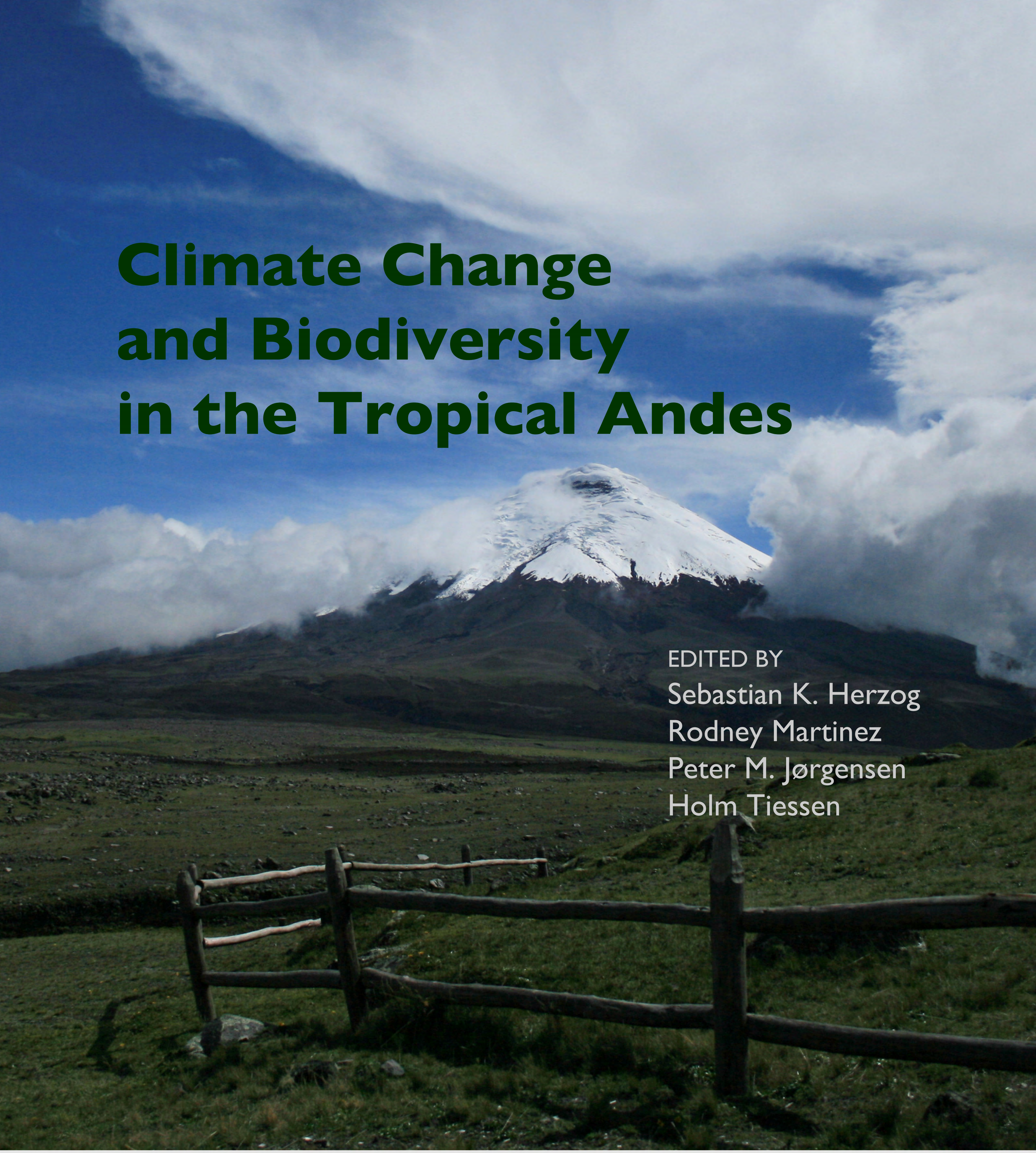

Climate Change and Biodiversity in the Tropical Andes

EDITED BY
Sebastian K. Herzog
Rodney Martinez
Peter M. Jørgensen
Holm Tiessen

MacArthur Foundation

IAI
INTER-AMERICAN INSTITUTE FOR GLOBAL CHANGE RESEARCH

SCOPE

Climate Change and Biodiversity in the Tropical Andes

Edited by: Sebastian K. Herzog, Rodney Martínez, Peter M. Jørgensen, Holm Tiessen.
2011. Inter-American Institute for Global Change Research (IAI) and Scientific
Committee on Problems of the Environment (SCOPE), 348 pp.
ISBN: 978-85-99875-05-6

Cover photo: Borja Santos Porras

About SCOPE

The Scientific Committee on Problems of the Environment (SCOPE) was established in 1969 to identify and undertake analyses of emerging environmental issues that are caused by or impact on humans and the environment. Over the past four decades SCOPE has provided authoritative, independent and influential scientific analyses on issues including i.a. environmental risk assessment, ecotoxicology, the major biogeochemical cycles, global climate change, indicators of sustainable development, biological invasions and biodiversity, and has advanced the development of global environmental programs throughout the world.

Today, SCOPE brings together scientists and experts in significant and innovative global and regional focus assessments through a cross-sectoral approach. It has recently initiated a broader membership base involving technology and engineering sciences and the business and industry sectors, while continuing to foster partnerships with UN agencies and other non- and inter-governmental bodies. SCOPE, a non-governmental organization, actively collaborates with the policy and decision-making sectors, affirming its role as a catalyst for the next generation of environmental assessments and contributions to inform research agendas and conventions relative to the environment and natural resources.

About IAI

The Inter-American Institute for Global Change Research (IAI) is an intergovernmental organization established in 1992 and supported by 19 countries in the Americas dedicated to pursuing the principles of scientific excellence, international cooperation, and the full and open exchange of scientific information to increase the understanding of global change phenomena and their socio-economic implications. With the recognition for the need to better understand the natural and social processes which drive large scale environmental change, the IAI encourages interactive exchanges between scientists and policy makers. The goal of the IAI is to augment the scientific capacity of the region and to provide information in a useful and timely manner to policy makers. Its primary objective is to encourage research beyond the scope of national programs by advancing comparative and focused studies based on scientific issues important to the region as a whole. The mission of the IAI is to develop the capacity of understanding the integrated impact of present and future global change on regional and continental environments in the Americas and to promote collaborative research and informed action at all levels.

Contents

Part I: Cross-Cutting Chapters

Part II: Background Chapters

Foreword

By Peter Raven
President, Missouri Botanical Garden, St. Louis, Missouri, USA

The tropical Andes, which are the subject of this path-breaking volume, are probably richer in biodiversity than any comparable area on Earth: the interactions between the species that make up the diverse and wonderful array of ecosystems in the area must therefore be even more complex than they are elsewhere. It is likely that approximately one sixth of the world's biodiversity occurs in the four countries of this region, presenting a degree of richness that would amount to at least two million species of eukaryotic organisms (all organisms other than bacteria) alone – animals, plants, fungi, and microorganisms. Probably less than 10% of the species of these groups that occur in the region have been cataloged and given names; therefore, the great majority of them are still unknown scientifically.

Only a very small fraction of these species are known in any degree of detail at all, and the progress in identifying and naming the others is exceedingly slow, probably amounting to no more than 2,000 species a year – a rate of discovery and description at which it would take centuries to complete our inventory. We thus have every reason to be discouraged at our collective lack of progress since Gonzalo Fernándo de Oviedo y Valdés wrote nearly five centuries ago and only a few years after Columbus' voyages (1526) that "the trees of these Andes are a thing that cannot be explained for their multitude." Since the time of extensive travels of Alexander von Humboldt in South America from 1799 to 1803, we have had a reasonably good idea of the richness of the representation of organismic diversity in the region, but have accomplished relatively little in learning about its details.

The enormous biological diversity of the tropical Andes must be understood against the background of the geologically recent uplift of the region, most of which occurred during the past 10 million years. As these incredibly beautiful peaks and impressive ranges were churned up as a result of the collision between the South American and Andean tectonic plates, many habitats came into existence in the region that were not present earlier. As this process continued, a number of kinds of organisms that existed earlier in the southern part of the continent migrated north along the Andes and formed constellations of species in the newly-formed upland habitats. Other kinds of organisms that existed in the lowlands of the region migrated into the newly-formed habitats at middle and higher elevations, and diversified greatly there. The *frailejones* and their relatives in the subtribe Espeliitinae of the plant family Asteraceae provide a spectacular example from a family that may well have originated in South American and certainly underwent much of its early diversification there. Still other organisms, the plant genera *Draba, Poa,* and *Astragalus* being representative of this sort of biogeographical pattern, moved along the mountains by dispersal over moderate to long distances from temperate and cooler habitats in the Northern Hemisphere, subsequently diversifying in the southern mountains.

It is in this geologically and biologically complex region that we must struggle to mount the best, highly selective effort possible to increase our level of knowledge. The slow progress of conventional modern taxonomy cannot possibly discover and name more than a small proportion of the species that occur in the tropical Andean region during the course of this century or even the next. We must find ways to gain and synthesize whatever information we can and make it widely available so that it can be applied efficiently to the conservation of some of the world's most impressive biological riches.

The area's species are suffering from a devastating onslaught that is related to human population growth and its consequences, a major one of which, the subject of this impressive volume, is global climate change. The roughly 100 million people that live in the region are projected to grow to 135 million by mid-century, with their levels of consumption doubtless increasing even more rapidly. The numbers of these people and their increasing needs will clearly have profound effects on the ecosystems they inhabit, and which support their lives. As a result of global climate change, average regional temperatures are likely to increase by a minimum of 2°C over the next few decades, and a larger increase is certainly possible. Accompanying these changes in average temperature will be large fluctuations and long-lasting changes in the distribution and amount of precipitation in the region. Most of the major cities of the Andes depend to a large extent on snowfall and glaciers that are diminishing rapidly, and there are likely to be human problems far beyond anything that we can imagine now.

Against this background, we congratulate those responsible for the appearance of this landmark volume: the John D. and Catherine T. MacArthur Foundation, sponsor of this compilation, and the many talented participants that contributed to its success. Their papers have been edited and collected in this volume; they will form an important guide to managing the biological resources of the tropical Andes in the future. Here is presented the first ever synthesis of the biogeographical patterns in the region as well as the first comprehensive assessment of how climate change is expected to affect tropical Andean biodiversity. The consequences of these factors for conservation planning and adaptation strategies are both timely and of fundamental importance. All those interested in the biodiversity of the region and its future will find that this book contains a rich storehouse of material of great interest for them. The findings and analyses presented here will lead to an enhancement of their efforts at a time when highly focused actions are needed to deal with the problems we are confronting. The chapters of this book are sound scientifically but written in such a way as to be readily accessible to the people who are working to understand and maintain the ecological integrity of the region, which is of fundamental importance to the welfare of its people and indirectly for the entire world.

All biodiversity is of concern to every person on Earth and necessary for our common survival. It provides all of our food, the majority of our medicines, building materials, ecosystem services, and simply beauty that enriches our lives and makes them much more enjoyable than they would be without it. We simply cannot afford to squander a high proportion of this biodiversity to meet our short-term needs or because we do not have the will to work together for our common good. We greatly and appropriately fear the effects of global climate change on all aspects of human life, but there is no area of our existence for which these effects will have more far-reaching and serious consequences than in the loss of biodiversity on which we depend for our lives and for the possibility of improving them in a sustainable context in the future.

Biodiversity is our common patrimony, presenting our best chance to build a sustainable world in the centuries to come. It is however facing its most serious challenges now since the close of the Cretaceous Period, 65 million years ago, and we are the cause of all those change.

The very nature of the world in which we live for the rest of our lives and our descendants thereafter will depend on the effectiveness of the actions we take now. To that end, this fine volume has made an invaluable contribution.

Introduction

Holm Tiessen

The tropical Andes are not only a center but also a cradle of South-American biodiversity (Hoorn et al. 2010). Their tectonic uplift caused highly differentiated rainfall regimes to develop between their eastern and western flanks. Erosion and sedimentation on the wet eastern portion are the source of much of the Amazonian plain and also of sediments in Andean intramontane basins, providing for landscapes of highly diverse soils and ecosystems. The same tectonic processes caused the closure of the Panama isthmus some 3.5 million years ago which, together with the subsequent ice age, resulted in extensive migration of species into South America - the Great American Biotic Interchange (Hoorn et al. 2010). Geologic and climatic differentiation, together with migrations, are the foundation of biodiversity of the tropical Andes. Landscape and soil diversity, elevation, rainfall and temperature gradients have isolated populations, favouring speciation. Seasonality, too, varies in the region from nearly aseasonal Ecuador to the highly seasonal Bolivian Altiplano, resulting in ecosystems adapted to very different climatic patterns.

The rising Andes thus created a vast region of exceptional biodiversity, and their differentiated climate and relief have maintained and enhanced this biodiversity. High elevation environments act as islands in which endemic species develop and survive however without the possibility of migration and mixing with other populations. Altitudinal belts also support different activities by human populations such as agriculture, forestry or animal husbandry. Such different land uses modify ecosystems, generate additional barriers to species movements and affect species survival. The result is a close interaction of natural climatic and human factors that determine biodiversity patterns in the region.

Temperature change due to global warming has affected high elevations more than the lowlands. One of the more obvious signs is the progressing deglaciation of the tropical high Andes. Just as significant for Andean ecosystems are changes in cloud dynamics, such as the lifting up-slope of the dew point. This changes the moisture regimes for cloud forests which may find themselves below the clouds and exposed to intermittent rainfall instead of common fog. One of the outstanding phenomena of climate change and cyclicity is the intensity and recurrence of the El-Niño Southern Oscillation which greatly affects rainfall in the tropical Andes. The region is therefore not only susceptible to future climate change but is already experiencing significant shifts in temperatures, rainfall regimes and seasonal weather patterns.

The exceptional biodiversity and endemism of the Andes, which are closely related to orography and differential climatic patterns, and their long history of intense land use, which has modified ecosystems and hydrological regimes, all make the ecosystems of the tropical Andes highly vulnerable to climate change. Understanding the nature of this vulnerability is still limited because climate and biological sciences have not yet collaborated to the degree needed. Further, knowledge of species and their diversity, distribution and dependence on Andean environments is very incomplete.

This volume brings together current knowledge, examines knowledge gaps, and charts both future research and decision-making needs in the face of ongoing climate change. Some patterns of regional differences in biodiversity emerge from the chapters: species richness is generally greatest on the environmentally favourable lower slopes, up to some 2000 m elevation. In addition to trends of decreasing biodiversity with elevation, a gradient of decreasing moisture towards the south generally reduces biodiversity. Endemism on the other hand is associated with higher elevation "islands" where species remain isolated. It often increases with elevation and is highest at the upper boundary of the cloud forest, which also support moderate species richness, and in high-elevation forest patches. At the highest elevations, particularly for aquatic species, there are many endemics. Hotspots of biodiversity have been reported for various areas on the Andean slopes, but this knowledge may be affected by the patchiness of available information. Knowledge on biodiversity is based on a small number of studies, and several authors estimate that only about half the species in the region are known. Therefore, we do not know if patterns of biodiversity, such as hotspots, are related to more intensive study of these areas, or if they reflect true diversity patterns.

Knowledge gaps, even at basic taxonomic level are substantial. Species interactions and ecosystem functioning are little explored in the region. Factors that determine vulnerability such as population densities, biological traits, ecological and physiological requirements are poorly understood. Biodiversity hotspots, as for instance identified for birds, may guide the identification of areas for conservation. But clearly considerable effort is still needed if a systematic understanding of biodiversity at the ecosystem level is to guide adaptation to climate change.

Like all high mountain areas, the Andes are already experiencing visible climate change. Retreating glaciers and snow lines, and an up-slope advance of agriculture bear witness to increasing temperatures. Although the mean temperature increase over the past 60 years of some 0.7°C is similar to global data, its effect on frost lines, elevation of dew point and other environmental factors has significantly greater impact on ecosystem function than at low elevations. Temperature effects have been amplified by a trend of decreasing annual precipitation throughout the region with a few localized exceptions.

The understanding of climate change processes that affect ecosystems and species is still poor, largely because of the dominant effects of orography which limit the usefulness of larger scale climate models. In particular, vertical and convection processes such as up-slope shifts in cloud formation, and changes in temporal patterns of temperature and precipitation need to be understood at the regional and even local level. To this end it is crucial to collect and evaluate climate data from different elevations within the same region. This will require an expansion of monitoring networks.

Modeled future temperature increases in the Andes exceed those in surrounding lowlands, but global circulation models upon which such predictions are based are unreliable along the Cordillera. Even so, extrapolations of current climate trends make it clear that ecosystems will be further affected and that biodiversity management must consider vulnerabilities and adaptive possibilities. Responses of species to continuing climate change may include tolerance and adaptation, migration to follow emerging gradients, or inability to adapt or move, resulting in extinction. The "island" effect of high elevations increases the extinction risk since such isolated species have nowhere to go. On the other hand, much of the high elevation terrain above 3000 m, has evolved under significant inter-annual temperature variability as a result of the El Niño Southern Oscillation. Species at high elevations may therefore be tolerant to a considerable range of future climates.

Theoretically, the most vulnerable species are those with a very specialized habitat, narrow environmental tolerance, or which depend on environmental resources or species interactions that are disrupted by climate change. Which species and ecosystems will in fact be most affected is largely unknown because of critical knowledge gaps. Species distribution modeling may help integrate the available knowledge and advance the understanding needed for designing adaptation measures.

In discussing strategies for adapting biodiversity management to climate change, the authors in this book concentrate on the role of conservation areas. To be useful under climate change, conservation areas should contain environmental gradients. Andean protected areas should therefore include contiguous corridors across elevations which facilitate species' and ecosystems' up-slope movement as they avoid temperature increases. The needed connectivity between conservation areas is being improved in several of the region's national conservation systems. At the same time, the Andes represent an ancient cultural landscape, and human interactions with ecosystems are important. Land use management that takes the conservation of biodiversity into account will therefore be critical to the success of adaptation to climate change. A mix of protected area systems and strategies for sustainable land use that considers biodiversity will be needed. For such management decisions to be effective, the valuing of ecosystems needs to reflect not just commercial or marketable worth, but also less tangible values of biodiversity that are difficult to quantify.

A significant contribution of this book is the first ever synthesis of region-wide biodiversity patterns for a broad range of taxonomic groups. In addition, the cross-cutting analysis integrating climate change and biodiversity contributes towards a more strategic understanding needed for adaptation in the face of critical knowledge gaps. Adaptive management (Hole et al., Chapter 2, this volume) will be needed to reduce uncertainties in strategic planning by an iterative process of decision making followed by system-level monitoring and subsequent revision and optimization of decisions. This is particularly important since changes in ecosystem function will affect ecosystem services upon which Andean populations depend (Anderson et al., Chapter 1, this volume). Human dependence on ecosystem services such as the water storage and buffering in highland bogs is an example that already requires management and conservation decisions that have generated schemes of ecosystem service payments. This book is a first much needed step in charting what we know as well as the knowledge gaps and decision-making challenges in this unique and vulnerable region.

Literature Cited

Hoorn, C, F. P. Wesselingh, H. ter Steege, M. A. Bermudez, A. Mora, J. Sevink, I. Sanmartín, A. Sanchez-Meseguer, C. L. Anderson, J. P. Figueiredo, C. Jaramillo, D. Riff, F. R. Negri, H. Hooghiemstra, J. Lundberg, T. Stadler, T. Särkinen, and A. Antonelli. 2010. Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* 330: 927-931. DOI: 10.1126/science.1194585

Acknowledgments

This book is a product of the project "An assessment of research and institutional needs to cope with the effects of Climate Change on Andean Biodiversity" carried out by the Inter-American Institute for Global Change Research (IAI) and funded by the John D. and Catherine T. MacArthur Foundation.

We thank the John D. and Catherine T. MacArthur Foundation for sponsoring this project, and wish to express our special appreciation to Steve Cornelius, program officer, of the Foundation's Conservation and Sustainable Development for his support throughout the development of this book.

We are very grateful to Harold A. Mooney, of Stanford University, for dedicating his time in reviewing the book.

Our special thanks to Dirk Hoffmann, José Luis Mena, Maria Paula Quiceño, Mónica Cuéllar, Peter M. Jørgensen, Rodney Martínez, Sebastian K. Herzog, Stephan R. P. Halloy, members of the project Steering Committee, for their guidance in the development of the book content; Véronique Plocq-Fichelet and Susan Greenwood-Etienne, from the SCOPE Secretariat, for their assistance before and during the project's scientific workshop; and the IAI staff, who have provided essential support to facilitate the development of this publication.

Holm Tiessen, IAI Director
IAI Directorate
Ave. dos Astronautas, 1758
12227-010 São José dos Campos, SP, Brazil

1

Consequences of Climate Change for Ecosystems and Ecosystem Services in the Tropical Andes

Elizabeth P. Anderson, José Marengo, Ricardo Villalba, Stephan Halloy, Bruce Young, Doris Cordero, Fernando Gast, Ena Jaimes, and Daniel Ruiz

The tropical Andes[1] harbor extraordinary biological and cultural diversity, contained in a mosaic of ecosystems (Josse et al. 2009). The region's complex topography, coupled with elevational and latitudinal gradients, results in varied physical conditions that create unique habitats and barriers for species movement. Temporal variability of climatic conditions, such as temperature, wind, and precipitation, also occurs across the tropical Andes over inter-annual and decadal time scales, as driven by the interplay between the tropical Pacific and Atlantic Oceans, and Amazonian influences (Marengo et al. 2004). Both humans and biota have adapted to the heterogeneity of the tropical Andean landscape and fluctuations in climatic conditions. An estimated 45,000 plant and 3400 vertebrate species (excluding fishes) have been documented from tropical Andean ecosystems, representing approximately 15% and 12% of species known globally, respectively. Nearly half of these species are endemic (Myers et al. 2000). The well-being of human populations has been linked to the functioning of tropical Andean ecosystems over a history that extends more than 10,000 years. Today, millions of people depend on these ecosystems as a source of fresh water, food, cultural importance, and many other ecosystem goods and services (Josse et al. 2009).

Recently, the range of natural climatic variability in the tropical Andes has started to exceed historically documented thresholds. Of particular concern is the general warming trend and its implications for the integrity of ecosystems and the human populations that depend on them. In this chapter, we explore current knowledge of the effects of climate change on tropical Andean ecosystems and ecosystem services. At present, other than unambiguous indications of a pronounced warming trend, the overall picture of the climatic future of the tropical Andes remains uncertain, making predictions about the fate of ecosystems difficult. Some studies on recent climate variability have been published, but much information remains observational or

---

[1] Many studies use 800 meters elevation as the lower limit of the tropical Andes. For central and southern Bolivia, this limit often extends to 600 meters. For Colombia 500 meters is often considered the lower limit.

anecdotal. The information presented here was gathered from discussions among climatologists, ecologists, anthropologists, and natural resource managers with expertise in the tropical Andes during a weeklong workshop designed to facilitate transfer of knowledge on climate change and tropical Andean biodiversity, together with a review of literature and other available information.

Climate Change Patterns in the Tropical Andes

Climate change in high elevation tropical locales, such as the tropical Andes, is not well simulated in current global General Circulation Models (GCMs), in part because of the models' coarse spatial resolution and the rugged topography of the long, relatively narrow Andean mountain chains (Marengo 2007; Urrutia and Vuille 2009). Climate projections from regional models show increased warming with elevation in the tropical Andes, with more pronounced warming at higher elevations (above 4000 m) on both eastern and western Andean slopes (Solman et al. 2008; Marengo et al. 2009; Urrutia and Vuille 2009). The magnitude of warming projected at high elevations in the tropical Andes is similar to that predicted for polar regions (Bradley et al. 2004; 2006). The consequences of climate change in the tropical Andes are of special concern because of the diverse nature of their ecosystems and the effects that changes in these ecosystems will have on a large human population directly dependent on the services they provide (Vuille et al. 2008). The combined population of the countries of Colombia, Ecuador, Peru, and Bolivia was close to 100 million people in 2009. Of these, Josse et al. (2009) estimate that 40 million depend directly on Andean ecosystems.

While recognizing uncertainties in climate change projections, we suggest that the climatic fate of ecosystems and ecosystem services in the tropical Andean region will be largely related to a few key trends. First, there is widespread evidence of increasing air temperature across the region (+0.11°C / decade over the past 60 years), a trend that has intensified in the past 25 years (+0.34°C / decade; Vuille and Bradley 2000; see Marengo et al., Chapter 7 this volume). Recent studies have suggested that warming across the region is more evident in the minimum than maximum temperature time series (Vuille et al. 2008; see Marengo et al., Chapter 7 this volume). Second, there is some evidence of change in patterns of precipitation, but these changes vary between eastern and western slopes of the Andes and inter-Andean valleys. Third, changes in cloud cover may also be significant for ecosystems, both in terms of rising cloud levels (Foster 2001; Ruiz et al. 2008; 2009) and in terms of the sunshine to cloud ratio. Some evidence suggests a decrease in occurrence of cloudy weather in the northern Andes, a trend that leads to more hours of sun exposure (Ruiz et al. 2008; 2009; Chapter 12, this volume).

Several factors influence these climate trends. Natural climatic variations have affected climatic conditions across much of the planet in the past, including the Andes, and will continue to be influential in the future. Examples are the great ice ages at millennial scales, multi-centennial shifts such as the AD 1500-1880 Little Ice Age, and decadal climate shifts around 1850 (Thompson et al. 2006) and in the 1910s, 1940s, 1970s and 2000 (Marengo et al. 2004). At inter-annual and decadal time scales, warming has been detected in the high Andean mountains, together with a decrease in rainfall in the southern tropical Andes (see Marengo et al. Chapter 7, this volume; and see Figure 1.1). Inter-annual and decadal variability of precipitation has traditionally been related to Pacific Ocean influences through the El Niño Southern Oscillation (ENSO) and ENSO-like decadal modes of variability. However, variability in the moisture transport and intensity of trade winds from the tropical Atlantic Ocean also affects the tropical

Andes (Marengo et al. 2004). On intra-annual time scales, coupled interactions between sea-surface temperature (SST) anomalies, wind patterns, and the latitudinal displacement of the Inter-Tropical Convergence Zone (ITCZ) drive variations in regional cloudiness (Vuille and Keimig 2004).

Climate change may increase extreme events, such as droughts, heat and cold waves, or intense rainfall. For instance, in the central inter-Andean valleys of Peru above 3500 meters elevation, the number of intense rainfall events and early freezes has recently increased (E. Jaimes, SENAMHI, unpublished data). Some evidence of an increased occurrence of unusually heavy rainfall events has also been reported locally in the central Colombian Andes region (Ruiz et al. 2008).

Effects of Climate Change on Andean Ecosystems

Josse et al. (2009) recognize 133 different ecosystem types for the northern and central Andes, classified into nine major groupings. Elevation ranges, temperature, and precipitation regimes are among the factors that distinguish these ecosystems (Table 1.1). Both direct (e.g., changes in climatic factors) and indirect (e.g., resultant ecosystem responses) effects of climate change have already been observed in the tropical Andes, and we can hypothesize about what may occur in the next 100 years in each of the nine major ecosystem groupings. Table 1.2 summarizes these observations and hypotheses.

Certain characteristics of each grouping of tropical Andean ecosystems make them uniquely vulnerable to climate change (see Young et al., Chapter 8, this volume). For example, the extent and future viability of high Andean superpáramo and Puna ecosystems is of concern because of their occurrence at high elevations. Here, a 3°C increase in temperature could result in a theoretical 600 meter upward movement of species, and the resulting loss of habitat area for species that would have to move to keep up with their current habitat optimum could significantly affect their viability. Major changes are predicted for páramo ecosystems, based in part on their island-like distribution and highly endemic biota. For northern Andean páramos, Cuesta Camacho (2007) estimates that around 35% of bird species (102 species) and 60% of plant species (125 species) would become extinct or critically endangered by 2080, based on A2 high emission scenarios (IPCC 2007). The vulnerability of cloud forest ecosystems relates to their dependence on the level of cloud bases, which is predicted to shift with climate change. Rising cloud bases and a reduction in horizontal precipitation could lead to decreased moisture, with consequences for diverse epiphytes and the animal communities they support. Many species in cloud forests are adapted to narrow elevational ranges on steep slopes. Spatial heterogeneity of climate change could lead to collapse of populations or increased vulnerability to extinction.

Several factors make aquatic systems vulnerable to climate change. Warming temperatures may cause increased evaporation in lakes and wetlands, with concomitant reduction of habitat and potential changes in water quality (e.g., temperature, salinity), particularly where precipitation declines are predicted. In areas where water bodies are fed by glacial runoff, water levels have been augmented while water reserves stored in glacial ice are released by accelerated melting, but will decline when glacial mass disappears (Vuille et al. 2008). Wetlands, in particular cushion bogs (e.g., *bofedales*, *turberas*, *vegas*) located along margins of rivers and springs in high mountain grasslands and deserts, function as archipelagos of diversity. Climate change could result in reduced water availability, salinization, area reduction, and increased carbon emissions (CO_2 in particular) in these ecosystems.

Beyond expected changes or vulnerabilities by ecosystem grouping, some general predictions about the effects of climate change on the tropical Andean landscape mosaic can also be made. First, contractions or expansions of ecosystems in terms of geographic area (e.g., contractions predicted for páramo and superpáramo), and a changing physical environment, will likely result in species disappearance or migration (see Larsen et al., Chapter 3, this volume). For example, in the Peruvian Andes, recent studies have already documented the disappearance of six threatened frog species from their historical ranges (von May et al. 2008), and three frog species have expanded their ranges upwards following recent deglaciation (T.A. Seimon et al. 2007). These kinds of species movements have implications for ecosystem structure (e.g., in terms of community dynamics) as well as ecosystem function (e.g., the role of different species in maintaining ecosystem processes).

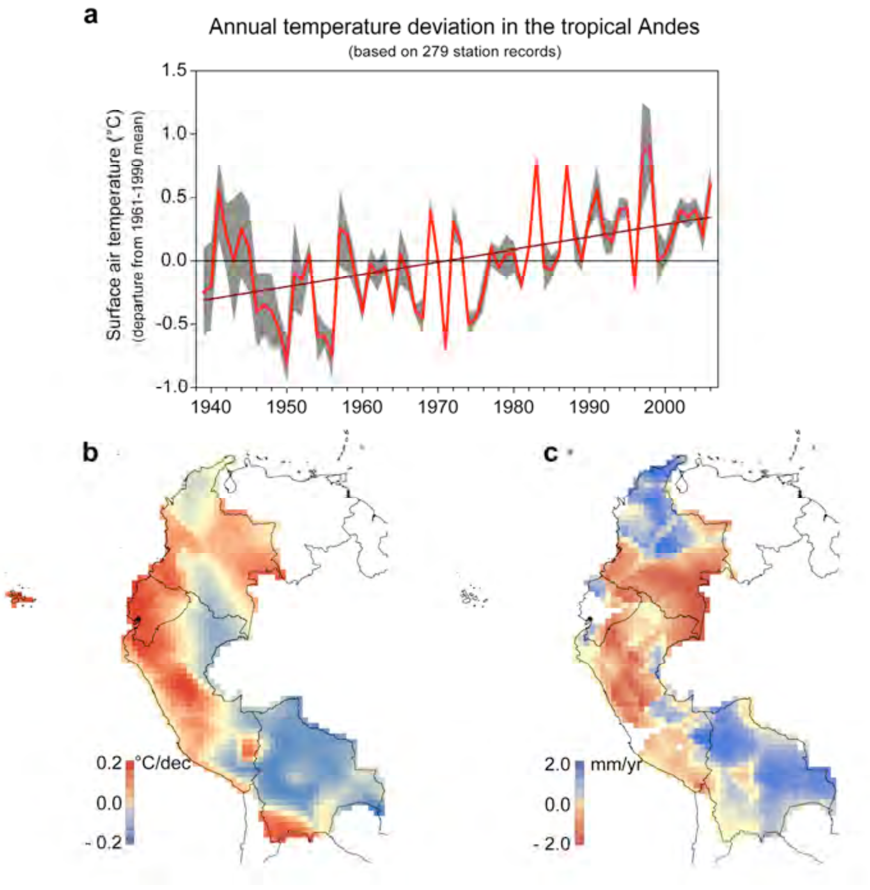

Figure 1.1. Temporal and spatial changes in mean temperature and precipitation in the tropical Andes. (a) Annual temperature anomaly with respect to 1961-90 average in the tropical Andes (1°N-23°S) from 1939 and 2006. Gray shading indicates ±2standard errors of the mean. The long-term warming trend (0.10°C/decade) is also indicated (from Vuille et al., 2008). (b) Mean decadal temperature trends across the tropical Andes of Colombia, Ecuador, Peru and Bolivia estimated over the interval 1951-2001. (c) Total annual precipitation trends across the tropical Andes of Colombia, Ecuador, Peru and Bolivia estimated over the interval 1951-2001.(b) and (c) from ClimateWizard (www.climatewizard.org). Figure prepared by R. Villalba.

Table 1.1. Characteristics of major ecosystem groupings in the northern and central Andes. Based on Josse et al. 2009.

Ecosystem	**Altitudinal range**	**General characteristics of terrestrial components and distribution**	**Important species**
Páramo	>3000 m	High elevation humid shrublands occurring from Venezuela to northern Peru in relatively thin strips along the top of the northern Andes, fragmenting into small patches in the south to Argentina and harboring high levels of endemism.	*Espeletia* spp, *Chusquea, Jamesonia, Azorella biloba, Gynoxis*, Ericaceae, *Loricaria*, *Werneria*, many mosses, lichens and ferns
Humid Puna	2000-6000 m	Dominated by grasses, shrubs, and cacti, replacing páramo to the south where precipitation is lower, extending from northern Peru to Bolivia and Argentina	*Festuca, Calamagrostis, Stipa, Poa* spp. Liolaemus, llamas, alpacas, flamingos
Dry Puna	2000-6000 m	Almost desert-like vegetation in southern Peru through Bolivia to northern Argentina with low spiny shrubs	*Festuca, Stipa, Deyeuxiay, Parastrephia* spp. llamas
High Andean / Superpáramo	>4500 m	The very highest places on mountaintops or just below snow fields or glaciers with permanent vegetation, usually consisting of very small stature plants, lichens, and mosses. Occur throughout the tropical and temperate Andes.	*Azorella* spp. *Nototriche*, *Aschersoniodoxa*, *Menonvillea Attagis gayii*, Vicuña, high levels of endemism
Cloud Forest	1000-3500 m – to 600 m in southern Peru and Bolivia	Very humid forests receiving a significant amount of precipitation in the form of cloud-borne mist that is intercepted by trees, and have a highly endemic, closed canopy forest with high epiphyte loads. Occur throughout the tropical Andes.	*Ceroxylon, Dyctocaryum, Podocarpus, Calatola, Gustavia, Clusia* spp.
Seasonal Andean Forest	800-3100 m	Areas that experience 3-5 month dry seasons and reduced precipitation, with medium stature forests made up in part by deciduous trees. Occur throughout the tropical Andes, but more extensive in Peru and Bolivia.	*Roupala, pseudocordata, Psidium caudatum, Tipuana tipu, Calycophyllum multiflorum*
Dry Andean Forest	800-4100 m	Forests that typically have low stature trees with thick stems and leaves for water storage and abundant spines and chemical defenses. Occur primarily in Inter-Andean valleys in Ecuador, Peru, and Bolivia.	*Schinopsis haenkeana, Prosopis alba, Bursera* spp., *Plumeria* spp, *Jacaranda* spp.
Inter-Andean Valleys	1900-3500 m	Landscapes that have been heavily altered by humans for many millennia and are characterized by shrublands with seasonal herbs with adaptations to dry periods. Occur throughout the tropical Andes.	*Acacia feddeana, Caracidium andicola, Jatropha* spp, *Croton* spp, *Salvia* spp, *Tecoma arequipensis.* numerous Cactaceae species
Aquatic Habitats	>800 m	Lakes, wetlands, cushion bogs, streams, rivers. Occur throughout the tropical Andes.	*Orestias* spp, *Astroblepus* spp., *Chaetostoma* spp., *Phoenicoparrus* spp, *Theristicus* spp. *Telmatobius, Isoetes,* Ephemeroptera

Table 1.2. Observed and hypothesized ecosystem responses to changes in climatic factors in the tropical Andes. Information presented is based on discussions with climate scientists and ecologists with knowledge of the Andes and select references. Degrees of confidence in changes to climatic factors are indicated as: +low ++medium +++high

OBSERVED CHANGES			**HYPOTHESIZED CHANGES**	
Climatic factors	**Ecosystem responses**	**References**	**Climatic factors**	**Ecosystem responses**
ANDEAN LAKES AND WETLANDS				
Increased temperature +++ Changes in water balance ++ Rise of lower limit of solid precipitation +++	Decreasing lake levels and drying of cushion bogs across the altiplano Rising elevation of highest lakes Upward movement of species (e.g., amphibians, nesting flamingos) Decline in populations of certain species (e.g., amphibians) and extinctions of local endemics (e.g., *Isoetes*)	Halloy 1983; A. Seimon et al. 2007	Increased temperatures, on the order of 2-4ºC +++ Increased number of extreme events ++ Changes in water balance +++	Altered hydrologic regimes and sediment loads Increased chance of eutrophication, decreased oxygen, and increased salinity in lakes Decreased carbon storage in cushion bogs Declines in species diversity and abundance, especially among endemics
HIGH ANDEAN / SUPERPARAMO				
Increased temperature +++ Changes in water balance ++ Rise of lower limit of solid precipitation +++ Increased insolation +	Upward migration of species and colonization by new species (e.g., *Pleurodema*, *Telmatobius*, *Liolaemus, Diuca speculifera*) Epidermis burning of vegetation (e.g., *Loricaria colombiana,* Cactaceae spp.) Shifts in species occurrence and responses (birds, mammals, plants) Upward shift of cultivation and grazing activities	T. A. Seimon et al. 2007; Hardy and Hardy 2008 Daniel Ruiz, unpublished data; Halloy 1981 Halloy 1985; Halloy 2002 Halloy et al. 2005a; Halloy et al. 2005b	Increased temperature, on the order of 3-4ºC +++ Slight increase in precipitation, but variable across region + Increased number of extreme events + Changes in water balance +++ Increased insolation + Increased wind + Changes in seasonality, particularly onset of conditions+ Increasing partial pressure of carbon dioxide +++	Glaciers virtually disappear Decrease in habitat area, with consequences for species interactions Declines in species diversity and abundance, increase in endangerment (e.g., *Polylepis*) and extinctions, and disappearance of indicator species CO_2 fertilization of landscape, with effects on water, soil and vegetation
PUNA				
Increased temperature +++ Changes in water balance ++ Rise of lower limit of solid precipitation +++	Increased dryness and salinity Burning of vegetation from		Increased temperature, on the order of 3-4ºC +++ Decrease in water balance ++	Extinction rates high among locally-adapted species

Increasing insolation + Changes in onset of seasons +	increased insolation (e.g. Cactaceae) Increased reports of sunburn, eye problems in human populations	Ulloa and Yager 2008; Yager et al. 2009)	Increase in extreme events + Increase in insolation + Increase in wind + Changes in onset of seasons + Changes in horizontal precipitation and cloudiness +	Colonization by species previously characteristic of lower elevations Increased human inhabitation of the landscape, adding further stress to climate induced changes
PARAMO				
Increased temperature +++ Rising lower limit of solid precipitation +++ Increasing insolation + More frequent and intense rainfall events, interrupted by longer dry periods +	Effects on soils: water saturation, nutrient lixiviation, erosion Increased sediment loads in streams Upward rise of species, pests, and diseases from lower altitudes Vegetation stress from alternation of heavy rains and dry periods		Increased temperature, on the order of 3-4ºC +++ Decrease in water balance ++ Increase in extreme events + Rise of lower limit of solid precipitation +++ Increasing insolation / decreasing cloud cover ++	Severe loss of habitat (up to 60%; F. Cuesta, pers. comm..) and high extinction risks Upward migration of species from lower altitude areas, and increased human influence on landscape Changing fire regime Reduction in water retention and filtration Reduction in carbon retention and sequestration
CLOUD FOREST				
Changing precipitation regimes, with increases or decreases in different areas ++ Upward movement of the condensation belt + Reduction in cloud cover in the northern Andes + Increased insolation + Changing seasonality, including shifts from two pluvial peaks to one during rainy season in the Northern Andes +	Extreme events like drought linked to tree die-offs (e.g., 2005 drought event) Increasing erosion and landslides on steep slopes Flooding events Upward migration of agriculture and human settlements	Ken Young, pers. comm. (Colwell et al., 2008; Svenning and Condit, 2008; Tewksbury et al., 2008)	Increased temperature ++ Changes in precipitation, with variability across the region + Change in ratio of horizontal to vertical rainfall, with decreased mist and clouds + Upward displacement of condensation belt, therefore less fog + Increased insolation +	Decrease or endangerment of heat and drought sensitive species (e.g., amphibians, epiphytes), and endemic species Reduced slope stability Increased human settlement, expansion of agriculture and grazing Increased risk of fire
DRY AND SEASONAL ANDEAN FORESTS				
Changing precipitation regimes, with increases or decreases in different areas +	Upward migration of pioneering species (e.g., *Cecropia* in Colombia) Landslides and erosion in areas	Gustavo Kattan, pers. comm. Rodney Martinez,	Increased temperature, on the order of 2-3ºC ++ Increase in annual precipitation, on the order of 400-500 mm	Increase in landslides and soil erosion in areas of increased annual precipitation Increase in growth rate of trees in

	with increased precipitation (e.g, western Ecuador) Variations in water temperature of aquatic environments	pers. comm. Ricardo Villalba, unpublished data	(Urrutia and Vuille 2009), and intensity of precipitation++	previously dry areas Declines or endangerment of sensitive species (e.g, certain rodents, nectarivorous bats, amphibians, fishes) Increased human settlement, expansion of agriculture and grazing Increased risk of fire
INTERANDEAN VALLEYS				
Changing precipitation regimes, with increases or decreases in different areas + Changes in seasonality, especially onset of seasons + Increased heterogeneity of climatic conditions between geographical areas +	Increased threat from human activities Reduced agricultural productivity Increased incidence of vector-borne diseases (e.g., malaria, dengue fever)	(López and Zambrana-Torrelio, 2006) Daniel Ruiz, unpublished data	Increased temperature, on the order of 3-4.5ºC + Moderate increase in precipitation in lower elevation valleys +	Changes in water balance, with increased water deficit, leading to reduced agricultural production and increased dependence on irrigation water and expanding infrastructural developments Changing fire regime Increased threat to slow-growing and long-lived vegetation

The expansion of geographic ranges is in some ways analogous to the introduction of exotic species into new landscapes, where newly colonizing species can alter the identity and strength of direct and indirect biotic interactions (Levine et al. 2004; White et al. 2006), as well as change the physical structure of ecosystems (Crooks 2002) and alter the strength of disturbance regimes (Brooks et al. 2004). Formation of no-analog communities (e.g., species assemblages that are currently unknown to occur) is also a potential outcome of climate change (Fox 2007; le Roux and McGeoch 2008). As community structures shift, an important question is whether or not the functional roles of disappearing species will be replaced by new migrants to ecosystems (Vos et al. 2008).

Second, the changes in climatic factors are also likely to influence abiotic functional processes of ecosystems. Increased erosion and landslides could accompany changes in precipitation regimes, particularly in ecosystems that span steep slopes, like montane or cloud forests. An increase in the ratio of vertical (rain) to horizontal (wind-blown mist) precipitation has been predicted for some ecosystems traditionally dominated by mist, such as the páramo; this change could affect the water retention and filtration capacity of the páramo. Also important is a rise in the elevational level of solid (snow, graupel) precipitation. For areas with vegetation and geomorphology in equilibrium with solid precipitation (which infiltrates slowly as it melts), a shift to liquid precipitation leads to increases in runoff, siltation, and erosion. Effects of climate change on nutrient cycling are uncertain. In aquatic systems, rising temperatures may lead to a decrease in dissolved oxygen and an increased potential for eutrophication. Wetlands and the páramo could shift from being sinks to sources of carbon in the short term with warming and drying.

Finally, the synergistic, interactive effects of climate change with other stressors to tropical Andean ecosystems—such as habitat modification, exotic species, and water pollution—may be severe and unexpected. For example, previous studies have shown that, at a species level, pesticide exposure at sublethal concentration in the presence of predation risk can cause massive mortality in amphibian larvae (Sih et al. 2004). Although these studies were not conducted on tropical Andean species, they do provide a window into the possible fates of species in landscapes with multiple stressors. It remains to be seen if and how changing climatic factors will interact with biotic (predation, disease, poor food supply) and abiotic (suboptimal habitat conditions) stressors to affect tropical Andean species. Beyond the species level, páramos provide an example of the potential for interactive effects of climate change with human-induced stressors at a larger scale. As climate warms, their lower margins may become more suitable to agriculture and thus more threatened by human activities. A combination of climate change and increased human influence on the páramo may also increase the spread of anthropogenic fires, considered a serious threat to integrity of this ecosystem (see Ruiz et al., Chapter 12, this volume).

Changing Ecosystem Services in the Andes

In the tropical Andes and elsewhere, the well-being and progress of human populations depend on the integrity of ecosystems (Table 1.3). The benefits people receive from ecosystems are known as ecosystem services, grouped by the Millennium Ecosystem Assessment (2005) into four general categories: *provisioning services* (e.g., water, food, timber, fiber), *regulating services* (e.g., climate regulation, flood control, down-slope safety, water purification), *supporting services* (e.g., soil formation, photosynthesis, nutrient cycling, pollination, waste disposal), and *cultural services* (e.g., recreation, aesthetics, spiritual values). The ability of ecosystems to provide these services to humans depends on a typically high degree of integrity or health of ecosystems. Nevertheless, as human demands on ecosystems increase with growth of population and consumption, and increased technology, there is greater potential for ecosystem degradation and intensification of trade offs related to ecosystem services. Climate change adds another dimension, as an additional driver of ecosystem change and a cause of shifts in human resource use. Although refuges and protected areas are seen as one way to buffer these services against threats (Dudley and Stolton 2003), climate change could jeopardize tropical Andean ecosystems' capacity to provide ecosystem services, as discussed below.

Vast changes are expected to water-related ecosystem services. Human populations in the Andes and adjacent lowland areas have long relied on Andean ecosystems for water-related services, in particular water supply, flow regulation, energy, and waste assimilation (Bradley et al. 2006; Buytaert et al. 2006; Vuille et al. 2008; also see Anderson et al., Chapter 23, this volume). These services fall into categories of *provisioning* and *regulating* services (Millennium Ecosystem Assessment 2005), and the ability of Andean ecosystems to provide these services in the future will be affected by climate change. Of specific concern in the region are the effects of warming on glaciers and degradation of vegetative cover. Mountain glaciers, Andean wetlands (including peat bogs), and the spongy páramo act as buffers of highly seasonal precipitation, providing water even during periods of little rainfall (Vuille et al. 2008). At present, páramo streams supply the majority of water to several of the region's largest cities, including Bogotá (~8 million inhabitants) and Quito (~2 million inhabitants; Bradley et al. 2006; Buytaert et al. 2006; Vuille et al. 2008). Andean rivers (both glacier- and páramo-fed) provide most irrigation water for croplands (FAO 2003; Buytaert et al. 2006), and through hydropower plants, generate ~50% of regional electricity (see Anderson et al., Chapter 23, this volume). Wastewater from most human settlements in the Andes is also discharged directly into rivers without prior treatment; reduced flow would mean reduced capacity of these systems for waste dilution and assimilation. Glacier retreat and drying of wetland and páramo areas are processes that could substantially alter stream flow patterns, presenting threats to water supply and energy generation. The density and size of human populations that depend on tropical Andean ecosystems for water and energy create a critical, urgent need to develop adaptation strategies to climate change (Bradley et al. 2006; Vergara et al. 2007).

Shifts in services related to agricultural production could occur as a consequence of climate change and changing patterns of human settlement. Tropical Andean ecosystems impart benefits that facilitate crop cultivation, livestock grazing, and timber production, among other agricultural activities. These benefits fall into categories of *provisioning* and *supporting* services (Millennium Ecosystem Assessment 2005). Over millennia, tropical Andean populations have developed highly diverse agricultural systems, and shaped landscapes (Erickson 2000; Mann 2000). In fact, the tropical Andean region is considered an important global center of agricultural biodiversity, containing a large number of the wild relatives of some of the world's most important food and fiber crops (e.g., potato, tomato, corn, peanuts; Halloy et al. 2005a).

Future changes in patterns of precipitation and temperature, as well as increased atmospheric CO_2, will affect agricultural production in the Andes. Consequences of these climatic changes might include intensification of agriculture in existing cropland or grazing areas, or expansion of the agricultural frontier both upwards to higher elevations (already being observed, as described in Chapter 2, this volume, and Halloy et al. 2005a) and downslope into

Table 1.3. Examples of ecosystem services provided by tropical Andean ecosystems.
Key: + Relevant ++ Important +++ Very important

Ecosystem	Provisioning services								Regulating services		Supporting services	Cultural services	
	Food			Fresh water	Fuel	Timber	Wild harvest medicinal plants	Hydro energy	Carbon storage	Down slope safety	Soil fertility	Recreation	Spiritual and sacred values*
	Agriculture	Grazing	Agro biodiversity										
Lakes and wetlands		++	+	+++	+			++	+++	+	++	+++	+++
High Andean / Superpáramo		+		+++			++	++	+	++	+	+++	+++
Puna	++	++	+++	+	++		++		+		+	+++	+
Páramo	+	++	+++	+++	++		++	++	+++	+++	+	+++	+
Cloud forest		+		+++	+++	+++	++	+++	+++	+++	+	+++	+
Interandean valleys	+++	+++	+++	+	++	+	+++	+	+	+	++	+++	++
Dry / seasonal Andean forest	+	+	++	+++	+++	+++	++	+++	+++	+++	+	+++	+

* Related to ancestral and spiritual traditions that do not have substitutes

lowland tropical forests. Crops may also be increasingly susceptible to damage by insect herbivores and pests under warmer conditions and rises in atmospheric CO_2 (Perez et al. 2010). Analyses of fossil leaves from 55.8 million years ago, when a sudden, transient elevation in temperature and atmospheric CO_2 occurred between the Paleocene and Eocene epochs, linked these climatic shifts to a significant rise in the percentage of damaged leaves and diversity of damage by insect herbivores (DeLucia et al. 2008). Additionally, many cultivated species are closely dependent on pollination from insects, birds, and bats. Climate change related effects on these species, or on other food species upon which they may depend for part of the year, could affect crop yields (see Buchmann and Nabhan 1996 for North American examples). Decreases in native agrobiodiversity could substantially increase risk of crop failure from extreme climatic events and increase crop vulnerability to disease (Garrett 2008). The combined pressure of climate change and anthropogenic degradation of agricultural landscapes may place many ecosystems at risk and affect future food security in the tropical Andes (Altieri and Merrick 1987; Nabhan 1989; FAO 1996; Brack 2005; Halloy et al. 2005a; Halloy et al. 2005b).

Decreased down-slope stability and safety is expected. In steep mountain landscapes, ecosystems, particularly forests, play an essential role in erosion control and slope stability. These services fall into the category of *regulating services* and depend on the presence and continuity of vegetative land cover, and also climatic variables like precipitation. Two projected effects of climate change in the tropical Andes are noteworthy here, as they could influence erosion and slope stability. Shifts from misty precipitation (horizontal rainfall and fog) to more liquid precipitation (vertical rainfall) in areas like the páramo and cloud forests could lead to greater erosion. At higher elevations, the shift from solid precipitation (snow and graupel, or *garrotillo*) to pluvial precipitation similarly leads to decreasing infiltration and increasing surface runoff and erosion. The more frequent occurrence of extreme events, such as heavy or prolonged rainfall, could have important implications for slope stability and consequently the safety of human settlements in downslope areas.

Ability of ecosystems to provide cultural services may be compromised by climate change. The cultural history and natural history of the tropical Andes are interwoven. Human cultures, knowledge systems, religions, and social interactions of Andean peoples all reflect a strong connection to the landscape and the importance of a sense of place. High mountains, lakes, certain trees and animals, and many other geographic and biological entities have sacred status in Andean cosmology (Bauer and Stanish 2001). These sacred sites and beliefs influence landscape management strategies. Tropical Andean ecosystems in good ecological condition also provide recreation areas and a basis for environment-based tourism, an important source of revenue for tropical Andean countries. Climate-related changes could influence ecosystems' ability to provide cultural services, and may degrade the identity of natural areas (e.g, visual, iconic biodiversity elements). The impact of loss of cultural services is difficult to measure but merits attention, as it relates to the overall well-being of human populations in the region.

Contribution of Andean ecosystems to climate regulation may change. Andean ecosystems, particularly Andean forests, the páramo, and wetlands (e.g., cushion bogs), contain important global reserves of carbon. Carbon storage falls into the category of *regulating services* and depends on climatic conditions like temperature, as well as human influences on the landscape. Under scenarios of future warming, the ability of these ecosystems to store or sequester carbon from the atmosphere could be reduced and they may become net sources of greenhouse gases.

Climate change-induced shifts in species distribution and abundance may affect biodiversity-related ecosystem services. Biodiversity influences the provision of ecosystem services, through the strong links of biological species to processes like pollination, climate regulation, and disease control, among others (Millennium Ecosystem Assessment 2005). In high Andean landscapes, correlations between biodiversity and human population density suggest that people have long depended on biodiversity-related ecosystem services (Fjeldså 2007). Key to the provision of biodiversity-related services is often species composition, not necessarily the number of species inhabiting an ecosystem. With climate change in the Andes, loss of sensitive species or range shifts could affect composition of ecological communities, with implications for disease control and agricultural activities.

Interactions between climate change, its consequences on Andean ecosystems and their services, and human use of resources are likely. Shifts in human behavior are expected to occur in response to climate change; these shifts could exacerbate impacts of climate change on ecosystems. Aquatic systems also provide a good example. As patterns of water flows are altered by climate change, increased modifications of freshwater systems by dams and water withdrawals are likely to occur. For example, in the case of glacier-fed rivers, it is projected that river flows will first increase as glaciers melt, but then recede to lower levels than historically reported once glaciers vanish. In the case of páramo-fed rivers, warmer temperatures could dry páramos and compromise their function as slow releases of water to rivers. Consequently, the buffer that currently exists to maintain river flows regardless of seasonal variability in rainfall could disappear with the glaciers and with drying páramos. When river flows exhibit more marked seasonal differences in flow, there may be more pressure to alter the timing of discharge through construction of storage dams to meet human needs for water. Alternatively, improving or increasing Andean cushion bogs could be a way to ameliorate water regulation (Yager et al. 2008, Yager 2009, Benítez et al. 2010). This is just one example of the kinds of feedbacks that might occur in the future as climate change affects the ecosystem services upon which human populations depend in the tropical Andes.

Conclusions

The effects of climate change have been documented on every continent, and observed biological changes have subsequently been attributed to climate change in many places (see Parmesan 2006 for a review). Published information establishing this link is still scant for the tropical Andes in terms of individual species or taxonomic groups, and perhaps even more so in terms of ecosystem level trends. The summary of observed and hypothesized effects of climate change on tropical Andean ecosystems presented in this volume provides a first attempt at filling this gap in current knowledge.

Regional models predict the magnitude of climate change in the high tropical Andes to be among the most severe globally, comparable to that of the Northern Hemisphere's high latitudes, particularly in terms of warming at high elevations. The difference in the tropical Andes is the direct impacts climate change will have on the lives and livelihoods of millions of people, many who are economically vulnerable and directly dependent on the goods and services that tropical Andean ecosystems impart. A clear cultural link exists between human societies and surrounding ecosystems, as established by the long history of human inhabitance and use of the tropical Andean landscape. Anticipated climate induced changes to the availability of water and agriculture-related ecosystem services are of particular concern in the near future in the tropical Andes. The value of ecosystem services at risk from climate change is high. Once lost, many of these services may be irreplaceable.

Human activities (e.g., forest clearing, river alteration, mining, grazing) already exert increasing pressure on tropical Andean ecosystems and their ability to provide key ecosystem services (Jarvis et al. 2010). Climate change is superimposed on these other human-induced alterations of the landscape. While the uncertainty of future climate change projections presents a challenge to resource management decisions, immediate efforts to mitigate the negative consequences of other stressors in the region should be encouraged. Strategies for more integrated and adaptive management of natural resources are necessary for addressing present and future effects of climate change on tropical Andean ecosystems, and reducing the vulnerability of human populations to subsequent reduction and loss of critical ecosystem services (Andrade-Pérez et al. 2010).

Acknowledgments

We thank S. Herzog, P. Jorgensen, J. Maldonado, M. Maldonado, H. Mooney, P. Olivas, A. Seimon, H. Tiessen, C. Toledo, J. Watling, and all participants at the May 2009 workshop for information and suggestions that helped improve this chapter.

Literature Cited

Altieri, M. A., and L. Merrick. 1987. In situ conservation of crop genetic resources through maintenance of traditional farming systems. *Economic Botany* 41(2):86-96.

Andrade Pérez, A., B. Herrera Fernández, and R. Cazzolla Gatti (eds). 2010. *Building resilience to climate change: ecosystem-based adaptation and lessons from the field*. Gland: International Union for the Conservation of Nature. 164 pp.

Bauer, B. S., and C. Stanish. 2001. *Ritual and pilgramage in the ancient Andes: the islands of the sun and the moon.* Austin: University of Texas Press.

Benítez, S., A. Blanco, J. Cole, M. Ibáñez, J. J. Rodríguez, and S. Halloy. 2010. Using water funds to finance watershed conservation in the Andes and Costa Rica. *Mountain Forum* 10:71-73.

Brack, A. 2005. *Deuda genética: los países pobres y la seguridad alimentaria de los países ricos*. Online: http://groups.yahoo.com/group/Biodiversidad_PERU/

Bradley, R. S., F. T. Keimig, and H. F. Diaz. 2004. Projected temperature changes along the American cordillera and the planned GCOS network. *Geophysical Research Letters* 31:L16210.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 312:1755-1756.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. Di Tomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677-688.

Buchmann, S. L., and G. P. Nabhan. 1996. *The forgotten pollinators*. Washington, DC: Island Press.

Buytaert, W., R. Celleri, B. DeBievre, F. Cisneros, G. Wyseure, J. Deckers, and R. Hofstede. 2006. Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews* 29:53-72

Colwell, R. K., G. Brehm, C. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261.

Cuesta Camacho, F. 2007. *Efectos del cambio climático en el rango de distribución de especies en los Andes del Norte*. La Paz: Curso GLORIA, Bolivia.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153-166.

DeLucia, E. H., C. L. Casteel, P. D. Nabity, and B. F. O'Neill. 2008. Insects take a bigger bite out of plants in a warmer, higher carbon dioxide world. *Proceedings of the National Academy of Sciences of the United States of America* 105:1781-1782.

Dudley, N., and S. Stolton. 2003. Ecological and socio-economic benefits of protected areas in dealing with climate change. Pp. 215-231 in *Buying time: a user's manual for building resistance and resilience to climate change in natural systems*, edited by L. J. Hansen, J. L. Biringer, and J. R. Hoffman. Berlin: WWF. 246 pp.

Erickson, C. L. 2000. The Lake Titicaca Basin – a Precolumbian built landscape. Pp. 311-354 in *Imperfect balance: landscape transformations in the Precolumbian Americas*, edited by D. Lenz. New York: Columbia University Press.

FAO. 1996. *The state of the world's plant genetic resources for food and agriculture*. Rome: Food and Agriculture Organization.

FAO. 2003. *Review of world water resources by country. FAO Technical Papers, Water Reports 23*. Rome: Food and Agriculture Organization.

Fjeldså, J. 2007. The relationship between biodiversity and population centres: the high Andes region as an example. *Biodiversity and Conservation* 16:2739-2751.

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55:73-106.

Fox, D. 2007. Back to the no-analog future. *Science* 316:823-825.

Garrett, K. A. 2008. Climate change and plant disease risk. Pp. 143-155 in *Global climate change and extreme weather events: understanding the contributions to infectious disease emergence*, edited by D. A. Relman, M. A. Hamburg, E. R. Choffnes, and A. Mack. Washington, DC: National Academies Press.

Halloy, S. R. P. 1981. La presión de anhidrido carbónico como limitante altitudinal de las plantas. *Lilloa* 35:159-167.

Halloy, S. R. P. 1983. El límite superior de aridez, límite de vegetación y el problema de los lagos, nevés y glaciares activos en el "Núcleo Arido" de la Cordillera Andina. *Actas 1era Reunión Grupo Periglacial Argentino, Mendoza. Anales 83, IANIGLA* 5:91-108.

Halloy, S. R. P. 1985. Reencuentro de *Azorella biloba* (Schlecht.) Wedd. en Tucumán. *Lilloa* 36:267-269.

Halloy, S. R. P. 2002. Variations in community structure and growth rates of high-Andean plants with climatic fluctuations. Pp. 227-239 in *Mountain biodiversity: a global assessment*, edited by C. Körner and E. M. Spehn. London: Parthenon Publishing.

Halloy, S. R. P., R. Ortega Dueñas, K. Yager, and A. Seimon. 2005a. Traditional Andean cultivation systems and implications for sustainable land use. *Acta Horticulturae* 670:31-55.

Halloy, S. R. P., A. Seimon, K. Yager, and A. Tupayachi Herrera. 2005b. Multidimensional (climate, biodiversity, socio-economics, agriculture) context of changes in land use in the Vilcanota watershed, Peru. Pp. 323-337 in *Land use changes and mountain biodiversity*, edited by E. M. Spehn, M. Liberman Cruz, and C. Körner. Boca Raton FL: CRC Press LLC.

Hardy, D. R., and S. P. Hardy. 2008. White-winged Diuca Finch (*Diuca speculifera*) Nesting on Quelccaya Ice Cap, Peru. *Wilson Journal of Ornithology* 120:613-617.

IPCC. 2007. Summary for Policymakers. Pp. 7-22 in *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson. Cambridge: Cambridge University Press.

Jarvis, A., J. L. Touval, M. Castro Schmitz, L. Sotomayor, and G. G. Hyman. 2010. Assessment of threats to ecosystems in South America. *Journal for Nature Conservation* 18:180-188.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009a. *Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela*. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

le Roux, P. C., and M. A. McGeoch. 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14:2950-2962.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7:975-989.

López, R. P., and C. Zambrana-Torrelio. 2006. Representation of Andean dry ecoregions in the protected areas of Bolivia: the situation in relation to the new phytogeographical findings. *Biodiversity and Conservation* 15:2163-2175.

Mann, C. C. 2000. Earthmovers of the Amazon. *Science* 287:786-789.

Marengo, J. A. 2007. *Mudanças climáticas globais e seus efeitos sobre a biodiversidade. Caracterização do clima atual e definição das alterações climáticas para o território brasileiro ao longo do Século XXI*. Brasilia: Ministerio do Meio Ambiente. 214 pp.

Marengo, J. A., W. R. Soares, C. Saulo, and M. Nicolini. 2004. Climatology of the Low Level Jet east of the Andes as derived from the NCEP-NCAR reanalyses: characteristics and temporal variability. *Journal of Climate* 17:2261-2280.

Marengo, J. A., R. Jones, L. Alves, and M. Valverde. 2009. Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. *International Journal of Climatology* 29:2241-2255.

Millennium Ecosystem Assessment. 2005. *Millennium Ecosystem Assessment synthesis report.* Washington, DC: Island Press.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-58.

Nabhan, G. P. 1989. *Enduring seeds: Native American agriculture and wild plant conservation.* California: North Point Press.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637-69.

Perez, C., C. Nicklin, O. Dangles, S. Vanek, S. Sherwood, S. Halloy, K. Garrett, and G. Forbes. 2010. Climate change in the high Andes: implications and adaptation strategies for small-scale farmers. *International Journal of Environmental, Cultural, Economic and Social Sustainability* 6:1-16.

Ruiz, D., H. A. Moreno, M. E. Gutierrez, and P. A. Zapata. 2008. Changing climate and endangered high mountain ecosystems in Colombia. *Science of the Total Environment* 398:122-132.

Ruiz, D., M. P. Arroyave, A. M. Molina, J. F. Barros, M. E. Gutierrez, and P. A. Zapata. 2009. *Signals of climate variability/change in surface water supply of high-mountain watersheds - case study: Claro River high mountain basin, Los Nevados Natural Park, Andean Central Mountain Range, Colombia*. World Bank Group, 207 pp.

Seimon, A., S. R. P. Halloy, and T. A. Seimon. 2007. Global high-altitude limits for aquatic vascular plants. *Arctic, Antarctic, and Alpine Research* 39:340-341.

Seimon, T. A., A. Seimon, P. Daszak, S. R. P. Halloy, L. M. Schloegel, C. A. Aguilar, P. Sowell, A. D. Hyatt, B. Konecky, and J. E. Simmons. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology* 13:288-299.

Sih, A., A. M. Bell, and J. L. Kerby. 2004. Two stressors are far deadlier than one. *Trends in Ecology and Evolution* 19:274-276.

Solman S., M. Nuñez, and M. F. Cabré. 2008. Regional climate change experiments over southern South America. I: Present Climate. *Climate Dynamics* 30:533-552.

Svenning, J. C., and R. Condit. 2008. Biodiversity in a warmer world. *Science* 322:206-207.

Tewksbury, J. J., R. B. Huey, and C. A. Deutsch. 2008. Putting the heat on tropical Animals. *Science* 320:1296-1297.

Thompson, L. G., E. Mosley-Thompson, H. Brecher, M. Davis, B. Leon, D. Les, P. N. Lin, T. Mashiotta, and K. Mountain. 2006. Abrupt tropical climate change: past and present. *Proceedings of the National Academy of Sciences of the United States of America* 103:10536-10543.

Ulloa, D., and K. Yager. 2008. *El cambio climático: ¿cómo lo sentimos y qué proponemos para adaptarnos?* La Paz: Conservation International. 28 pp.

Urrutia, R., and M. Vuille. 2009. Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research* 114:D02108.

Vergara, W., A. Deeb, A. Valencia, R. Bradley, B. Francou, A. Zarzar, A. Grünwaldt, and S. Haeussling. 2007. Economic impacts of rapid glacier retreat in the Andes. *EOS, Transactions, American Geophysical Union* 88:261-263.

von May, R., A. Catenazzi, A. Angulo, J. L. Brown, J. Carrillo, G. Chavez, J. H. Cordova, A. Curo, A. Delgado, M. A. Enciso, R. Gutierrez, E. Lehr, J. L. Martinez, M. Medina-Mueller, A. Miranda, D. R. Neira, J. A. Ochoa, A. J. Quiroz, D. A. Rodriguez, L. O. Rodriguez, A. W. Salas, T. Seimon, A. Seimon, K. Siu-Ting, J. Suarez, C. Torres, and E. Twomey. 2008. Current state of conservation knowledge on threatened amphibian species in Peru. *Tropical Conservation Science* 1:376-396.

Vos, C. C., P. Berry, P. Opdam, H. Baveco, B. Nijhof, J. O'Hanley, C. Bell, and H. Kuipers. 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology* 45:1722-1731.

Vuille, M., and R. S. Bradley. 2000. Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophysical Research Letters* 27:3885-3888.

Vuille, M., and F. Keimig. 2004. Interannual variability of summertime convective cloudiness and precipitation in the central Andes derived from ISCCP-B3 data. *Journal of Climatology* 17:3334-3348.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. *Earth Science Reviews* 89:79-96.

White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions* 12:443-455.

Yager, K. 2009. *A herder's landscape: deglaciation, desiccation and managing green pastures in the Andean puna*. PhD thesis. New Haven: Yale University.

Yager, K., H. Resnikowski, and S. R. P. Halloy. 2008. Grazing and climatic variability in Sajama National Park, Bolivia. *Pirineo* 163:97-109.

Yager, K., D. Ulloa, and S. R. P. Halloy. 2009. *Conducting an interdisciplinary workshop on climate change: facilitating awareness and adaptation in Sajama National Park, Bolivia*. Hamburg: Hamburg University of Applied Sciences.

2

Adaptive Management for Biodiversity Conservation under Climate Change – a Tropical Andean Perspective

David G. Hole, Kenneth R. Young, Anton Seimon, Carla Gomez Wichtendahl, Dirk Hoffmann, Klaus Schutze Paez, Silvia Sanchez, Douglas Muchoney, H. Ricardo Grau, and Edson Ramirez

The tropical Andes are a globally significant region for biodiversity (Mittermeier et al. 2004). Dramatic environmental heterogeneity across the region including steep gradients in elevation and humidity, and complex mosaics of bedrocks and soils (Young, Chapter 8, this volume), together with the wide range of historical variability in Andean climates (Chapter 5, this volume), have helped shape this remarkable biological diversity (e.g., Trenel et al. 2008; Antonelli et al. 2009; Guarnizo et al. 2009). These same processes have also shaped the human context and provided natural resources that now sustain the wellbeing of millions of people, including lands for farming and grazing, water for households, irrigation and industries, and space for settlements. The region is one of the key places in the world for the development of early human societies, from organized settlements, to irrigated agriculture and the domestication of plant and animal species (Denevan 2001). Hence, it now contains large expanses of human-dominated landscapes, from highly urbanized centers to more rural areas, where native forests have been replaced by agriculture and non-native tree plantations. Even the dry environments and high elevation sites are often used for extensive grazing of livestock. This leaves relatively few areas without a human presence, principal exceptions being the cool, moist cloud forests and the very humid paramos on the high mountains of the northern Andes. As a result of these historical and contemporary land-use patterns, there have long been tensions among the needs for conservation and protection of natural biodiversity, versus those for economic development and the reduction of social inequalities (Terborgh 1999). These tensions substantially increase the complexities of conservation planning in the region.

Historically, the rate of change in the land cover of tropical landscapes is unlikely to have occurred as rapidly as it has in the last 50 years (Young 2007). Deforestation and conversion of land has led to an unprecedented loss of natural habitats in recent decades, with profound ramifications for the continued functioning of entire ecosystems (MEA 2005). Ongoing and projected climate change adds a substantial new component to this mix. Dramatic changes to both biotic and abiotic systems and processes are already being seen across the tropical Andes, with glacial ice diminishing and upward biotic range extensions occuring even into high alpine areas (Seimon et al. 2007), with local people already altering their land uses in response (Postigo et al. 2008; Young 2008). Such changes are having profound impacts on species' phenologies, distributions and abundance (Parmesan 2006) that will increase in magnitude in the future. Of particular conservation concern are the likely changes in representation and abundance of species within existing protected areas and across networks (Araujo et al. 2004; Hole et al. 2009), as well as the high likelihood of profound changes in the location and continued functioning of many Andean ecosystems (Anderson et al. Chapter 1, this volume). Indeed, such changes are likely to result in the formation of 'no-analog' communities (i.e. species assemblages for which there are no present-day examples) (Williams and Jackson 2007). Given the projected pace and likely consequences of climate change, magnified as they are in regions such as the high Andes (Bradley et al. 2006; IPCC 2007), it is critical that we adapt conservation management strategies in an effort to maintain their effectiveness under climate change. Without such effort, the region risks losing substantial components of its biodiversity (Larsen et al. Chapter 3, this volume), loss of key ecological processes (Aguirre et al. Chapter 4, this volume) and disruption of its ecosystems and consequent reduction or loss of the services they provide (Anderson et al. Chapter 1, this volume).

In this chapter, we will focus on the conservation spotlight on adaptive management. It is not intended to be exhaustive in its coverage - the topics included are broad and need consideration in greater detail. Instead, we begin the process of identifying the range of risks and opportunities for biodiversity conservation and adaptive management presented by climate change within the unique context of the tropical Andean region. We highlight some of the principal tools available for assessing the vulnerability of biodiversity and ecosystems, and describe a range of conservation and management options that might be selected, based on the degree of manipulation and use required in order to maintain human wellbeing. In some cases, strict protection of very fragile ecosystems and endangered wild species is likely to be needed. In other cases, a mix of conservation through protected area systems and integrated planning for sustainable land use will likely be more appropriate. We then look briefly at options for monitoring climate change impacts and the effectiveness of management actions, before highlighting the opportunities (however limited) that climate change may bring for conservation. Finally, we identify critical institutional capacity needs within the region that are urgently required in order to effectively, efficiently, and equitably enable adaptation to the profound challenges posed by climate change.

Current Status of Andean Biodiversity Conservation

Protected areas are the single most important tool for biodiversity conservation in the tropical Andes region and have seen a substantial increase in number and area covered over the past 15 years (Hoffmann et al. Chapter 22, this volume). Currently, around 15% of the four Andean nations' land area is under national protected area status. While designation of protected areas has generally been based on biodiversity targets, it has not necessarily resulted in the representation of the most biologically pristine or valuable areas within priority ecosystems. More recently, protected areas have in many cases been created simply on the basis of socio-political opportunity.

Even though robust assessments of the representativeness of the different protected area systems have not been carried out in a systematic manner, around 70-80% of species are likely to be represented within national protected areas (excluding municipal and departmental level protected areas, indigenous and community conservation areas, and indigenous communal lands). However, representation is biased towards lowlands and foothills, and little attention has been paid to ecological processes, especially in western regions.

Capacity and data limitations mean that potential gaps in the network under climate change are largely unknown. However, there is now a push to integrate the large number of additional conservation areas managed at local and regional levels, into the National Protected Area Systems (Hoffmann 2009; Hoffmann et al. Chapter 22, this volume), in some cases led by municipal governments, and in others by native peoples, which could play a vital role in adapting national biodiversity conservation efforts to the challenges of climate change. There are also efforts under way to define national and regional conservation corridors that serve to link protected areas (e.g., Vilcanota-Amboró Corridor in Bolivia and Peru; three altitudinal corridors on the Eastern slopes in Colombia). Only in Colombia, however, has climate change recently been incorporated as an explicit component of the conservation planning process behind these efforts (see Appendix 2.1 and Hoffmann et al. Chapter 22, this volume, for further details). Hence, substantial basic research, including gathering of baseline data, as well as modelling of potential future shifts in species distributions and consequent changes in the provision of ecosystem services, is a critical priority for the tropical Andes region.

Adaptive Management and the Identification of Future Vulnerabilities and Opportunities

If we are to be proactive in addressing climate change, the identification of likely vulnerabilities and evaluation of possible adaptation responses, as well as the identification of potential opportunities, is paramount. Proactive strategies are likely to prove both more cost-effective (Hannah et al. 2007) and ethically responsible - in terms of preventing or ameliorating some of the worst potential impacts of climate change (Adger et al. 2009). However, given the magnitude of uncertainty in projections of climate change and in species, ecosystems and human responses, conservation planning must be set in the context of a range of potential future scenarios. Such an approach is not an excuse for inaction, but a call for adaptive management.

Adaptive management is an iterative process of optimal decision making in the face of uncertainty, that attempts to reduce that uncertainty over time by system-level monitoring (see Sutherland 2006 for more details). Broadly speaking, such an approach has five stages (Figure 2.1): 1) define plausible future scenarios and set conservation targets within this plausible range; 2) perform conservation actions; 3) actions will lead to new behaviour within the system; 4) monitor to detect changes in the system; 5) analyze impacts of conservation actions and adjust initial targets accordingly. The cycle is then repeated.

However, the high degree of historical and contemporary variability in Andean climate presents a substantial challenge to the identification of future scenario's (Figure 2.1, Stage 1) in relation to climate change impacts on species, processes and ecosystems. For example, for much of the high Andean region above 3000 m, climatological data indicates that inter-annual thermal variability is regionally synchronous and largely controlled by the phases of the El Niño Southern Oscillation (ENSO), whereas the precipitation pattern varies spatially. At Cusco in

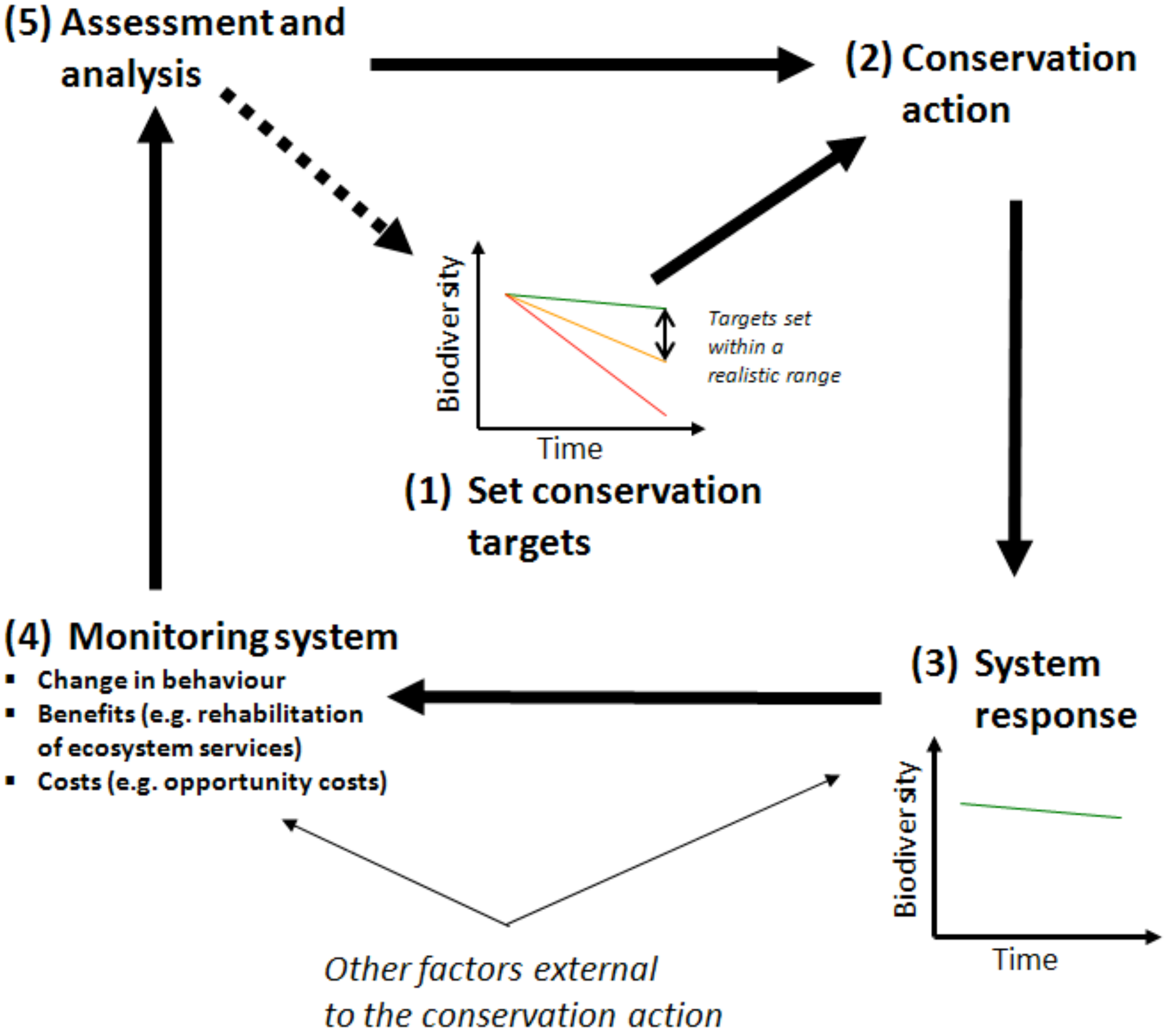

Figure 2.1. Simple schematic of the five stages of the adaptive management process: 1) Define plausible future scenarios based on modelling and/or expert opinion and set conservation targets within this plausible range; 2) Perform conservation actions; 3) Actions will lead to new behaviour within the system, which will also be subject to influence by multiple external factors; 4) Monitor to detect changes in the behaviour of the system, as well as the influence of external factors, including measurement of the direct and indirect costs of management actions, both positive (e.g. rehabilitation of ecosystem services) and negative (e.g. opportunity cost of foregone agricultural production); 5) Feed these data into an analysis of the impacts of the conservation actions, and adjust the initial models/scenario's and targets accordingly. This cycle is then repeated at appropriate time intervals.

southern Peru, the inter-annual range of variation in daily maximum temperature over the summer growing season has been as much as 3.8^0C (from $+2.5^0$C accompanying a strong El Niño event in 1983, to -1.3^0C under La Niña conditions in 1984). Historically, such a range of variability is likely the norm, although glaciological evidence suggests downward shifts in baseline mean temperature followed by a rebound to present levels probably occurred during the Little Ice Age (1500-1900 AD).

Such natural climatic variability creates two challenges. Firstly, it translates into greater uncertainty in projections of future climatic change in the region, particularly at the relatively fine scales required for most spatial planning needs (Vuille et al. 2008). Secondly, it has shaped the evolutionary environment of regional biodiversity, potentially enhancing the resilience of species and ecosystems to sequential climatic extremes. Moreover, the amplitude of change of such short term climatic shocks (i.e. 3.8^0C) exceeds the expected net thermal increase projected for the end of the 21st century under all but the most extreme emissions scenarios depicted by climate models for the Andes. Hence, there is a risk that some assessments could overestimate the impacts of climate change, projecting extinction in regions where a species or component populations are, at least potentially, pre-adapted. Perhaps more pertinent, however, is the capacity of individual species and ecological systems to adapt to a shifting thermal baseline that increasingly biases the distribution towards higher temperatures likely to surpass historical experience. Hence, the Andean context highlights a key issue in the development of scenarios of potential climate change impacts: what is the level of acceptable uncertainty? Practically however, when considering biodiversity targets, such uncertainty necessitates the use of multiple, but necessarily limited data sources, and therefore a judicious assessment of vulnerability.

Assessing Vulnerability

Direct Impacts

Broadly speaking, the vulnerability of a species to climate change is a product of its susceptibility (defined by its intrinsic biological traits), its exposure (does it occur in a region of high climatic change?) and its adaptive capacity (can it adapt to climatic change?) (Figure 2.2). The vulnerability of an ecosystem can then be defined by the likely complex interactions and synergies between the relative vulnerabilities of its component species and proximate abiotic processes (see Chapter 4 for a discussion of the complexity of the interactions).

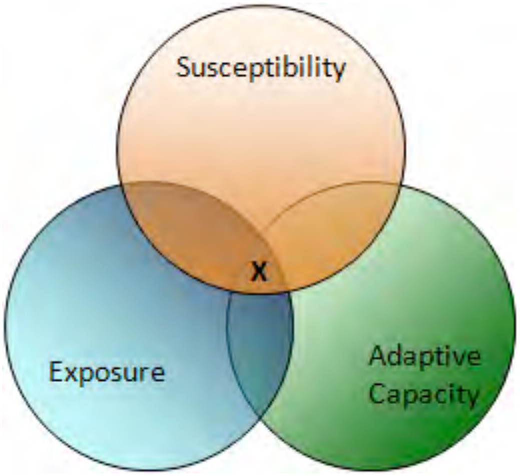

Figure 2.2. Schematic representation of a species vulnerability to climate change, where each component varies from 'low' to 'high' according to the colour gradient, such that 'X' represents greatest vulnerability (i.e., the intersection of the three components – high susceptibility, high exposure and low adaptive capacity)

These three components can be estimated using a variety of data sources and methodologies requiring varying degrees of technical capacity, input data quality and quantity, ability to provide robust future projections, definition of operational scale, and – critically – the associated uncertainties (Table 2.1). The simplest approach is to identify those biological traits of individual species (or across a taxon) that, based on expert opinion, are likely to predispose a species to being susceptible to climate change (Foden et al. 2009). Such traits might include a narrow altitudinal range at a high elevation, a high degree of habitat specialization, or a dependency on only a few prey or host species. Similarly, a species' adaptive capacity might be deemed limited if it is a poor disperser, or if its genetic diversity is low. Exposure can then be estimated based on, for example, its thermal tolerance (Jiguet et al. 2006) in comparison to projected climatic anomalies across its area of occupancy. Such an approach has many advantages – for example, it relates directly to a specie's ecology; it avoids the need to develop a more complex model of the relationship between climate and species distribution; and it is data 'light' in that it can be applied to a wide range of species and taxa. Disadvantages are that it provides limited information on the likely future spatial distribution of biodiversity that is critical for conservation planning and interactions between components of vulnerability may be missed.

Table 2.1. Examples of the methods currently available for assessing vulnerability and identifying future scenarios of biodiversity pattern.

Method	**Description**	**Identifies**	**Example Reference**
Trait-based assessments	Expert derived identification of broad life-history characteristics that predispose susceptibility	Susceptibility; Adaptive capacity	(Foden et al. 2009)
Shifts in climatic parameters	Spatial representation of shifts in climatic parameters derived from GCM or RCM outputs	Exposure; Refugia	(Ohlemuller et al. 2006; Williams et al. 2007)
Species distribution models (SDMs)	Modelled statistical association between a species present-day distribution and current climate – can then project relationship onto future climates (e.g. Maxent; Generalized Additive Models; Boosted-Regression Trees)	Susceptibility via e.g. present and future range overlap or change in future range extent; Exposure; Spatially explicit projections	(Pearson and Dawson 2003; Hole et al. 2009)
Dynamic [global] vegetation models (D[G]VMs)	Process based models that simulate shifts in, and dynamics of, vegetation, in response to climate and other drivers (e.g. LPJ; VECODE; BIOME)	Susceptibility of individual modelled plant species; Susceptibility of other species via spatially explicit projections of future presence of suitable habitat	(Scott et al. 2002; Hannah et al. 2008)
Population viability analysis (PVA)	Data-intensive, species-specific model that determines viability of one or more populations over time, based on internal and external drivers of population dynamics	Vulnerability	(Brito and Figueiredo 2003; Vargas et al. 2007)

Towards the other extreme of the data requirement spectrum is species distribution modelling (SDM) (Graham et al. Chapter 21, this volume; Pearson and Dawson 2003). Given adequate and robust gridded data on the presence and absence of a species across its entire range, or sufficient accurate and fine-scale presence localities across an environmentally representative sample of its range, together with technical capacity in statistical analysis and GIS, it is now relatively easy to generate present and future projections of individual species distributions at local, regional or continental scales (although interpretation of model outputs still requires ecological expertise). Advantages include quantified estimates of sensitivity (e.g., reduction/increase in future range extent), and spatially explicit projections of species' potential future distributions – a product that is unavailable by any other means. Disadvantages include the wide-range of assumptions that such models rely on (see Graham et al. Chapter 21, this volume) and the consequent requirement for judicious interpretation. Recent advances in the development of the next generation of SDMs seek to overcome many of these disadvantages and assumptions (e.g., Keith et al. 2008), by incorporating habitat requirements, population dynamics and dispersal into the bioclimatic modelling framework. On the downside, such models will require a vastly improved understanding of a specie's ecology. The pros and cons inherent across these methodologies should therefore be carefully considered when applying analyses to inform the adaptive management process.

Indirect Impacts

An understanding of the direct impacts of climate change on biodiversity is beginning to emerge in the Andean region, as is an awareness of the diversity and magnitude of the responses by people whose lives and livelihoods are altered by climate change (Young and Lipton 2006). However almost no attention has been paid to the impacts that human responses to climate change will have upon biodiversity. Yet these 'indirect' impacts have the potential to be of a magnitude and scope that will rival or exceed the direct impacts. Here we identify several areas in which the interactions between people, biodiversity and climate change in the tropical Andes have the potential to be critical and which urgently warrant further research and consideration in the adaptive management process.

Food: Climate change will have profound impacts on our ability to grow food. Regions currently suitable for a particular crop may become unsuitable, as climate change pushes local microclimates beyond the crop's temperature or water tolerance (Lobell et al. 2008). Unless new varietals can be developed, cropping practices adapted, or alternative crops identified, farmers may be forced to migrate to new areas (Warner et al. 2009), putting increased pressure on natural habitats or urban zones. Of course the converse may also be true, with changes in climate generating increases in yield and allowing some crops to be grown in areas that were previously unsuitable. In Peru's Cordillera Vilcanota for example, cultivation practices on highland slopes have moved progressively higher in recent decades as moderating temperatures have expanded the domain of a viable growing season upward. Studies at Nunoa performed in 1964-65 identified a relatively frost-free 5-month period representing a suitable growing season at 4,236m, close to the highest tilled fields at that time. A nearby climate station meanwhile, at 4,543m, recorded frosts throughout the year (Winterhalder and Thomas 1978). By 2003, however, potato cultivation in the nearby Pitumarca valley had moved to 4,550m around several communities. The warming regional climate has thus been accompanied by a rise in the limit of cultivation by as much as 300m over the 38 year period (Halloy et al. 2005; Figure 2.3). Further upward shifts in cultivation may put still largely pristine high elevation habitats under pressure. In the Cordillera Apolobamba in Bolivia, the upward shift in agricultural activities has displaced livestock (*camélidos*) to even greater elevations, with consequent impacts on high altitude ecosystems in the region (Schulte 1996). Where higher elevations have limited area, the same number of animals is often packed into a smaller area resulting in increased erosion. Yields of cash-crops crucial to livelihoods in the region, such as coffee, will also respond to changes in temperature, as projected for other regions of the America's (e.g., Mexico; Schroth et al. 2009). Increased pressures on upslope protected areas, as cost-effective yields of *Coffea arabica* become increasingly limited to higher elevations, are a likely consequence.

Water: Deglaciation caused by climate change over the past several decades, has led to a significant reduction in dry season flows in glacier-fed rivers (Francou et al. 2005; Vergara et al. 2007). This has necessitated the creation of upstream reservoir capacity to provide a buffer to ensure sufficient flow for hydropower generation and agricultural needs downstream. For example, the largest high-alpine lake in the Andes, Peru's 32 km^2 Laguna Sibinacocha at 4,900 m, which provides habitat for thousands of flamingos and other waterfowl, was artificially enlarged by a dam in the mid-1990s to augment diminishing dry season flow far downstream at the Machu Picchu hydroelectric generation plant on the Vilcanota-Urubamba river (Seimon 2001). Anecdotal evidence suggests that avian diversity and abundance on the lake may have decreased as a result, due to inundation of traditional nesting areas (see Anderson et al. Chapter 1, this volume for further examples).

Health: A major potential impact of climate change on human health is the change in the incidence and geographic range of vector-borne diseases (Martens 1998; Patz et al. 2002). Changes in ambient temperatures and rainfall have affected the seasonality, duration of outbreaks and morbidity profiles of both malaria and dengue fever, diseases whose transmission, distribution and seasonality are linked to climatic conditions (Poveda et al. 2001; Ruiz et al. 2006). Projected increases in temperature under climate change may now drive these diseases into formerly mosquito-free territories. As in the past, communities may choose to seek out malarial-free areas (Gade 1999) beyond the expanding disease front, putting further pressure on natural habitats within these regions.

Energy: Biofuels have been proposed as one method for mitigating greenhouse gas emissions. Whether or not biofuels actually offer carbon savings depends on how they are produced. In many regions the production of food crop-based biofuels is leading to the conversion of rainforests, savannas, peatlands, grasslands and other natural ecosystems to agriculture, generating a substantial "carbon debt" (Fargione et al. 2008), while simultaneously causing widespread degradation of natural ecosystems. In the Andean region, it is unclear as yet whether the increase in biofuel demand will have substantial negative impacts on Andean biodiversity as a result of deforestation and other legal, illegal or politically motivated land use changes. Although laws have been passed recently in Bolivia for example, encouraging biofuel production for national consumption, the government has so far opposed producing biofuels for exports, because of the potentially negative impacts on food security and on small farmers.

Hydroelectric power generation meanwhile is affected by changes in climate and stream flows. In Peru, the prospect of decreasing dry season flows from glacier-fed rivers has motivated an adaptive electricity generation strategy shifting away from hydropower, which formerly contributed 90% of the country's power supply, to greenhouse gas producing gas/thermoelectric power generation facilities (Vergara et al. 2007).

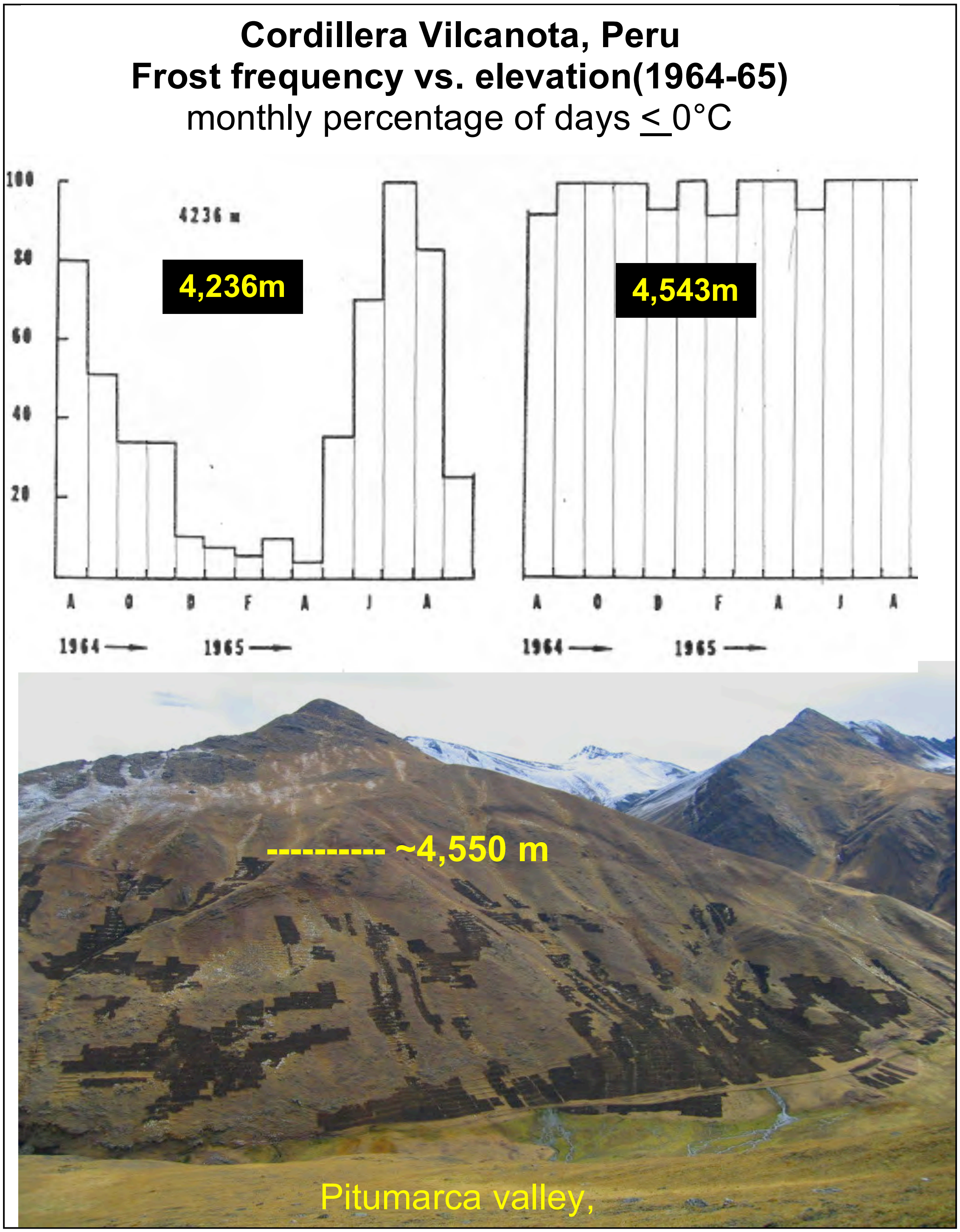

Figure 2.3. Rising altitudinal limit to cultivation in the Andes associated with regional warming. Photograph © Anton Seimon 2003

Human migration: Large-scale displacements of people resulting from climate change is already a reality, with the United Nations High Commissioner for Refugees in 2008 arguing for the first time that the increase in displaced people globally was at least partly attributable to climate change-related conflict. However, even in the absence of conflict, this trend is likely to increase substantially in synergy with many of the drivers outlined above, generating new, or modifying existing patterns. Rural-urban migration is already significant in the Andes, and will be further enhanced by the increased unpredictability of agricultural production. While this process may result in socioeconomic improvements, as well as more efficient use of natural resources, it is also likely to result in increased human pressure in urban areas, local increases in water demand and water diversion, with consequent impacts on freshwater and terrestrial ecosystems. Conversely, the reduction in the human footprint in rural areas could lead to a beneficial indirect impact on biodiversity (Grau et al. 2003; Grau and Aide, 2007), assuming the land has not been badly degraded and is allowed, or actively encouraged to revert to a natural state.

Adaptive Management Responses

Mitigating identified vulnerabilities to climate change in the tropical Andean region will be challenging, given the complex patterns and associated interactions of biodiversity and human land use. Here we highlight key adaptive management responses (see Heller and Zavaleta 2009 for a more comprehensive review), noting that these responses require coordination and integration at local, national and regional levels (Figure 2.4) if they are to be effective. Although here we break these responses down into species-, site- and landscape-level approaches, such distinctions must become necessarily blurred when developing a holistic adaptation strategy under climate change.

Regional planning process

A systematic conservation planning process (Margules and Pressey 2000) for the region is a critical research and policy requirement for the near term. While the potential foundations for such a process exist (e.g., the Estrategia Regional de Biodiversidad para los Paises del Tropico Andino), climate change is at best a marginal component in such plans. Any process must also be cognizant of the specific national and local contexts in which biodiversity conservation will be carried out.

Species-level approaches

Removing current stresses and threats to a vulnerable species or ecosystem (e.g., hunting pressure, habitat fragmentation) requires minimal knowledge of potential climate change impacts, yet it is a practical way to increase resilience since a system facing multiple stressors is less able to cope with additional pressures from climate change. The Andean bear (*Tremarctos ornatus*) is one example that would likely benefit from such an approach, given its large home-range and lack therefore of site-specific conservation options. ***Individual species action plans*** such as the Biodiversity Action Plans (BAPs) in Europe, or the US Endangered Species Program that are backed up by legal enforcement, also reduce the vulnerability of a species to climate change. A limited number of such plans already exist in the Andean region, e.g., for *Polylepis* in the Callejon de Conchucos in Ancash, Peru; and Southern Horned Curassow *Pauxi unicornis* in

Bolivia. Identification of further species for which alternative adaption options are unlikely to be sufficient to maintain viable populations should be a priority.

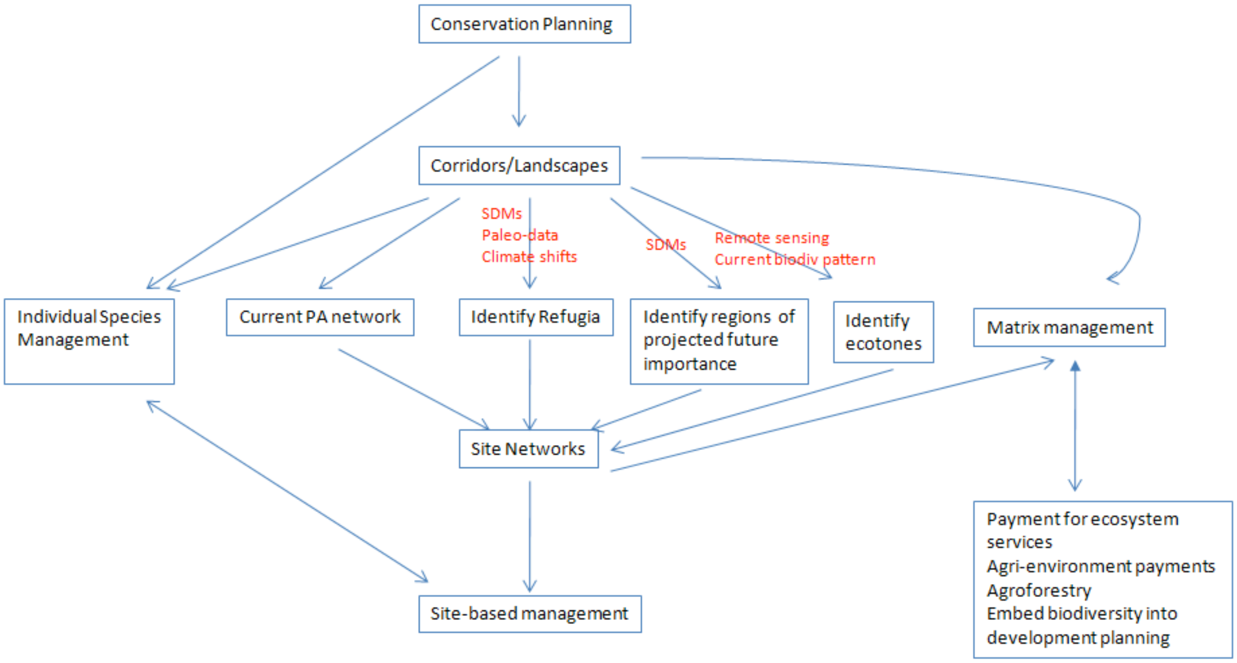

Figure 2.4. Adaptive management options for increasing resilience to biodiversity, across spatial scales.

Where a species is imminently at risk of extinction, its ***translocation (or assisted migration)*** to suitable but inaccessible habitat (perhaps due to distance from the species' current range) and **ex situ *conservation*** have to be seriously considered, despite acknowledged costs, difficulties and risks (e.g., Hoegh-Guldberg et al. 2008). For example, following precipitous population declines caused principally by Chytridiomycosis (Pounds et al. 2006), many Andean amphibians now require an *ex situ* approach, namely bringing the most threatened species into captive breeding until release back into the wild becomes feasible. In other situations, this may be done *in situ*, translocating plants and animals to sites that will be buffered from the effects of climate change (see 'refugia' below) or at sites that can be managed such that the negative effects of climate change are mitigated. Crucially, translocation will also likely have to include long-lived elements of critical habitat types, such as seedlings of trees that upon maturity will provide food, shelter and other resources, for the range of species and taxa that will be shifting their distributions into these newly climatically suitable sites/regions.

Site-level approaches

Protected areas (PAs) and PA networks remain the optimal strategy for conserving global biodiversity (Bruner et al. 2001). Increasing the coverage of the global PA network in order to fill 'gaps' (i.e., species whose ranges are not included in the current network (Rodrigues et al. 2004)) is an urgent conservation priority. However, under climate change simply trying to achieve adequate representation of current biodiversity pattern when choosing new sites is likely to be insufficient. Instead, other considerations, particularly potential shifts in both biodiversity pattern and process, must be explicitly considered.

Relict forest patches above the mean closed timberline are a common feature on many steep mountain slopes up to 5,400 m, especially along the eastern Andes. Composed primarily of *Polylepis* and *Gynoxys* (Fjeldså and Kessler 1996; Coblentz and Keating 2008), these forest islands harbour assemblages of other species including endemic fauna and flora such as the critically endangered bird, the Royal Cinclodes (*Cinclodes aricomae*). Indeed, these patches have likely functioned as ***biological refugia*** through climatically stressful epochs in the past, including most recently the Little Ice Age. Their apparent stability therefore suggests resilience in the face of climate change. It has therefore been argued that they should be considered high priority targets for conservation, both for their current ecological function and for their potential to serve as refugia under the changed climatic conditions of the future. However, some caution is needed since these relict patches could simply represent remnants of much more extensive forests fragmented by humans over centuries or millennia (Fjeldså and Kessler 1996; Fjeldså 2002; Kessler 2002), raising doubt over their ability to act as future refugia. Other putative refugia have also been identified in the Andean region, including areas with stable mist formation on the Pacific slope and the intermontane basins (Fjeldså et al. 1999). Clearly, the robust identification of functional refugia in the tropical Andes must be a research priority.

Environmental gradients containing sufficient natural habitat to create land-use mosaics that will maintain functional habitat connectivity, should be incorporated into conservation units wherever possible (e.g. sites, corridors, watersheds). Both short, sharp, and broad, diffuse gradients should be considered where relevant, because of the different options they provide for rapid dispersal of species or adaptation through genetic plasticity (Killeen and Solorzano 2008). Gradients of particular relevance to the Andes include elevational, edaphic, and humidity gradients. This strategy is already being utilized in Peru, where three large national parks have been created that include entire elevational gradients (Rio Abiseo, Yanachaga-Chemillen, and Manu National Parks) (Young and Lipton 2006), in Bolivia (Madidi, Carrasco, and Amboró National Parks), in Ecuador (La Reserva Cofanes-Chingual), and in Colombia.

The ***tracking of ecotones*** (the transition between two ecosystems or biomes) offers a further adaptive management option. An important example in the Andean context is the treeline, the dynamics of which are sensitive to both climatic and human impacts (Bader et al. 2007; Young and Leon 2007). Given the relatively high environmental and climatic variability at ecotones, populations in or near these areas are likely to be pre-adapted to a relatively high level of physiological stress and may possess adaptive genetic traits that are absent from core populations (Killeen and Solorzano 2008). Monitoring and tracking of ecotones is now feasible thanks to recent advances in remote sensing (see Monitoring section).

Riverine forest corridors have served as pathways or refugia for many forest taxa (e.g., in Madagascar; Wilme et al. 2006) and are likely to continue to do so under climate change. By connecting higher elevation watersheds to the lowlands, they incorporate many of the environmental gradients already highlighted as key targets in the Andean region. Examples include the Topo and Palora rivers in Ecuador, whose watersheds are protected by the Llangantes and Sangay National Parks, thereby covering an elevational gradient of almost 3000 m.

Maintaining riverine forest can reduce the build up of sediment and/or chemicals leaching into the water from the surrounding landscape, preserving water quality for aquatic species. The rivers themselves are also critical for both freshwater and biodiversity.

In order to reduce or remove threats to a vulnerable species or ecosystems, strict protection of some localities within PAs, or of entire PAs, will be required. Most tropical Andean national protected area systems include ***strict protection*** as a management option, typically defining specific vulnerable zones as "no impact" or "no visit". Use of this management option is likely to become even more crucial under climate change and sensitivity will need to be shown in deriving the correct balance between sustainable use of an area by local communities and the preservation of species and key habitats.

SDM projections provide a means of ***identifying regions or even sites that could represent concentrations of future species richness*** and/or regions projected to experience large numbers of species moving through them, as species' ranges shift. As a result, they have begun to be incorporated into adaptive management planning, e.g. for the Cape Proteaceae in South Africa (Williams et al. 2005); for the African IBA network (Hole et al. in press). If the assumptions and uncertainties in such modelling exercises are fully acknowledged, these techniques currently provide the only method of proactively identifying future regions of potentially high conservation value that may not be included in current conservation plans.

Similarly, use of SDM and dynamic vegetation models (DVM) projections provide a means of ***informing future site-based management strategies*** by identifying and targeting broad management strategies across networks of conservation sites, that reflect potential changes in the species composition of those sites. Broad strategies can be characterized from SDM derived projections of inter-site differences in the number of immigrant, emigrant and persistent species across a network of sites (e.g., for the African IBA network; Hole et al. in press), or based on DVM projections of future vegetation patterns within sites (e.g., the Canadian Parks system; Scott et al. 2002).

Landscape-level approaches – corridors and landscape permeability

Large protected areas may include sufficient environmental gradients such that they can be managed as a single landscape unit (Figure 2.5 A). Within such sites, species range shifts will likely leave relict distributions in addition to forming new species assemblages along elevation and humidity gradients. A variety of approaches may then be viable for preservation, translocation, and restoration. Most Andean landscapes, however, include a wide variety of human land uses, creating mosaics within which conservation strategies are more constrained (Figure 2.5 B). Given the potential speed and magnitude of species range shifts in response to climate change, and the very high likelihood of substantial species turnover within conservation areas (Hole et al. 2009), most site-based conservation strategies will continue to fulfil their role only if the landscapes within which they are embedded (i.e., the matrix) allow species to move through them across ecologically relevant temporal and spatial scales (Gascon et al. 1999). Corridors are landscape scale conservation and management units (Soule and Terborgh 1999) that have already been defined across parts of the Andean region. Within such landscape units, promotion of land use efficiency may prove to be key. Encouraging the concentration of agricultural production within restricted, but high yield areas, may favour de-intensification in

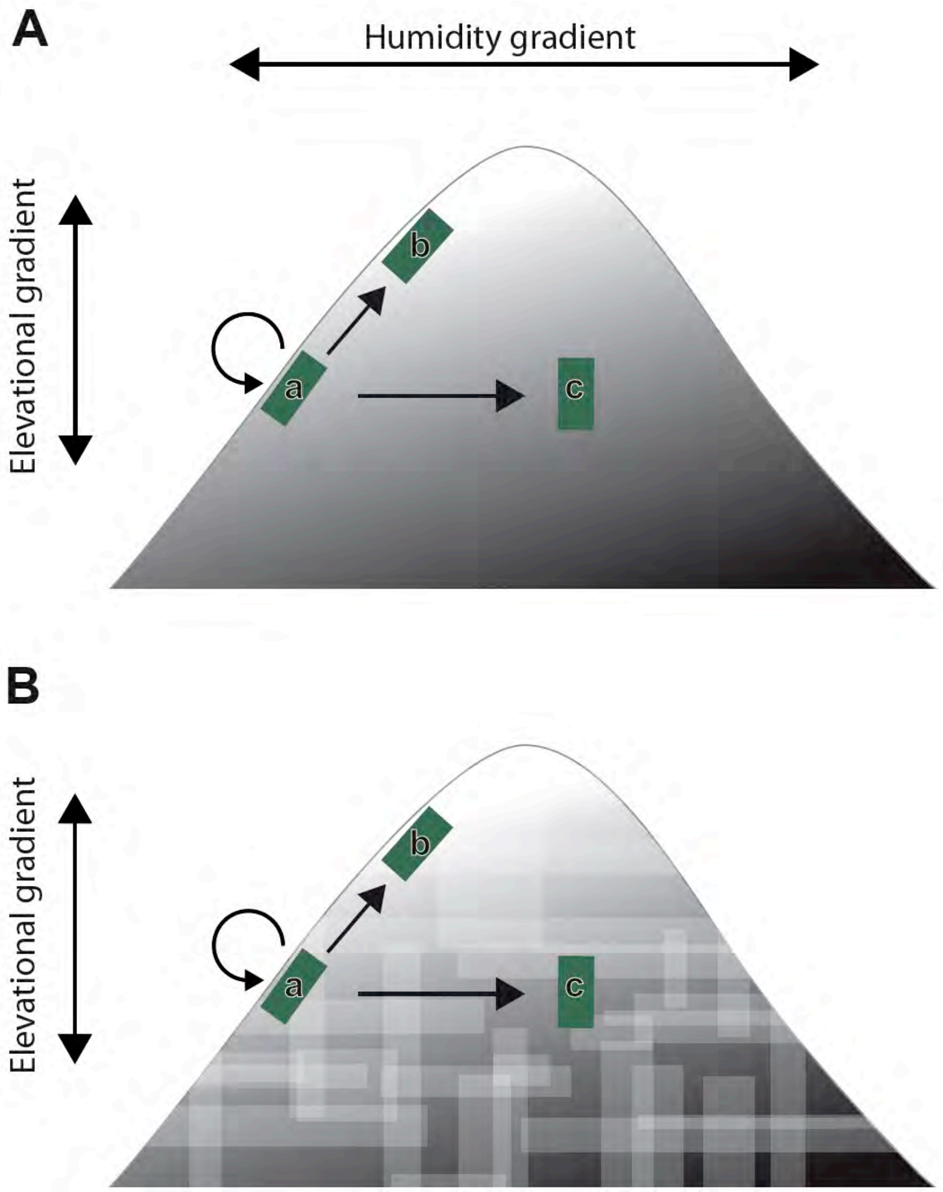

Figure 2.5. Andean landscapes have strong environmental gradients, with dramatic changes in elevation joined by shifts in humidity, mediated through rainfall amounts, degree of seasonality, and soil moisture.

XA, represents a protected landscape, wherein the goals of biodiversity conservation take priority. Climate change can force species shifts along the elevational gradient (b), along the humidity gradient (c), or in some cases may not cause species shifts or may not affect a particular site (a). Strategies within this protected area may include special attention to a, given it serves as a conservation refugia, while facilitated transformation of important habitat elements (e.g., tree plantings) and translocation of species of concern to places predicted to be important for altitudinal shifts (b) and range shifts to wetter or drier sites (c).

XB, represents an inhabited landscape, utilized by people and with multiple land owners and land tenures. Here there could also be refugia (a), elevational shifts (b) and shifts with changing humidity regimes (c), but the conservation strategies may be more constrained in deference to competing needs for land use. Instead management strategies or conservation incentives could be used to lessen the landscape matrix's resistance to species movements, through formal conservation corridors or through land uses such as agroforestry or shade coffee. The refugia (a) could be particularly important conservation targets, requiring active management interventions including strict protection and habitat management.

less productive and more vulnerable areas (e.g., on slopes and at higher elevations) and reduce encroachment on natural habitats (Green et al. 2005; Grau and Aide 2007), although the effectiveness of such ‘land sparing’ remains questionable (Ewers et al. 2009).

Monitoring

Monitoring is a critical component of the adaptive management process (Figure 2.1, Stage 4). It provides baseline assessments of biodiversity and environmental parameters of interest (e.g., climate) from which to interpret current and potential future changes; a means to validate model outputs (e.g. is a species range shifting in the manner projected by its SDM?); an early-warning mechanism of unexpected climate change impacts; and a measure of the effectiveness of a conservation action, that must then be fed back into adaptive management. Choosing the correct indicators to monitor can be challenging given limited resources, and they will depend on the goal of the monitoring. Suitable indicators can be individual species (e.g., amphibians with a recognized sensitivity to climatic conditions); assemblages (repeat censusing of floral assemblages is already underway through the GLORIA initiative but is otherwise lacking in the Andes); ecosystems (e.g., paramos are a crucial ecosystem to monitor since there is nowhere ‘upwards’ for constituent species to go (Anderson et al. Chapter 1, this volume)); processes or interactions (e.g., the well documented relationship between fig trees (*Ficus* spp.) and their fig-wasp pollinators (*Agaoninae*) represents a powerful indicator since its disruption through climate change would resonate across communities or even entire ecosystems); composites of these (e.g., GLORIA http://www.gloria.ac.at/?a=20 and TEAM http://www.teamnetwork.org/en/ networks); or derived products from remote sensing (e.g., NDVI to assess seasonal ‘greening’). Utilizing a broad range of indicators increases our ability to detect climate change signals and rapidly adapt management responses accordingly. Long-term data series are also vital for understanding the natural range of variability of systems, yet standardized long-term monitoring records are lacking throughout the majority of the tropical Andes.

The utility of remote sensing data for monitoring purposes has increased rapidly over the past decade and merits closer inspection, given its potential for relatively cheap, standardized monitoring over much of the globe, including the tropical Andes. There is now a wide array of current and/or planned Earth observing systems (satellite, aerial, and *in situ*) at local, national and regional scales, that collect and disseminate monitoring data. The Global Earth Observing System of Systems (GEOSS) is coordinating the collection, distribution and use of these data across multiple themes of importance to society: climate, weather, energy, health, agriculture, water, disasters, biodiversity, and ecosystems. Recent changes in data policy have made remote sensing data available at little or no cost. Table 2.2 provides an overview of current satellite and associated sensors most relevant to monitoring climate change effects on biodiversity and ecosystems in the tropical Andes. As an example of the utility of such data, satellite and aerial photography, together with radar and LIDAR data, when coupled with field-based calibration and validation, now provide an operational means of defining and monitoring ecotones, including changes in treelines, through estimation of tree height, basal area and stem volume (Holmgren 2004), treeline structure (Rees 2007), species composition (Holmgren and Persson 2004), tree migration (Næsset and Nelson 2007), and changes in treeline over time (Zhang et al. 2009). The number of satellite-borne sensors has increased dramatically and many hyperspectral, radar, and LIDAR missions are on-going or planned. Yet access to this high data volume, to usable, derived products, and to technical capacity for interpretation remain limiting factors for monitoring climate change impacts on biodiversity.

Table 2.2. An overview of principal current remote sensing data, of relevance to biodiversity and ecosystem monitoring in the tropical Andes . * = commercial system; Pan = panchromatic; XS = multispectral.

Satellite / Sensor	**Temporal Resolution (days)**	**Spatial Resolution (m)**	**Spectral Resolution / Band**	**Program Life**	**Derivative Products**
Moderate-resolution (250-8000m)					
AVHRR	1	1000-8000	XS, thermal	1982-	IGBP Land Cover, GIMMS NDVI
SeaWIFS	1	1000	XS	1998-	Ocean Color
SPOT-Vegetation (VGT)	2	1000	XS	1998-	GLC 2000, GIMMS NDVI
MODIS	1	250-1000	36 channels in visible - thermal	2000-	MODIS LAI/fPAR, VI, NPP, Land Cover, Fire. Land Surface Temperature
MERIS	1	300	36 channels in visible - thermal	2000-	GLC 2005
Medium-resolution optical (10-250m)					
Landsat 1-3 MSS	16	80	XS	1973-87	Global Land Survey 1970
Landsat 4-5 TM	16	28.5	XS, thermal	1984-	Global Land Survey 1970, 1990, 2000, 2005
Landsat 7 ETM	16	15-28.5m	XS, thermal. pan	1999-	Global Land Survey 2000, 2005
SPOT 1-5	2	10-20	Green, red, near-IR	1990-	
ASTER	16	15, 30, 90	XS, thermal	1999-	ASTER Global Digital Elevation Model
IRS	Variable	2.5, 20, 30	Pan, XS	1988-	
CBERS 1-3	5	20	XS, Pan	2003-	
ALOS	46	10	XS	2006-	
Medium-resolution radar(10-250m)					
ERS 1-2	35	25	C-band SAR	1996-	
JERS-1	44	10	L-band	1992-98	
Radarsat 1-2	24	8, 20, 50	C-band	1995-	
PALSAR	46	10, 100	L-band	2006-	
SRTM	short-lived	30,90, 1000	Interferometric radar	2002	SRTM30, SRTM90 DEMS
ENVISAT ASAR	35		C-band	2002-	
High-resolution (<10m)					
Ikonos *	Variable	1-4	Pan, XS	1998-	
GeoEye *	Variable	1	Pan, XS	2009-	
TerraSAR	11 days	1, 3, 6	X-band SAR	2007-	
RapidEye*	1	6.5	XS, Pan	2008-	

Opportunities – Demonstrating the Value of Maintaining Functional Ecosystems

Climate change is already having negative repercussions for both biodiversity and people and poses a multitude of future risks. If there is any positive side to this, it may be that climate change has helped push biodiversity, ecosystems and the services they provide, to finally being recognized and valued as critical components of the Earth system, rather than as a global commons to be used and abused without concern for the consequences. Attaching a 'value' to nature is seen as anathema by some and care must be taken to ensure that the value of an ecosystem reflects not just its direct commercial or marketable value (e.g., provision of hydrological services), but also those goods and services that are extremely difficult to quantify and value (e.g., cultural services such as spiritual value). Nevertheless, the lack of any sort of valuation is an underlying cause of the degradation of ecosystems and the loss of biodiversity that we see today (TEEB 2008). Such a valuation becomes even more critical given that the maintenance of functional ecosystem services is likely to represent the most cost-effective way to avoid and/or adapt to many of the projected impacts of climate change on human wellbeing. So-called 'ecosystem based adaptation' (an adaptation strategy now defined and endorsed by IUCN, the World Bank and many other international organizations) is likely to be of particular relevance in much of the developing world, where 'technical' adaptation options, such as the building of a large-scale water treatment plant in response to diminished freshwater quality, may be a far less pertinent adaptation option than, for example, maintaining or restoring forest-cover throughout a key watershed. In light of these developments, including a valuation (even a "back-of-the-envelope" calculation) of the ecosystem services preserved or restored as part of any adaptive management strategy, represents a key tool to leverage biodiversity-favourable policy across stakeholders.

Payment for Ecosystem Services (PES)

Paying individuals or communities for the services provided by natural ecosystems on their land is still rare in the Andean region. However, successful PES schemes do exist. For example, in the Los Negros river watershed in Bolivia, Fundación Natura has initiated a project that seeks to reduce or prevent reductions in water quality and quantity for downstream users (principally farmers relying on irrigation) caused by upstream deforestation. Through the scheme, these downstream irrigators agree to compensate upstream farmers to protect certain forests and restore others, thereby ensuring the quality of their water supply. In Ecuador meanwhile, the Pimampiro initiative places a specific fee for watershed forest protection onto the water bills of nearly 1300 families; 20% of these funds are then used to pay 19 upstream farmers to conserve their forests (390 ha of forest and 163 ha of paramo) (Camacho 2008). Major cities such as Bogotá in Colombia and Santa Cruz in Bolivia are now also beginning to utilize water-based PES schemes through small additions to water or electricity fees to pay for watershed conservation. In Quito, Ecuador, which receives its water supply from the high plateaus of the surrounding Andean range, a Water Conservation Fund (FONAG) was set up in 2000 to manage and direct revenue generated by a water consumption fee, to fund conservation and restoration projects in surrounding watershed. These projects include, for example, improving sheep and cattle production practices in order to reduce negative impacts on land cover and water quality.

On a potentially far greater scale, the introduction of REDD (Reduced Emissions from Deforestation and Degradation) as a climate change mitigation strategy, could provide a potentially massive increase in the funds available for forest conservation through their role in carbon sequestration and storage. The benefits to biodiversity could be increased further still if policymakers could agree to prioritize forests with high biodiversity for REDD funding. The potential for REDD to contribute to biodiversity conservation in the tropical Andean region is substantial and numerous pilot studies are being carried out. For example, a recent study in Peru's Cordillera Azul National Park, has demonstrated that management activities over the past six years have decreased deforestation rates in its buffer zone and prevented further deforestation in the park. However, without a continuous source of revenue, such as REDD could provide, continued management will be impossible and the park will likely succumb to threats from logging, oil extraction and the expansion of the agricultural frontier that have impacted the park in the past.

Incorporating Biodiversity Conservation into Development Planning

There is a growing awareness, from local NGOs to the large multilateral organizations, that poverty and biodiversity are intimately linked. The poor, especially in rural areas, depend on biodiversity for food, fuel, shelter, medicines and a wealth of other ecosystem services. Biodiversity loss therefore exacerbates poverty, while poverty in turn is a major threat to biodiversity, through unsustainable land use. The conservation and sustainable use of biodiversity also plays a critical role in the economic survival of a variety of production sectors such as fisheries, agriculture, and tourism. Consideration of biodiversity must therefore be integrated into the development process. This 'mainstreaming' of biodiversity into production sectors, poverty reduction plans and national sustainable development plans has been an internationally acknowledged goal for some time. For instance, goal 3.3 of the Strategic Plan of the Convention on Biodiversity (CBD), developed in 2002, requires that "biodiversity concerns are being integrated into relevant national sectoral and cross-sectoral plans, programmes and policies". Yet progress on achieving this goal in the Andean region, as elsewhere, has been limited. It must now become a priority, both in terms of collating the scientific and socio-economic evidence to support it, and the development of the policy initiatives to make it happen.

Obstacles – Institutional Capacity

Perhaps the single greatest limitation to robustly addressing the combination of the direct and indirect effects of climate change, together with the impacts of other global change (e.g., deforestation, species invasion) on biodiversity in the Andean Region, is the lack of institutional capacity. This lack is principally a result of competing and overlapping responsibilities, compounded by lack of interconnections between and among institutions, authorities and other stakeholders in the region. Although skilled and technically adept scientists and policy makers exist across the region, they are in profoundly short supply. In order to improve capacity therefore, there is a clear need to: 1) Develop interdisciplinary higher education programs, to train qualified local researchers in the processing and analysis of ever increasing quantities of data (e.g., by promoting international programmes for students to study in leading institutions in

Europe, Asia and North America). 2) Promote training opportunities for local leaders to facilitate their understanding and interpretation of complex analyses. 3) Involve the social, behavioral, and economic sciences in the necessary planning, implementation, and monitoring; advances are being made in the areas of environmental economics and common pool resource theory, used for understanding decisions relating to natural resource use and valuation. 4) Establish and promote social networks, for example, through the internet, to coordinate and facilitate information dissemination to decision makers and other stakeholders.

At the scale of the tropical Andes, institutions like the Comunidad Andina (CAN) could play a leading role in promoting and facilitating integration and adaptive practices among signatory countries. Ideally, this would result in a regional planning process at least every five years, timed to coincide with the availability of new assessments resulting from the IPCC process. The planning process may also need to expand to include the Venezuelan Andes, north-west Argentina and north-east Chile, given the extension of tropical Andean ecosystems across these country's borders. At the national level, there are existing planning initiatives in both the private and public sectors that could be expanded and replicated elsewhere. Not only should this involve the scientific community, but also social communicators. At the local level, municipalities and local communities will need access to results to allow them to assess and plan for locally-led initiatives. It will therefore be important to promote the provision of training to meet identified needs, so that local concerns are accounted for. In some regions, municipalities coordinate with protected area systems and should also be partners when setting climate change goals. Throughout the regional planning process, it will be crucial to facilitate public dissemination in order to ensure that the process is transparent and accountable.

Conclusions

Given the global importance of the tropical Andes for biodiversity, and the considerable risks posed by climate change, it is critical that both a regional and an international response be oriented to provide the necessary information and resources at the appropriate regional, national, and local scales, in order to inform robust adaptive management responses. Given current social inequalities which will likely be further exacerbated by climate change, the implementation of strategies that incorporate the use of economic, policy, and legal instruments for biodiversity conservation across the tropical Andean region will need to consider equity, fairness and distributional issues. How are these policies impacting stakeholders? Are they imposing burdens on the poorest sectors? These and other similar questions must be considered when designing and implementing integrated conservation and development policies. We highlight nine critical needs:

- Convene a region-wide systematic conservation planning process, that explicitly incorporates the impacts of climate change, and that reconvenes every five years, in order to coincide with the availability of new knowledge from the IPCC and other assessments.
- Continue to develop a comprehensive understanding of Andean climatology of the present and recent past to provide a baseline for detecting change and for assessing species and ecosystem capacities for resilience to climate stresses.
- Implement standardized monitoring protocols to provide baseline evaluations of species distributions, population status, and ecosystem integrity, drawing from taxonomy, field

ecology, and remote sensing. It is critical that data transparency and sharing is widely promoted.

- Continue to develop and test the next generation of SDMs for projecting species and ecosystem (or proxy) spatial responses to climate change, since these provide the only way of assessing potential synergies and conflicts with people in an uncertain future.
- Improve the understanding of the indirect impacts of climate change, resulting from planned and unplanned human adaptation and mitigation responses, on biodiversity and the provision of ecosystem services.
- Demonstrate the direct and indirect benefits of ecosystem based adaptation as a key tool for making lives and livelihoods more resilient to climate change.
- Build institutional capacity to design and implement robust adaptive management strategies, at regional, national and local scales, including all stakeholders.
- Incorporate consideration of biodiversity into local, national and regional development planning, across all economic and societal sectors. Biodiversity and the ecosystem services it underpins must be front and center with economic and other considerations.

Literature Cited

Adger, W. N., S. Dessai, M. Goulden, M. Hulme, I. Lorenzoni, D. R. Nelson, L. O. Naess, J. Wolf, and A. Wreford. 2009. Are there social limits to adaptation to climate change? *Climatic Change* 93:335-354.

Antonelli, A., J. A. A. Nylander, C. Persson, and I. Sanmartin. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences of the United States of America* 106:9749-9754.

Araujo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H.Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* 10:1618-1626.

Bader, M. Y., M. Rietkerk, and A. K. Bregt. 2007. Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic, Antarctic, and Alpine Research* 39:353-364.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 302:1755-1756.

Brito, D., and M. D. L. Figueiredo. 2003. Minimum viable population and conservation status of the Atlantic Forest spiny rat *Trinomys eliasi*. *Biological Conservation* 113:153-158.

Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* 291:125-128.

Camacho, D. C. 2008. Esquemas de pagos por servicios ambientales para la conservacion de cuencas hidrograficas en el Ecuador. *Investigacion Agraria: Sistemas y Recursos Forestales* 17:54-66.

Coblentz, D., and P. L. Keating. 2008. Topographic controls on the distribution of tree islands in the high Andes of south-western Ecuador. *Journal of Biogeography* 35:2026-2038.

Denevan, W. F. 2001. *Cultivated landscapes of native Amazonia and the Andes*. Oxford: Oxford University Press.

Ewers, R. M., J. P. W. Scharlemann, A. Balmford, and R. E. Green. 2009. Do increases in agricultural yield spare land for nature? *Global Change Biology* 15:1716-1726.

Fargione, J., J. Hill, D. Tilman, S. Polasky, and P. Hawthorne. 2008. Land clearing and the biofuel carbon debt. *Science* 319:1235-1238.

Fjeldså, J. 2002. *Polylepis* forests – vestiges of a vanishing ecosystem in the Andes. *Ecotropica* 8:111-123.

Fjeldså, J., and M. Kessler. 1996. *Conserving the biological diversity of* Polylepis *woodlands of the highland of Peru and Bolivia: a contribution to sustainable natural resource management in the Andes*. Copenhagen: NORDECO.

Fjeldså, J., E. Lambin, and B. Mertens. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography* 22:63-78.

Foden, W. B., G. M. Mace, J.-C. Vie, A. Angulo, S. H. M. Butchart, L. DeVantier, H. T. Dublin, A. Gutsche, S. Stuart, and E. Turak. 2009. Species susceptibility to climate change impacts. Pp. 77-88 in *Wildlife in a changing world – an analysis of the 2008 IUCN Red List of threatened species*, edited by J.-C. Vie, C. Hilton-Taylor, and S. N. Stuart. Gland: International Union for Conservation of Nature and Natural Resources. 180 pp.

Francou, B., P. Ribstein, P. Wagnon, E. Ramirez, and B. Pouyaud. 2005. Glaciers of the tropical Andes, indicators of the global climate variability. Pp. 197-204 in *Global change and mountain regions: a state of knowledge overview*, edited by U. Huber, K. M. Harald, and M. A. Reasoner. Dordrecht: Springer.

Gade, D. 1999. *Nature and culture in the Andes*. Madison: University of Wisconsin Press.

Gascon, C., T. E. Lovejoy, R. O. Bierregaard, J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91:223-229.

Grau, H. R., and T. M. Aide. 2007. Are rural-urban migration and sustainable development compatible in mountain systems? *Mountain Research and Development* 27:119-123.

Grau, H. R., T. M. Aide, J. K. Zimmerman, J. R. Thomlinson, E. Helmer, and X. Zou. 2003. The ecological consequences of socioeconomic and land use changes in post agricultural Puerto Rico. *BioScience* 53:1159-1168.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. *Science* 307:550-555.

Guarnizo, C. E., A. Amezquita, and E. Bermingham. 2009. The relative roles of vicariance versus elevational gradients in the genetic differentiation of the high Andean tree frog, *Dendropsophus labialis*. *Molecular Phylogenetics and Evolution* 50:84-92.

Halloy, S. R. P., A. Seimon, K. Yager, and A. Tupayachi Herrera. 2005. Multidimensional (climate, biodiversity, socio-economics, agriculture) context of changes in land use in the Vilcanota watershed, Peru. Pp. 323-337 in *Land use changes and mountain biodiversity*, edited by E. M.Spehn, M. Liberman Cruz, and C. Körner. Boca Raton FL: CRC Press LLC.

Hannah, L., R. Dave, P. P. Lowry, S. Andelman, M. Andrianarisata, L. Andriamaro, A. Cameron, R. Hijmans, C. Kremen, J. MacKinnon, H. H. Randrianasolo, S. Andriambololonera, A. Razafimpahanana, H. Randriamahazo, J. Randrianarisoa, P. Razafinjatovo, C. Raxworthy, G. E. Schatz, M. Tadross, and L. Wilmee. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters* 4:590-594.

Hannah, L., G. Midgley, S. Andelman, M. Araujo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5:131-138.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142:14-32.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* 321:345-346.

Hoffmann, D. 2009. Municipal protected areas as policy instruments to enhance ecosystem resilience. Lessons from Latin American experiences. *IOP Conference Series: Earth and Environmental Sciences* 6:312019.

Hole, D. G., B. Huntley, J. Arinaitwe, S. H. M. Butchart, Y. C. Collingham, L. D. Fishpool, D. J. Pain, and S. G. Willis. In press. Towards a management framework for key biodiversity networks in the face of climate change. *Conservation Biology*.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* 12:420-431.

Holmgren, J. 2004. Prediction of tree height, basal area and stem volume in forest stands using airborne laser scanning. *Scandinavian Journal of Forest Research* 19:543-553.

Holmgren, J., and A. Persson. 2004. Identifying species of individual trees using airborne laser scanner. *Remote Sensing of Environment* 90:415-423.

IPCC. 2007. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Soloman, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

Jiguet, F., R. Julliard, C. D. Thomas, O. Dehorter, S. E. Newson, and D. Couvet. 2006. Thermal range predicts bird population resilience to extreme high temperatures. *Ecology Letters* 9:1321-1330.

Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araujo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4:560-563.

Kessler, M. 2002. The "*Polylepis* problem": where do we stand? *Ecotropica* 8:97-110.

Killeen, T. J., and L. A. Solorzano. 2008. Conservation strategies to mitigate impacts from climate change in Amazonia. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 363:1881-1888.

Lobell, D. B., M. B., Burke, C. Tebaldi, M. D. Mastrandrea, W. P. Falcon, and R. L. Naylor. 2008. Prioritizing climate change adaptation needs for food security in 2030. *Science* 319:607-610.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.

Martens, W. J. M. 1998. Health impacts of climate change and ozone depletion: an eco-epidemiological modelling approach. *Environmental Health Perspectives* 106(Suppl. 1):241-251.

MEA, 2005. *Ecosystems and human well-being: synthesis*. Washington, DC: Island Press.

Mittermeier, R. A., P. Robles Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, and G. A. B. da Fonseca. 2004. *Hotspots revisited*. Mexico City: CEMEX.

Naesset, E., and R. Nelson. 2007. Using airborne laser scanning to monitor tree migration in the boreal-alpine transition zone. *Remote Sensing of Environment* 110:357-369.

Ohlemuller, R., E. S. Gritti, M. T. Sykes, and C. D. Thomas. 2006. Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931-2100. *Global Ecology and Biogeography* 15:395-405.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637-669.

Patz, J. A., M. Hulme, C. Rosenzweig, T. D. Mitchell, R. A. Goldberg, A. K. Githeko, S. Lele, A. J. McMichael, and D. Le Sueur. 2002. Climate change - regional warming and malaria resurgence. *Nature* 420:627-628.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361-371.

Postigo, J., K. R. Young, and K. A. Crews. 2008. Change and continuity in a pastoralist community in the high Peruvian Andes. *Human Ecology* 36:535-551.

Pounds, J. A., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, R. Puschendorf, S. R. Ron, G. A. Sanchez-Azofeifa, C. J. Still, and B. E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161-167.

Poveda, G., W. Rojas, M. L. Quinones, I. D. Velez, R. I. Mantilla, D. Ruiz, J. S. Zuluaga, and G. L. Rua. 2001. Coupling between annual and ENSO timescales in the malaria-climate association in Colombia. *Environmental Health Perspectives* 109:489-493.

Rees, W. G. 2007. Characterization of arctic treelines by LiDAR and multispectral imagery. *Polar Record* 227:345-352.

Rodrigues, A. S. L., S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. da Fonseca, K. J. Gaston, M. Hoffmann, J. S. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. N. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts, and X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428:640-643.

Ruiz, D., G. Poveda, I. D. Velez, M. L. Quinones, G. L. Rua, L. E. Velasquez, and J. S. Zuluaga. 2006. Modelling entomological-climatic interactions of *Plasmodium falciparum* malaria transmission in two Colombian endemic-regions: contributions to a national malaria early warning system. *Malaria Journal* 5:66.

Schroth, G., P. Laderach, J. Dempewolf, S. Philpott, J. Haggar, H. Eakin, T. Castillejos, J. G. Moreno, L. S. Pinto, R. Hernandez, A. Eitzinger, and J. Ramirez-Villegas. 2009. Towards a climate change adaptation strategy for coffee communities and ecosystems in the Sierra Madre de Chiapas, Mexico. *Mitigation and Adaptation Strategies for Global Change* 1:605-625.

Schulte, M. 1996. Tecnología agrícola altoandina. La Paz: Plural Editores – CID.

Scott, D., J. R. Malcolm, and C. Lemieux. 2002. Climate change and modelled biome representation in Canada's national park system: implications for system planning and park mandates. *Global Ecology and Biogeography* 11:475-484.

Seimon, A. 2001. Dilemmas of transport and energy development in Peru's Cordillera Carabaya. Pp. 26-27 in *Mountains of the world: mountains, energy, and transport*, edited by M. Price, T. Kohler, T. Wachs, and A. Zimmermann. Berne: Mountain Agenda and the Swiss Agency for Development. 53 pp.

Seimon, T. A., A. Seimon, P. Daszak, S. R. P. Halloy, L. M. Schloegel, C. A. Aguilar, P. Sowell, A. D. Hyatt, B. Konecky, and J. E. Simmons. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology* 13:288-299.

Soule, M. E., and J. W. Terborgh (eds.). 1999. *Continental conservation: scientific foundations of regional reserve networks*. Washington, DC: Island Press.

Sutherland, W.J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. *Journal of Applied Ecology* 43:599-616.

Terborgh, J. W. 1999. *Requiem for nature*. Washington, DC: Island Press.

The Economics of Ecosystems and Biodiversity. 2008. The economics of ecosystems and biodiversity: an interim report. European Communities. 68 pp.

Trenel, P., M. M. Hansen, S. Normand, and F. Borchsenius. 2008. Landscape genetics, historical isolation and cross-Andean gene flow in the wax palm, *Ceroxylon echinulatum* (Arecaceae). *Molecular Ecology* 17:3528-3540.

Vargas, F. H., R. C. Lacy, P. J. Johnson, A. Steinfurth, R. J. M. Crawford, P. D. Boersma, and D. W. Macdonald. 2007. Modelling the effect of El Niño on the persistence of small populations: the Galapagos penguin as a case study. *Biological Conservation* 137:138-148.

Vergara, W., A. Deeb, A. Valencia, R. Bradley, B. Francou, A. Zarzar, A. Grünwaldt, and S. Haeussling. 2007. Economic impacts of rapid glacier retreat in the Andes. *EOS, Transactions, American Geophysical Union* 88:261-263.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. *Earth-Science Reviews* 89:79-96.

Warner, K., C. Ehrhart, A. de Sherbinin, S. Adamo, and T. Chai-Onn. 2009. *In search of shelter – mapping the effects of climate change on human migration and displacement*. Available at: http://www.careclimatechange.org/.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475-482.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* 104:5738-5742.

Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* 19:1063-1074.

Wilme, L., S. M. Goodman, and J. U. Ganzhorn. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science* 312:1063-1065.

Winterhalder, B. P., and R. B. Thomas. 1978. *Geoecology of southern highland Peru: a human adaptation perspective*. *Occasional Paper 27*. Boulder: Institute of Arctic and Alpine Research, University of Colorado.

Young, K. R. 2007. Causality of current environmental change in tropical landscapes. *Geography Compass* 1:1299-1314.

Young, K. R. 2008. Stasis and flux in long-inhabited locales: change in rural Andean landscapes. Pp. 11-32 in *Land-change science in the tropics: changing agricultural landscapes*, edited by A. Millington and W. Jepson. New York: Springer.

Young, K. R., and B. Leon. 2007. Tree-line changes along the Andes: implications of spatial patterns and dynamics. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 362:263-272.

Young, K. R., and J. K. Lipton. 2006. Adaptive governance and climate change in the tropical highlands of western South America. *Climatic Change* 78:63-102.

Zhang, Y., M. Xu, J. Adams, and X. Wang. 2009. Can Landsat imagery detect tree line dynamics? *International Journal of Remote Sensing* 30:1327-1340.

Appendix 2.1. Summary information on the current PA systems in three of the four tropical Andean countries

1. What is the focus of the current PA system – i.e., is it selected on biodiversity targets or just the cheapest/unusable land?

Bolivia

In general, on biodiversity targets, but not necessarily in the best portions of the priority ecosystems in terms of conservation status and threat levels. Most recent PAs were created on the basis of socio-political opportunities (political will). Gap analysis at national level requires downscaling in order to better prioritize where future PAs need to be created.

Peru

At present what is being used are "marxan" type approximations, which are looking for sectors with maximum protection at minimum cost.

Ecuador

Apparently the design of PA systems is changing, not only looking for the opportunity to create spaces that might contain representative samples of biodiversity, but also to include concrete targets, such as a certain key or endangered species, certain natural monuments or specific ecosystem services. "Using the cheapest lands" has not been a common criteria for selection it seems.

2. How well does the current PA system likely represent current biodiversity pattern and process?

Bolivia

At species level, about 70-80% covered by national PAs (without considering municipal and departmental level PAs or indigenous and community conservation areas or indigenous communal lands (TCOs). There is a bias on representation of lowlands (and Andean foothills).

Peru

It seems that there is a lack of representation of ecological processes in the western part.

Ecuador

There is no definition (base line) about what to understand as "biodiversity pattern and process". Both GAP analysis in Ecuador (marine and terrestrial) consider maintaining representative samples of all ecosystems – vegetation formations of the country as main criteria (rather than processes).

3. What are the likely key gaps under climate change?

Bolivia

Altitudinal ranges and intersections between ecosystems (e.g. bosque seco chiquitano – pantanal).

Peru

Difficult to say, as there are not many climate change scenarios available for analysis of representativness in mountainous conditions. It seems the problem is more serious on the western side, because of the lower rate of PA coverage and the high number of population, especially in the valleys. This population generates a high demand of hydrological resources, that are being extracted from the high parts of the (Eastern slope?) watersheds.

Ecuador

Lack of information (e.g., a base line of how biodiversity would be affected by climate change). Existing climate models are not detailed enough, especially for the Andean region, and are not an adequate basis to define strategies.

What would be needed is a balance between practical mitigation actions and local adaptation measures, combining the following: biodiversity management, management of hydrological resources, risk management, agro-ecology, food security, poverty reduction strategies, conflict management, capacity development, territorial approach, among others.

Appendix 2.2. Definitions of key terms

Biological diversity: Variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. (CBD,Art.2)

Planning: Refers to a set of activities which leads to identifying i) issues, and goals; and to ii) formulating strategies and plans to be followed for the achievement of concrete goals.

Conservation: Protection and management of natural resources. The CBD identifies 2 biodiversity conservation options: i)"In-situ conservation" (in their natural habitats), ii)"Ex-situ conservation" (outside their natural habitats.) (CBD, Art. 2)

Natural resources management: Set of activities and actions or inactions carried out to either: exploit, use, conserve or preserve natural resources. These set of actions or inactions can lead to either positive or negative impacts on biodiversity.
Question: * whether conservation is a component of management/ or whether management is a component of conservation.

Climate change: A change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods. (UNFCCC, Art.1)

3

Range Shifts and Extinctions Driven by Climate Change in the Tropical Andes: Synthesis and Directions

Trond H. Larsen, Gunnar Brehm, Hugo Navarrete, Padu Franco,
Humberto Gomez, José Luis Mena, Victor Morales, Jaime Argollo,
Luis Blacutt, and Vanderlei Canhos

Global temperatures are rising, and climate change is driving biodiversity changes worldwide (Parmesan and Yohe 2003). Species extinctions, changes in abundance, and shifts in species ranges are profoundly altering ecological communities and ecosystem services (Lovejoy and Hannah 2005). Most evidence for the impacts of climate change on biodiversity has emerged from temperate regions (Root et al. 2003). However, recent research challenges the view that tropical species are less threatened than temperate species by climate change (Higgins 2007; Colwell et al. 2008; Deutsch et al. 2008; Raxworthy et al. 2008; Chen et al. 2009). When Janzen (1967) famously proposed forty years ago that tropical species are more physiologically constrained by climatic barriers in their environment than temperate species ('mountain passes are higher in the tropics'), he probably did not know the importance of this observation for climate driven extinctions today. Tropical species are adapted to a relatively uniform and narrow temperature range, making them among the most sensitive to climate change (Deutsch et al. 2008; McCain 2009; Feeley and Silman 2010). Species in tropical montane systems are likely to be even more vulnerable than lowland species, because changes in climate appear to be more pronounced at higher elevations (Bradley et al. 2006; Vuille et al. 2008).

With exceptionally high environmental heterogeneity across relatively short spatial scales, the tropical Andes are a region of unparalleled diversity and endemism and a global center of speciation (Myers et al. 2000; Fjeldså and Rahbek 2006). Restricted range size of many tropical Andean species is likely to make them especially extinction prone (see below). With climate warming paralleling predictions for the Arctic (Anderson et al., Chapter 1, this volume), but with intrinsically more sensitive species, the tropical Andes appears to be among Earth's most ecologically vulnerable regions to climate change (Bush 2002; Malcolm et al. 2006; Vuille et al. 2008; Lawler et al. 2009). Changing land-use patterns have already caused biodiversity loss in the region. That will be exacerbated by climate change. Despite these critical observations, virtually no studies have assessed the impacts of climate change on species in the tropical Andes.

Here we synthesize available information on observed and predicted impacts of climate change on species' geographic ranges and extinctions in the tropical Andes, and outline priorities to mitigate these effects.

Baseline Patterns of Diversity and Endemism

Diversity

Understanding patterns of diversity and endemism is fundamental for establishing baseline data and planning conservation strategies that minimize the impacts of climate change on biodiversity. As the largest tropical mountain range in the world, the Andes support exceptional biodiversity that is generated by the overlap of a broad latitudinal gradient with extended elevational and wet-dry gradients (Young, Chapter 11, this volume). The tropical Andes harbor global records of species richness for a range of taxa that include birds, mammals, amphibians and vascular plants, as well as less studied taxa such as beetles, butterflies and moths (see Chapters 13-20, this volume).

Diversity is not evenly distributed along the slopes of the Andes (see Chapters 13-20, this volume for patterns in each taxon). There are fewer species at high compared to low elevations, and species richness often peaks at low to mid elevations, both globally and in the Andes (Rahbek 1995). For example, in Peru, Ecuador, and Bolivia, vascular plant species richness is often fairly constant along an altitudinal gradient in the foothills up to 1500m, and then declines with increasing elevation (Jørgensen et al, Chapter 13 and Kessler et al., Chapter 14, this volume). However, when species richness is adjusted by the total available area at any given elevation, the same analysis shows a peak in diversity at mid elevations (usually between 1500-2500m).

Latitudinally, overall vascular plant diversity appears to peak near the equator in Ecuador (Jørgensen et al, Chapter 13 and Kessler et al., Chapter 14, this volume), whereas epiphyte and fern diversity does not vary strongly with latitude (Kessler et al., Chapter 14, this volume) and moss diversity is higher in Colombia and Bolivia than in Peru and Ecuador (Churchill, Chapter 16, this volume). Wetter habitats, especially forests, generally harbor more species than drier habitats (Chapters 13-19, this volume). Overall, the most species-rich areas include wet montane forests on the eastern Andean slopes in all countries, as well as the wet western slopes in Colombia and Ecuador (Chapters 13-19, this volume).

Understanding Andean diversity patterns is complicated by the fact that perhaps more than 50% of tropical Andean biodiversity remains undescribed, and many species may disappear before they are known to science. Birds and mammals are relatively well studied, yet new species are still being discovered (Ceballos and Ehrlich 2009). On average, every other day a new plant species is described from Ecuador alone (Jørgensen and León-Yánez 1999). In southern Ecuador, about 60% of geometrid moths and oribatid mites, but only 5% of fungi, are known to science (Brehm et al. 2008). Fish are probably the most poorly studied vertebrate group (Maldonado et al., Chapter 20, this volume).

Endemism

Many of the species found in the tropical Andes are endemic and range-restricted, occupying narrow altitudinal and latitudinal ranges (see Chapters 13-20 this volume; IUCN Red Lists published for Colombia, Ecuador, and Peru [plants, amphibians, mammals, birds, fish]; Churchill et al. 1995; Stotz et al. 1996; Jørgensen and León-Yánez 1999; Fjeldså and Rahbek 2006; Young 2007). At the regional scale, at least 25-50% of species in most taxonomic groups are endemic (e.g. 30% mosses, 25% vascular plants, 40% fish, 29% birds), making the Andes a global hotspot of endemism. Many species, particularly frogs and fishes, are known only from a single collecting locale (Young 2007).

Although species richness tends to decrease at higher elevations in the Andes, rates of endemism usually increase (see Chapters 13-20, this volume). Endemism is often concentrated in isolated bands or patches of habitat (e.g. cloud forests, *Polylepis* forest, isolated valleys, mountaintops). Overall, the habitat with the highest rate of endemism across taxa appears to be cloud forest just below tree line (Young 2007). Virtually all aquatic species found in high elevation streams and lakes are endemic (Maldonado et al., Chapter 20, this volume). High elevation lakes also support endemic frogs such as *Telmatobius* species.

Due to their small range and restricted requirements, endemic species are particularly threatened by anthropogenic disturbances and climate change. Evidence suggests that historical patterns of climate change have been important in shaping current distributions of endemism and in many cases may be more influential than geographic barriers. For example, centers of endemism for plants and birds often occur in areas that have remained ecologically stable, especially high precipitation areas (Churchill et al. 1995; Killeen et al. 2007). Identifying and conserving these ecologically stable areas may provide important refugia for species to persist in the face of anthropogenic climate change.

Although several reviews of diversity and endemism have been completed for specific taxa or regions (e.g. Kessler 2002; Ibisch and Mérida 2004; Young 2007) there has been little broad synthetic analysis across the tropical Andes (but see Myers et al. 2000). This type of synthesis is an urgent priority for establishing baseline data to monitor the impacts of climate change on biodiversity and also to develop appropriate conservation priorities and adaptation strategies.

Drivers of Species Response

Because most species are adapted to a specific range of environmental conditions, they are affected by many components of climate that alter these conditions (these climatic variables are discussed more completely in Anderson et al., Chapter 1, Mártinez et al., Chapter 6, and Marengo et al., Chapter 7, this volume). In addition to rising mean temperature, variability in temperature, rainfall, and humidity at various temporal and spatial scales strongly influences species distributions and persistence. Climatic extremes and changing climatic characteristics, such as dry season duration and severity, are important for many species.

Cloud and fog formation in the tropical Andes are being disrupted by climate change, often shifting uphill, and are critical for species persistence along wet Andean slopes and in the paramo (Anderson et al., Chapter 1, Ruiz et al., Chapter 12, this volume; Ruiz et al. 2008). A lifting cloud base appears to be driving upslope movement and extinctions, as has occurred in the past along the eastern Andean slopes (Bush 2002). Cloud and fog are also important for protecting Andean ecosystems from solar radiation at high elevations. Species may also be affected indirectly by climate; for example, decreases in the number of dry days per year appears to have altered leaf litter biomass, which in turn may have caused amphibian and reptile declines in Costa Rica (Whitfield et al. 2007). We still know very little about the complex suite of climatic variables that are driving ecological responses of species.

Species respond in many different ways to changing climatic conditions. In this chapter, we focus on geographic range shifts and on extinction of species that cannot successfully relocate. Climate-driven habitat loss, increased physiological stress, extreme climatic events, changes in fecundity, and other factors can also cause extinctions or population declines at a given site without any opportunity for a species to move elsewhere. Phenology, migration, trophic dynamics (including disease), species invasion and other ecological processes are also impacted by climate change, and are addressed in Aguirre et al., Chapter 4, this volume. Many of these responses to climate change are linked and can trigger cascading extinctions and abundance shifts. Here, we review the existing literature documenting historical, recent, and projected influence of climate change on species extinctions and range shifts in the tropical Andes.

Box 3.1. Research and conservation priorities to mitigate biodiversity loss with climate change in the tropical Andes

- Synthesize existing biodiversity data to identify cross-taxa diversity and endemism patterns across the Andes
- Focus on areas where diversity, endemism, and threat coincide (e.g. cloud forest, paramo, superparamo, dry inter-Andean valleys)
- Establish long-term monitoring sites using standardized sampling methods and standardized criteria for selecting focal taxa
- Maximize landscape connectivity, especially along altitudinal gradients and humidity/rainfall gradients
    - Establish protected areas, habitat corridors, land-use mosaics (promote alternative land-use strategies that maximize biodiversity, e.g. tree plantations, shade coffee)
- Plan conservation strategies that consider future shifts in the distribution of biodiversity and key habitats in response to climate change
- Identify traits that make species sensitive and/or vulnerable to climate change in the Andes
- Revisit/resample existing biodiversity datasets to assess recent species’ response to climate change (see Appendix)
- Improve data infrastructure and push for open accessibility
- Understand regional variation in species’ response to climate change within the Andes
- Understand the complexity of climate variables that directly and indirectly drive species’ response (e.g. not just upslope shifts caused by temperature increase)
- Build research capacity with improved taxonomy, field guides and identification tools
- Refine species modeling tools specifically for the Andes
- Identify mechanisms of species response using field and laboratory experiments

Box 3.2. Climate change and tropical Andean species

Palaeoecology and past climate change

Reconstructions of historical changes in Andean montane vegetation based on pollen records show that climate has strongly altered species distributions in the past (Chapter 5, this volume; Bush et al. 2004; Bush and Flenley 2007). During thermal optima of previous interglacial periods, montane forest appears to have extended 200 m further upslope than at present, while the lower limit is difficult to estimate. During cooling periods, montane forest species moved downslope by about 1000-1500 m and replaced lowland flora, probably following a lowering cloudbase and decreasing temperature (Bush and Flenley 2007).

Recent climate change

Alarmingly, we found only one published study that assessed the impacts of recent climate change on species in the tropical Andes. Seimon et al. (2007) found that three frog species expanded upwards in the Peruvian Andes following recent deglaciation. This increase in altitudinal limit appears to be the greatest so far observed for any species responding to climate change in the world. Chytrid fungus also moved uphill with the frogs, an example of the potential influence of climate change on infectious diseases and invasive species. Another amphibian study found that six threatened frog species appear to have disappeared recently from their historical range in Andean Peru, although the relative and possibly synergistic influence of climate change, habitat degradation, and chytrid fungus is unknown (von May et al. 2008). A few studies that have not yet been published have documented upslope shifts in taxa such as *Cecropia* trees and other plants, flamingos and vicuñas (see Table 1.2 in Anderson et al., Chapter 1, this volume for more details).

Projected impacts of climate change

Across North and South America, the Andes and northern tundra are predicted to show the highest turnover of bird, mammal, and amphibian species (over 90% change in some areas) in response to climate change under several emissions scenarios (Lawler et al. 2009). The same study predicted 20-50% species loss in the Andes due to climate-induced range contractions. Two studies, described in more detail in Graham et al., Chapter 21, this volume, estimate the response of species in the northern Andes using species distribution models. They predict that a high percentage of species, including birds and plants, will undergo range reductions and/or become critically endangered under future climate change scenarios. The most vulnerable species may be those restricted to specific habitats, especially paramo, dry valleys, and cloud forest. A third study, using single-species bioclimatic envelope models, predicted that 10-20% of 216 reptile species in the Andes of Bolivia will be extinct by 2080 (Embert et al. unpub. data, FAN-Bolivia).

Altitudinal and Latitudinal Range Shifts

Many different types of species response to recent climate change have been observed, but the dominant global trend is the poleward and/or upslope movement of species as they readjust to warming temperatures and changing precipitation (Parmesan and Yohe 2003). Similar range shifts have been observed during historical periods of climate change.

In contrast to temperate regions, altitudinal temperature gradients in the tropics are vastly steeper (>1000 times) than latitudinal temperature gradients, making upslope range shifts the most likely response of tropical species to climate warming (Colwell et al. 2008). A lifting cloudbase and changing precipitation also appear to be driving upslope range shifts in the tropics. Only a few cases of recent elevational range shifts have been documented in the tropics: amphibians and bats in Costa Rica (Pounds et al. 2005), amphibians and reptiles in Madagascar (Raxworthy et al. 2008) and geometrid moths in Borneo (Chen et al. 2009). The upslope range expansion of frogs following deglaciation in Peru (Seimon et al. 2007) is the only case we are aware of published for the tropical Andes.

Though poleward range shifts are less likely around the equator where the latitudinal temperature gradient is very shallow, the north-south orientation of much of the Andes may provide greater potential for poleward shifts than other mountain ranges (although several deep valleys act as barriers). Though few studies exist, no latitudinal range shifts due to recent climate change have yet been documented in the tropics.

Species redistribution does not always occur uphill or poleward (e.g. Moritz et al. 2008; Chen et al. 2009), especially when environmental changes (e.g. habitat type, microclimate, rainfall, humidity) caused by climate change occur in other directions. Such response patterns are poorly studied in the tropics. For example, aquatic species may be forced downhill if climate change causes high elevation habitats (where water flow is less than at lower elevations) to dry out. Changing precipitation may be an especially important driver of range shifts in the Amazonian lowlands where spatial and temporal patterns of rainfall vary strongly while temperature generally does not. Species redistribution also depends on species interactions and changing community dynamics, complicating generalized predictions (see Aguirre et al., Chapter 4, this volume). For example, tolerant species may move downhill taking advantage of newly vacant niches.

Range Shifts and Extinction Risk

Based on the tendency for many tropical species to move upslope, species in the Andes may be directly threatened by climate-induced range shifts in several ways (Figure 3.1) that include: 1) disappearance or decline of species in the lowlands and at lower elevations due to a net movement of species upslope (‘lowland biotic attrition’); 2) extinction of species on mountaintops for which no escape routes exist; 3) inability of species to shift into a newly suitable geographic range, often due to dispersal obstacles and/or insufficient dispersal capability (see next section). Extinction risk due to altered species interactions, phenology, resource availability, and other factors are addressed in Aguirre et al., Chapter 4, this volume.

The Amazon supports one of the most diverse communities on Earth, and many of its species are predicted to migrate towards wetter and cooler habitats as the lowlands heat up. As the largest and highest mountain range on the continent, the Andes may represent the only refuge for many Amazonian species. The proportion of lowland rainforest species that will shift their ranges upslope is currently unknown. Because no species from lower latitudes or below sea level are available to replace species that move upslope, lowland tropical rainforests (especially near the equator) are expected to suffer a net loss of species (Colwell et al. 2008). Lowland Amazonian species are likely to be highly vulnerable to climate change because their thermal niche is narrower than species in cooler areas (Feeley and Silman in press). Some areas in the Andes may actually increase in species richness due to immigration of lowland species, although these gains may be offset by other threats to biodiversity such as habitat loss. In parts of the Northern Andes, climate driven shifts of bird, mammal and amphibian species are predicted to lead to minimum average gains of 21% - 27% in species richness, based on two greenhouse-gas emissions scenarios (Lawler et al. 2009).

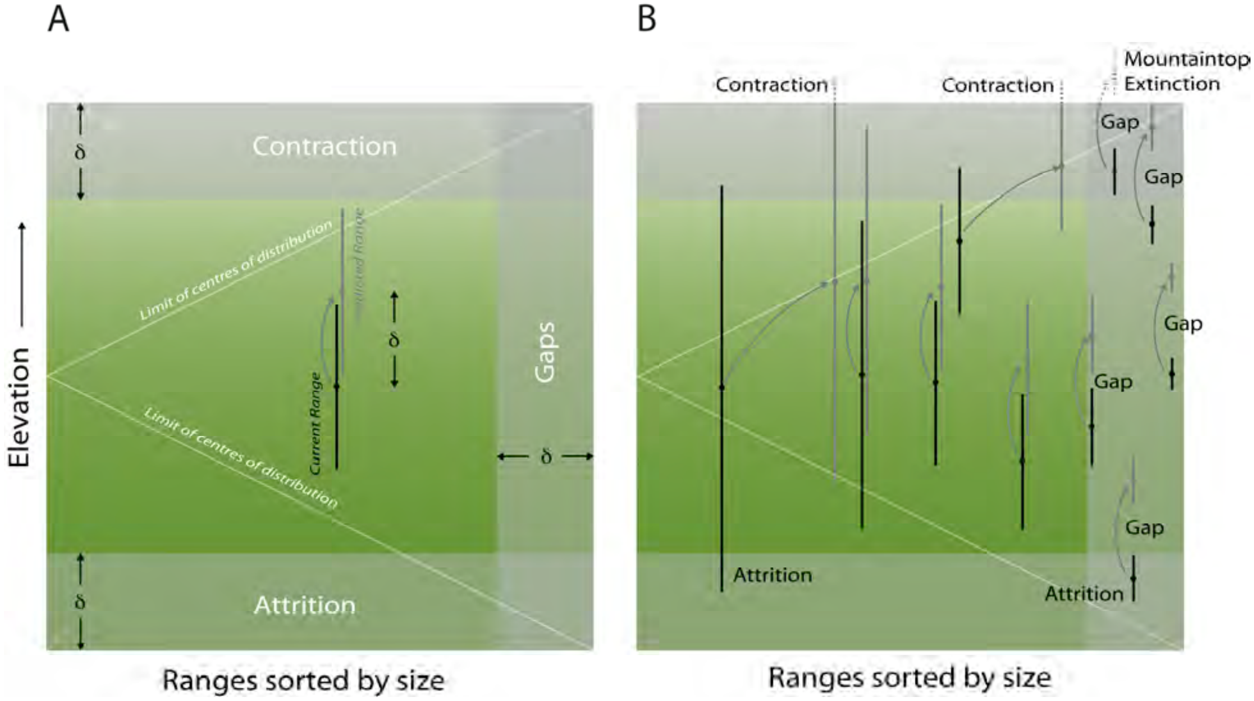

Figure 3.1. Conceptual model of elevational range shifts and associated extinction risk caused by climate warming in the Andes. **A.** An upslope shift in isotherms with warming climate is measured by δ. The model assumes a corresponding upslope shift of species ranges (shown by arrows). Three examples of species responses are: (a) range contraction of species at upper limit (possibly leading to mountaintop extinctions), (b) spatial discontinuity between species current range (black) and predicted range (grey) ('range shift gaps' – these species may need to shift upslope to survive), and (c) local species loss from lower elevations due to upslope range movement ('lowland biotic attrition'). **B**: Ten hypothetical species' ranges sorted by size. Wide-ranging species are most likely to be affected by range contraction and/or attrition. Restricted-range species are most likely to experience range shift gaps, and those at high elevations are prone to mountaintop extinction. Illustration by G. Brehm, modified from Colwell et al. (2008).

At the other elevational extreme, species that occur on mountaintops may go extinct with climate change because unlike species from lower elevations, they have nowhere to go. Total colonizable area generally decreases at higher elevations, exacerbating the problem (Figure 3.3). Mountaintop species become extinct unless they are able to adapt rapidly to changing conditions or are able to colonize nearby higher mountain ranges. Although diversity is relatively low on Andean mountaintops, a high proportion of species are endemic and likely to be especially sensitive, including several high elevation frog and plant species (see Table 1.1 in Anderson et al., Chapter 1, this volume). Because they can be observed easily and may respond particularly rapidly, mountaintop species are useful for monitoring the impacts of climate change (see below). So far, few data exist regarding mountaintop extinctions in tropical regions. Raxworthy et al. (2008) predicted the loss of three out of 30 species of amphibians and reptiles on a high massif in Madagascar under a 2°C warming scenario. Massive climate-driven extinctions of endemic vertebrates are predicted on mountaintops in the Australian tropics due to the loss of their core environment (Williams et al. 2003). On the other hand, Colwell et al. (2008) predicted an almost negligible rate of mountaintop extinctions for 1900 species of plants and insects distributed along a 2900 m elevational gradient in Costa Rica under a 3.2°C warming scenario, whereas about 50% of species were predicted to contribute to lowland biotic attrition or face spatial gaps between their current and predicted range.

Andean Landscape Connectivity and Climate Change

As demonstrated in the background chapters (Chapters 13 to 20, this volume), the majority of Andean species occupy relatively narrow altitudinal ranges. Restricted range species are likely to face 'range shift gaps', defined as a physical gap between the upper limit of a species' current altitudinal distribution and the lower limit of its predicted altitudinal distribution under a future climate scenario (Colwell et al. 2008). Restricted range species facing range shift gaps may be more vulnerable to climate change than wide ranging species because they must shift their entire distribution upslope in order to persist. Habitat loss causes range contractions that also make tropical restricted range species highly susceptible to climate change (Jetz et al. 2007).

Species under climate change stress face a range of dispersal barriers that may block redistribution, leading to extinction. The extreme topographic and climatic heterogeneity of the Andes creates many natural barriers to species movement. Although these biogeographic barriers may limit the ability of species to adapt to climate change, they have also driven speciation and endemism in the Andes and will continue to do so in the future. Many endemic plants and other taxa are restricted to a single valley by steep mountains on each side. Waterfalls create natural obstacles to movement of fish and other aquatic organisms. Dispersal of lake-dwelling organisms may be obstructed by a general absence of lakes at most mid-elevations. Snowline and treeline also form natural limits to distributions, although treeline has been heavily modified by humans in most areas.

Anthropogenic barriers are increasingly important in determining the ability of species to adapt to climate change. A long history of land-use and a rapidly advancing agricultural frontier have fragmented and isolated many habitats in the Andes. Species often must persist across a mosaic of habitat fragments embedded within a matrix of unsuitable habitat (e.g. cattle pasture and coffee plantation; see Suárez et al., Chapter 9, this volume for land-use details). Roads act as geographic barriers, as well as driving further deforestation and habitat loss. Roads may also provide corridors for the dispersal of weedy species, especially ecologically damaging invasive species (Urban et al. 2008). Riverine connectivity is disrupted by physical barriers (e.g. dams and hydroelectric plants), reductions in flow from water withdrawal or reduction in glacial melt, and changes in water quality (e.g. pesticides, fertilizers, sedimentation) (Anderson et al., Chapter 23, this volume). Land-use also interacts with fire frequency along the upper Andean slopes where fires are spreading downslope from grasslands, leading to further forest loss and creating an upper barrier to species movement (Bush et al. 2008).

Deforestation in the Andes often occurs along routes (rivers and roads) that connect human population centers at high elevations with those in the lowlands, a pattern that varies across the Andes (Young, Chapter 8, this volume; Etter et al. 2006). In Colombia these routes occur principally along the major rivers draining to the Caribbean, in Ecuador and Peru towards the Pacific lowlands and in Bolivia towards the Amazon lowlands. Current land transformation rates are highest along the eastern Andean slopes, where deforestation is advancing from above and below, and in some cases leaving a forested belt at intermediate elevations (~1500-2500m). Until now, steep slopes and limited accessibility have allowed many of these mid-elevation forests to persist. Land-use patterns are also influenced greatly by biophysical factors that vary by elevation and region (climate, slope, soil, etc.).

Maximizing Connectivity

Since most tropical species are expected to seek habitats that match their ecological requirements in response to climate change, protecting intact habitat corridors connecting lowlands to the cooler highlands may provide an escape route for many species from the megadiverse Amazon and Andean foothills. However, very few elevational gradients of intact habitat extend from the lowlands on either side of the Andes to treeline or above. Because forests often remain in isolated belts at intermediate elevations, many species are likely to be stuck in the middle of a climate-habitat sandwich – rising temperatures force them to shift upslope while they are simultaneously pushed downslope by expansion of human population centers and the advancing agricultural frontier. Furthermore, deforestation in the lowlands and along the base of the Andes is predicted to rapidly increase this century (Soares et al. 2006), driving further species declines and severing potential escape routes.

Perhaps the most successful strategy to maximize landscape connectivity and provide corridors for the greatest number of species is using protected areas (Killeen and Solorzano 2008). The relatively recent threat of anthropogenic climate change necessitates a new paradigm for planning and designing protected areas. Only few of the current protected areas protect sufficiently extensive corridors for species responding to climate change along altitudinal and latitudinal gradients. Only 8% of the tropical Andes is currently within protected areas, and the amount of land protected varies with altitude (Figure 3.2). Protected areas are urgently needed on the western slopes of the Andes, as well as along entire altitudinal gradients on both slopes.

Effective protected areas must incorporate future distributions of species responding to climate change, a critical consideration that was understandably not included in past protected area planning (see Hole et al., Chapter 2, this volume). Protected areas with stable high-precipitation regimes probably have the most favorable chance of preserving biodiversity in the long-term (Killeen and Solorzano 2008). Situating protected areas to encompass environmental gradients (not just altitudinal gradients), including temperature, rainfall and humidity, is also important. Environmental gradients are often centers of speciation, diversity, and endemism. Because they encompass a range of climatic variables across a relatively small geographic space, environmental gradients may provide the greatest potential for species to adapt to climate change.

Because the Andes are a human dominated landscape, effective biodiversity conservation strategies also need to incorporate land-use outside of parks. Alternative types of land-use can be adopted that provide direct economic benefits to people and biodiversity. For example, shade coffee and polyculture native tree plantations provide much more hospitable habitat for many species than more intensive forms of land-use such as cattle pasture (Philpott et al. 2008). At the very least, maintaining some trees and shrubs in pastures can foster much higher levels of biodiversity than grass alone. On the other hand, agricultural intensification or crop improvement may increase productivity over less area, allowing habitat restoration and regeneration on previously farmed land. The benefits of these alternative land-use strategies and agricultural intensification to local human communities depend on many complex regional and socioeconomic factors that need to be systematically addressed in each region.

The ability of organisms to move across the matrix of a fragmented landscape (permeability) depends not only on the configuration of the landscape (size, shape, and isolation of patches), but also on the environmental contrast (e.g. temperature and humidity) between matrix and natural habitat. Some species disperse easily across human modified landscapes, while others are unable to move even short distances across roads or clearings. A matrix that is more structurally similar to natural habitat facilitates dispersal by organisms that otherwise would be constrained physiologically or behaviorally. The most mature and structurally complex habitats (e.g., shade coffee, secondary forest) generally support the most species, especially species adapted to forests. Maintaining a heterogeneous landscape that includes many land-use types, particularly structurally complex habitats such as plantations, can help various plants and animals to disperse across the landscape.

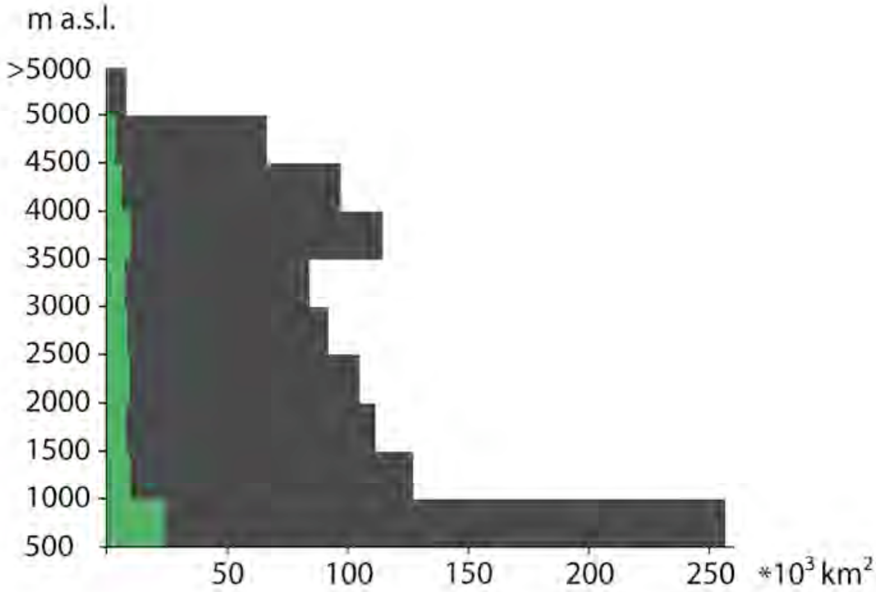

Figure 3.2. Proportion of total area with protected area status according to 500 m elevational bands in the Tropical Andes (Colombia, Ecuador, Peru, Bolivia). Grey: total surface area; Green: area of national parks and other national protected areas. Total area is 1,065,450 km^2. Only eight percent of the area (88,550 km^2) is currently legally protected. There is considerable variation between elevational bands as well as between countries (not shown). Data provided by I. Jimenez. Illustration by G. Brehm.

However, landscape fragmentation can also be exacerbated in other ways by climate change. For example, army ants are able to disperse between fragments across deforested areas, but only on cool, cloudy days (Meisel 2006). Climate change is likely to magnify the contrast between habitat patch and matrix and reduce the number of cool days that allow for dispersal, possibly leading to extinction.

Context-Dependent Species Response

Predicting how species will respond to changing land-use and climate is complicated by the fact that taxa in different regions and at different elevations respond in different ways depending on their ecology, environment, and evolutionary history. For example, the same tree species may shift in response to climate change at one site, but not in another, depending on its local climate and other environmental factors (Daniels and Veblen 2004). Dung beetle communities in Mexico, which historically have inhabited a wide range of habitats (holarctic and afrotropical origin), tolerate conversion of forest to pasture, whereas dung beetles in Colombia do not (Larsen et al., Chapter 17, this volume). Many high elevation dung beetle species in Colombia and Peru also tolerate a wider range of habitats, including tree plantations, than low elevation species, possibly due to relaxed competition and broader ecological niches at naturally depauperate high elevation sites (Larsen et al., Chapter 17, this volume). High elevation species may be better suited to tolerate climate change than low elevation species because they are adapted to an environment experiencing greater natural variation in temperature (McCain 2009).

On the other hand, high elevation species may be less able to adapt to climate change because they have less colonizable upslope habitat available than low elevation species. This is because the total surface area of land and water generally decreases at higher elevations simply due to the shape of the mountain (Figure 3.3). The southern Andes are somewhat distinct however in that they have broad areas of high elevation grasslands, possibly providing a buffer for species responding to climate change (Figure 3.3). Aquatic organisms are also faced with less habitat at higher elevations, especially near headwaters with less water flow.

To improve our understanding of species' complex response to climate change, further work is needed to identify regional patterns and differences within the Andes and also to identify generalizable species traits and variables.

Traits of Vulnerable Species

Identifying the response of each individual species to climate change is beyond the limits of time and funding in the diverse tropical Andes. However, determining traits associated with species response to climate change facilitates the development of a generalized framework for predicting response that can be applied across different systems. An excellent global review of these traits is provided by IUCN (Foden et al. 2009). These traits fall into five categories: 1) specialized habitat and/or microhabitat requirements; 2) narrow environmental tolerances or thresholds; 3) dependence on specific environmental triggers or cues that are likely to be disrupted by climate change; 4) dependence on interspecific interactions that are likely to be disrupted by climate change; 5) poor ability to disperse to or colonize a new or more suitable range.

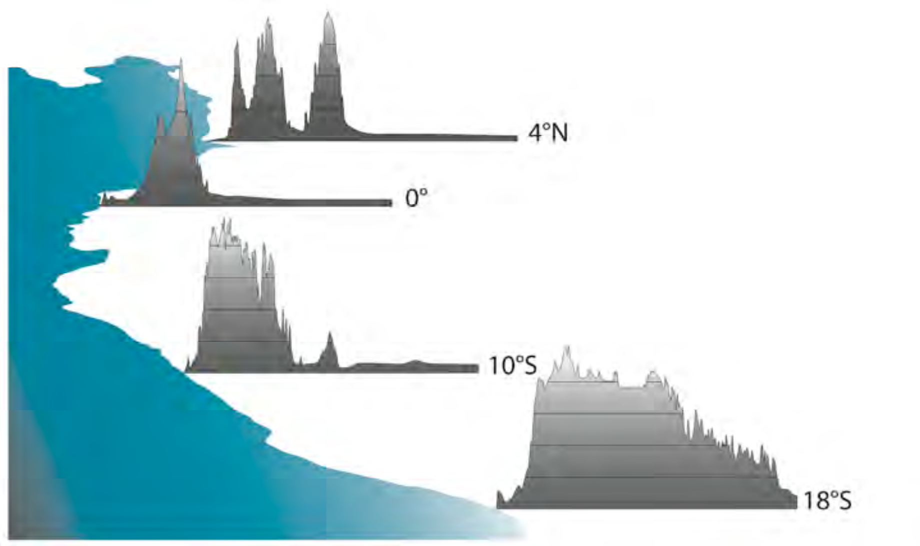

Figure 3.3. Cross sections (with 1000 m isolines) through the tropical Andes at 4° N (Colombia), 0° (Ecuador), 10°S (Peru) and 18° S (Bolivia). Surface area generally declines with increasing elevation, but this pattern varies regionally. While the northern tropical Andes are characterized by triangle shaped cordilleras, the southern tropical Andes contain extensive areas of altiplano at high elevation. Data provided by P. Franco and C. Rios (WCS). Illustration by G. Brehm.

Because the tropical Andes support a much higher proportion of specialists than temperate regions, several of these trait categories are likely to apply especially strongly to species in this region (McCain 2009). For example, a relatively high number of tropical Andean species are endemic habitat specialists, are adapted to narrow physiological ranges, and are co-evolved with other species or dependent on specialized resources. Many tropical plants depend on animals rather than wind for pollination and seed dispersal, making them potentially sensitive to indirect as well as direct effects of climate change. Tropical ectotherms, such as insects, comprise the vast majority of biodiversity in the Andes and elsewhere, and are predicted to be among the most sensitive taxa worldwide to climate change. This is because their body temperature depends largely on their environment, and in the tropics, they have a narrow range of physiological tolerance and already occur at or near their thermal optimum (Deutsch et al. 2008). Most species in temperate regions tolerate a relatively wide temperature range, especially seasonally. Some high elevation Andean species may also be subjected to relatively large temperature variation (especially across the course of the day).

The response of species to climate change also depends on their ability to adapt locally. Some species may not have the opportunity or capability to shift their range in response to rapidly changing climatic conditions. Species with phenotypic plasticity can behaviorally adjust to changing microclimates by moving between habitats at a local scale (Huey et al. 2009). The high local heterogeneity of the Andes may favor the ability of species to adapt to climate change by shifting their microclimatic associations within their current range. Some species may evolve rapidly in situ to changing climate, without the need to shift their distribution (Reusch and Wood 2007). The relative role of phenotypic plasticity versus genetic change (microevolution) in adapting to climate change is currently under debate (Gienapp et al. 2008).

Long Term Monitoring

Our understanding of recent and future changes in biodiversity in response to climate change is severely limited by a lack of data. Most species data for the Andes are difficult to compare because they were not collected using standardized and rigorous sampling methods. Biological inventories, such as those conducted by the Field Museum and Conservation International, have provided valuable baseline data, but many areas remain poorly studied. The Global Observation Research Initiative in Alpine Environments (GLORIA) has begun a coordinated, strategic program to monitor biodiversity and climate in alpine ecological zones across the world, focused on high elevation plants. Expansion of networks such as GLORIA is urgently needed, particularly multi-taxa monitoring along broad latitudinal and altitudinal gradients in the Andes. Areas where high diversity and endemism coincide with high vulnerability to climate change (e.g. paramo, superparamo, dry inter-Andean valleys, cloud forests; see Anderson et al., Chapter 1, this volume for more details) are priorities for monitoring. Superhumid and dry regions that may act as refugia for species during climate change are also critical to consider (Fjeldså et al. 1999; Killeen et al. 2007).

Selection of appropriate focal taxa is important for monitoring the impacts of climate change. Many of the traits of vulnerable species (described above) also apply to the selection of focal taxa. However, the traits of sensitive early warning indicator species are also important and may differ from vulnerability traits. For example, pioneer plant species with potential for rapid colonization and growth or other widely dispersing ‘weedy’ plant or animal species may be the first to take advantage of habitats recently created by climate change, such as those following glacial retreat. Although sensitive species are not necessarily vulnerable to climate change, they are useful for measuring the rate and magnitude of biodiversity response in different areas.

To maximize cost-effectiveness of monitoring, priority taxa should be relatively easy, cheap, and rapid to sample using standardized methods and should respond distinctly to each type of disturbance, including climate change and land-use regimes. Ideally, focal taxa should also be representative of changes occurring in other taxa. No single taxon embodies all of these criteria for monitoring the effects of climate change. However, several priority groups, which are discussed in more detail in the background chapters, include amphibians, insects (e.g. dung beetles, moths, and ants), plants (especially high Andean flora), lichens, fish, and certain groups of bats and birds. Biodiversity monitoring is also needed for poorly studied groups (both taxonomically and geographically).

Taking Advantage of Existing Data

Despite the general paucity of long term monitoring, several existing datasets, particularly those at least 10 years old, provide potential for assessing recent impacts of climate change. Revisitation of these previously inventoried sites, using a similar methodology, could provide a relatively cheap and easy way to understand how species are responding to climate change. Assessing the ecological consequences of climate change that have already occurred is also important for developing strategies to mitigate future changes. In Appendix 3.1, we provide a list of these datasets that we hope will be resampled.

Other cost-effective ways to assess recent biodiversity changes include time-series analysis of historical aerial photographs and satellite images. Certain images can be used to detect spatial shifts in vegetation structure, including individual plant species. Many species data remain unused in museum and local collections.

Conservation planning requires detailed understanding of species distributions across the Andes. Although many data exist, especially in unpublished databases and grey literature, there has been no comprehensive synthesis, partly due to limited data accessibility, poor data infrastructure, and lack of standardized protocols. For example, from the 175 million records currently available at the Global Biodiversity Information Facility (www.gbif.org) less than 1 million are from the Andes-Amazon region. For the Andes, 82% of the data available are from just two collections: Missouri Botanical Garden (69.17%) and the Herbarium of the University of Aarhus (13.20%). Tools and funding are needed to promote publication of these materials and make them more accessible.

An emerging example of one strategy to address this problem is the Amazon Basin Biodiversity Information Facility (www.abbif.net). ABBIF is being developed as a regional institutionally driven effort to integrate worldwide distributed species and specimen information on the fauna, flora, and micro-biota of the Amazon Basin. The goal is to digitize and integrate all relevant biodiversity data in a structured manner, with the adoption of standards and protocols that allow transparent data integration and systems interoperability.

Additional Recommendations

- Field and laboratory experiments are important for identifying mechanisms underlying species response to climate change (e.g. climate-dependent competition, growth, dispersal, etc.). Understanding the causes of changes to biodiversity is critical for identifying strategies to mitigate future loss.
- Greater taxonomical work and availability of species guides is essential for facilitating the biodiversity inventories and monitoring that are needed for assessing climate change impacts. Many studies in the tropical Andes cannot be compared because species are identified only to the morphospecies level, if at all. Diverse but poorly known groups (e.g. insects, fungi) merit taxonomic priority since such a low proportion of species are described. Type specimen information from museums must be made digitally available, including images. Rapid color guides managed by the Field Museum are an excellent example of these kinds of tools, and include many species from the tropical Andes (http://fm2.fieldmuseum.org/plantguides).
- Since few long-term monitoring data exist, modeling tools are an important way to assess the likely impacts of climate change on biodiversity (Graham et al., Chapter 21, this volume). Several modeling approaches have been developed to predict extinctions and range shifts in response to climate change. However, these tools need to be made more applicable to the Andes and refined at finer spatial resolution.

Acknowledgments

We thank W. Aguirre, E. Anderson, A. Catenazzi, R. Colwell, D. Cordero, S. Halloy, S.K. Herzog, D. Hole, I. Jimenez, P. Jørgensen, M. Kessler, M. Maldonado, D. Ruiz, A. Seimon, C. Toledo and B. Young for providing comments and suggestions that improved the manuscript.

Literature Cited

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 312:1755-1756.

Brehm, G., J. Homeier, K. Fiedler, I. Kottke, J. Illig, N. M. Noeske, F. A. Werner, and S. W. Breckle. 2008. Mountain rain forests in southern Ecuador as a hotspot of biodiversity – limited knowledge and diverging patterns. Pp. 15-23 in *Gradients in a tropical mountain ecosystem of Ecuador*, edited by E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl. Berlin: Springer.

Bush, M. B. 2002 Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecology and Biogeography* 11:463-473.

Bush, M. B., M. R. Silman, and D. H. Urrego. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science* 303:827-829.

Bush, M. B., and J. R. Flenley. 2007. *Tropical rainforest responses to climatic change*. Berlin: Springer.

Bush, M. B., M. R. Silman, C. McMichael, and S. Saatchi. 2008. Fire, climate change and biodiversity in Amazonia: a Late-Holocene perspective. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 363:1795-1802.

Ceballos, G., and P. R. Ehrlich. 2009. Discoveries of new mammal species and their implications for conservation and ecosystem services. *Proceedings of the National Academy of Sciences of the United States of America* 106:3841-3846.

Chen, I. C., H. J. Shiu, S. Benedick, J. D. Holloway, V. K. Cheye, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America* 106:1479-1483.

Churchill, S. P., H. Balslev, E. Forero, and J. L. Luteyn (eds.). 1995. *Biodiversity and conservation of Neotropical montane forests*. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21-26 June 1993. New York: The New York Botanical Garden. 702 pp.

Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261.

Daniels, L. D., and T. T. Veblen. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology* 85:1284-1296.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105:6668-6672.

Etter, A., C. McAlpine, K. Wilson, S. Phinn, and H. Possingham. 2006. Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture Ecosystems and Environment* 114:369-386.

Feeley, K. J., and M. R. Silman. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology* 16:1830-1836.

Fjeldså, J., E. Lambin, and B. Mertens. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography* 22:63-78.

Fjeldså, J., and C. Rahbek. 2006. Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. *Integrative and Comparative Biology* 46:72-81.

Foden, W. B., G. M. Mace, J.-C. Vie, A. Angulo, S. H. M. Butchart, L. DeVantier, H. T. Dublin, A. Gutsche, S. Stuart, and E. Turak. 2009. Species susceptibility to climate change impacts. Pp. 77-88 in *Wildlife in a changing world – an analysis of the 2008 IUCN Red List of threatened species*, edited by J.-C. Vie, C. Hilton-Taylor, and S. N. Stuart. Gland: International Union for Conservation of Nature and Natural Resources. 180 pp.

Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merila. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* 17:167-178.

Higgins, P. A. T. 2007. Biodiversity loss under existing land use and climate change: an illustration using northern South America. *Global Ecology and Biogeography* 16:197-204.

Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. A. Perez, and T. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B, Biological Sciences* 276:1939-1948.

Ibisch, P. L., and G. Merida. 2004. *Biodiversity: the richness of Bolivia.* Santa Cruz de la Sierra: Editorial FAN.

Janzen, D. H. 1967. Why mountain passes are higher in tropics. *American Naturalist* 101:233-249.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211-1219.

Jørgensen, P. M., and S. León-Yánez (eds.). 1999. Catalogue of the vascular plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75. 1188 pp.

Kessler, M. 2002. The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. *Journal of Biogeography* 29:1159-1165.

Killeen, T. J., M. Douglas, T. Consiglio, P. M. Jørgensen, and J. Mejia. 2007. Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography* 34:1357-1373.

Killeen, T. J., and L.A. Solorzano. 2008. Conservation strategies to mitigate impacts from climate change in Amazonia. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 363:1881-1888.

Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588-597.

Lovejoy, T. E., and L. Hannah. 2005. *Climate change and biodiversity*. New Haven: Yale University Press.

Malcolm, J. R., C. R. Liu, R. P. Neilson, L. Hansen, and L. Hannah. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20:538-548.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters* 12:550-560.

Meisel, J. E. 2006. Thermal ecology of the Neotropical army ant *Eciton burchellii*. *Ecological Applications* 16:913-922.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger, 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261-264.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

Philpott, S. M., W. J. Arendt, I. Armbrecht, P. Bichier, T. V. Dietsch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams-Linera, J. Valenzuela, and J. M. Zolotoff. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conservation Biology* 22:1093-1105.

Pounds, J. A., M. P. L. Fogden, and K. L. Masters 2005. Responses of natural communities to climate change in a highland tropical forest. Pp. 70-74 in *Climate change and biodiversity*, edited by T. E. Lovejoy and L. Hannah. New Haven: Yale University Press.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200-205.

Raxworthy, C. J., R. G. Pearson, N. Rabibisoa, A. M. Rakotondrazafy, J. B. Ramanamanjato, A. P. Raselimanana, S. Wu, R. A. Nussbaum, and D. A. Stone. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology* 14:1703-1720.

Reusch, T. B. H., and T. E. Wood. 2007. Molecular ecology of global change. *Molecular Ecology* 16:3973-3992.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57-60.

Ruiz, D., H. A. Moreno, M. E. Gutierrez, and P. A. Zapata. 2008. Changing climate and endangered high mountain ecosystems in Colombia. *Science of the Total Environment* 398:122-132.

Seimon, T. A., A. Seimon, P. Daszak, S. R. P. Halloy, L. M. Schloegel, C. A. Aguilar, P. Sowell, A. D. Hyatt, B. Konecky, and J. E. Simmons. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology* 13:288-299.

Soares, B. S., D. C. Nepstad, L. M. Curran, G. C. Cerqueira, R. A. Garcia, C. A. Ramos, E. Voll, A. McDonald, P. Lefebvre, and P. Schlesinger. 2006. Modeling conservation in the Amazon basin. *Nature* 440:520-523.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. *Neotropical birds: ecology and conservation.* Chicago: University of Chicago Press.

Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2008. A toad more traveled: the heterogeneous invasion dynamics of cane toads in Australia. *American Naturalist* 171:E134-E148.

von May, R., A. Catenazzi, A. Angulo, J. L. Brown, J. Carrillo, G. Chavez, J. H. Cordova, A. Curo, A. Delgado, M. A. Enciso, R. Gutierrez, E. Lehr, J. L. Martinez, M. Medina-Mueller, A. Miranda, D. R. Neira, J. A. Ochoa, A. J. Quiroz, D. A. Rodriguez, L. O. Rodriguez, A. W. Salas, T. Seimon, A. Seimon, K. Siu-Ting, J. Suarez, C. Torres, and E.

Twomey. 2008. Current state of conservation knowledge on threatened amphibian species in Peru. *Tropical Conservation Science* 1:376-396.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. *Earth-Science Reviews* 89:79-96.

Whitfield, S. M., K. E. Bell, T. Philippi, M. Sasa, F. Bolanos, G. Chaves, J. M. Savage, and M. A. Donnelly. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America* 104:8352-8356.

Williams, S. E., E. E. Bolitho, and S. Fox. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London B, Biological Sciences* 270:1887-1892.

Young, B. E. (ed.). 2007. *Endemic species distributions on the east slope of the Andes in Peru and Bolivia*. Arlington: NatureServe.

Appendix 3.1. Datasets from the tropical Andes that could be resampled to detect biodiversity changes associated with climate change.

Andrade, G. 1993. *Carpanta, selva nublada y páramo.* Bogotá: Fundacion Natura.

Bustamante, M., S. R. Ron, and L. Coloma. 2005. Cambios en la diversidad en siete comunidades de anuros en los Andes de Ecuador. *Biotropica* 37:180-189.

Canaday, R. L. 1986. Aves encontradas en el sector de Orocue del PNN Tama, Norte de Santander. Bogotá: INDERENA, Ministerio de Agricultura.

Churchill, S. P., H. Balslev, E. Forero, and J. L. Luteyn (eds.). 1995. *Biodiversity and conservation of Neotropical montane forests*. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21-26 June 1993. New York: The New York Botanical Garden. 702 pp. [Many datasets included here]

Cresswell, W., R. Mellanby, S. Bright, P. Catry, J. Chaves, J. Freile, A. Gabela, H. Martineau, R. MacLeod, F. McPhee, N. Anderson, S. Holt, S. Barabas, C. Chapel, and T. Sanchez. 1999. Birds of the Guandera Reserve, Carchi province, northeastern Ecuador. *Cotinga* 11:55-63.

Donegan, T. M., and L. Davalos. 1999. Ornithological observations from Reserva Natural Tambito, Cauca, south-west Colombia. *Cotinga* 12:48-55.

Duellman, W., and J. D. Lynch. 1988. Anuran amphibias from the Cordillera de Cucutú, Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 140:125-142.

Fawcett, D. 1994. Bats. Pp. 60-67 in *Surveys and conservation of biodiversity in the Chocó, south-west Colombia*, edited by P. G. W. Salaman. Cambridge: Birdlife International.

Gensini, M. E. 1985. *Estructura y composición de la comunidad aviaria de un bosque montano húmedo de la cordillera occidental*. Undergraduate thesis. Cali: Universidad del Valle.

Graham, G. L. 1983. Changes in bat species diversity along elevational gradient up the Peruvian Andes. *Journal of Mammalogy* 64:559-571.

Herzog, S. K., and M. Kessler. 2002. Biogeography and composition of dry forest bird communities in Bolivia. *Journal of Ornithology* 143:171-204.

Herzog, S. K., and M. Kessler. 2006. Local versus regional control on species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography* 15:163-172.

Herzog, S. K., M. Kessler, and K. Bach 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography* 28:209-222.

Hilty, S. L. 1997. Seasonal bird movements in Colombia. *Ornithological Monographs* 48:321-343.

Kessler, M. 2000a. Altitudinal zonation of Andean cryptogam communities. *Journal of Biogeography* 27:275-282.

Kessler, M. 2000b. Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecology* 149:181-193.

Kessler, M. 2000c. Upslope-directed mass effect in palms along an Andean elevational gradient: a cause for high diversity at mid-elevations? *Biotropica* 32:756-759.

Kessler, M. 2001. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation* 10:1897-1921.

Kessler, M., S. K. Herzog, J. Fjeldså, and K. Bach. 2001. Diversity and endemism of plants and birds along two gradients of elevation, humidity, and human land-use in the Bolivian Andes. *Diversity and Distributions* 7:61-77.

Krömer, T., M. Kessler, S. R. Gradstein, and A. Acebey 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* 32:1799-1809.

Krömer, T., M. Kessler, and S. K. Herzog. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica* 38:183-195.

Lynch, J. D., and P. A. Burrowes. 1990. The frogs of the genus *Eleutherodactylus* (family Leptodactylidae) at the La Planada reserve in southwestern Colombia, with descriptions of eight new species. *Occasional Papers of the Museum of Natural History, the University of Kansas* 136:1-31.

Muñoz, J. 1990. Diversidad y hábitos alimenticios de murciélagos en transectos altitudinales a través de la Cordillera Central de los Andes en Colombia. *Studies on Neotropical Fauna and Environment* 25:1-17.

Muñoz, J. 1993. Murciélagos del norte de Antioquia (Colombia). *Studies on Neotropical Fauna and Environment* 28:83-93.

Negret, A. J. 1994. Lista de aves registradas en el Parque Nacional Natural Munchique. *Novedades Colombianas* 6:69-83.

Orejuela, J. E., G. Cantillo, and M. S. Alberico. 1982. Estudio de las comunidades de aves y mamíferos en Nariño, Colombia. *Cespedesia* 41-42:41-67.

Orejuela, J. E., R. J. Raitt, and H. Alvarez-López. 1979. Relaciones ecológicas de las aves en la Reserva Forestal de Yotoco, Valle del Cauca. *Cespedesia* 8:7-27.

Osgood, W. H. 1914. Mammals of an expedition across northern Peru. *Fieldiana Zoology* 10:185.

Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593-607.

Pearson, O. P., and C. P. Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias del Museo de Historia Natural "Javier Prado"* 18:1-97.

Rangel, J. O. 1994. *Ucumarí: un caso típico de la diversidad biológica andina.* Pereira, Colombia: Corporación Autónoma Regional de Risaralda.

Ridgely, R. S., and S. J. C. Gaulin. 1980. The birds of Finca Meremberg, Huila Department, Colombia. *Condor* 82:379-391.

Rueda, J. V. 2000. La herpetofauna de los “Bosques de Florencia”, Caldas: una visión integrada sobre su composición diversidad y relaciones ecológicas. Manizales, Colombia: Corpocaldas.

Salaman, P. G., T. M. Donegan, and A. M. Cuervo. 1999. Ornithological surveys in Serrania de los Churumbelos, Southern Colombia. *Cotinga* 12:29-39.

Stiles, F. G., and C. I. Bohórquez 2000. Evaluando el estado de la biodiversidad el caso de la avifauna de la Serrania de las Quinchas, Boyaca, Colombia. *Caldasia* 22:61-92.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. *Neotropical birds: ecology and conservation.* Chicago: University of Chicago Press. [Many datasets included here]

Tamsitt, J. R. 1965. Aspects of altitudinal distribution of chiropterans in the Eastern Cordillera of Colombia. *American Zoology* 5:1-492.

Tamsitt J. R., D. Valdivieso, and J. Hernandez-Camacho. 1964. Bats of the Bogota Savanna, Colombia, with notes on the altitudinal distribution of Neotropical bats. *Revista Tropical de Biología* 12:107-115.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.

Villareal, H. 1998. Caracterización biológica del Parque Nacional Natural Tamá. Bogotá: Programa de Inventarios de Biodiversidad, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

4

Phenology and Interspecific Ecological Interactions of Andean Biota in the Face of Climate Change

Luis F. Aguirre, Elizabeth P. Anderson, Gunnar Brehm, Sebastian K. Herzog, Peter M. Jørgensen, Gustavo H. Kattan, Mabel Maldonado, Rodney Martínez, José Luis Mena, José Daniel Pabón, Anton Seimon, and Cecília Toledo.

The order of authors is alphabetical and does not necessarily reflect the relative contribution of each author to this chapter.

Complex links between phenology, the ecological interactions between species, and climate will determine the fate of species and ecosystems under climate change, but they are still poorly understood for the tropical Andes. In this chapter we use generalizations from temperate regions along with studies from the Andes and other tropical areas to discuss effects of climate on the phenology and interspecific interactions of tropical organisms, and to explore potential effects of climate change.

Phenology describes the timing of transitions between stages in organisms' life cycles. Phenology can be directly affected by climate (arrow 1 in Figure 4.1), for instance when organisms can only reproduce under certain climatic conditions because of physiological constraints (Morin 1999). Phenology plays a crucial role in the carbon balance of terrestrial ecosystems (Cleland et al. 2007) and vegetation feedback into the atmosphere (Schwartz 2003b).

Ecological interactions between species may affect the "fitness" of organisms, measured as their genetic contribution to the next generation, or they can affect population size (Futuyma 1998). Such ecological interactions include predation, competition, herbivory, parasitism, detritivore-detritus interactions, and mutualism (Ricklefs and Miller 2000). These interspecific interactions can be affected by climate in multiple ways (arrow 2 in Figure 4.1) when climate affects behavior (e.g., predator search efficiency) or physiology (e.g., herbivore metabolic rate). Interactions such as mutualisms between plants and mycorrhizal fungi play important roles in ecosystem carbon cycling (Pendall et al. 2004). Indeed, the functioning of virtually all ecosystems, and thus their impact on the atmosphere, depends on coevolved interspecific interactions (Thompson 2009).

Phenology can affect interspecific interactions (arrow 3, Figure 4.1) by altering the time overlap between interacting phenophases (Morin 1999), such as that between flowering or fruit set and pollinators or seed dispersers. Interspecific interactions can in turn affect phenology (arrow 4, Figure 4.1) because predators, competitors, herbivores, parasites, and mutualists exert pressures on the life cycle stages of other species (Morin 1999). Both phenology and interspecific interactions can to some extent also affect local climate (arrows 5 and 6 in Figure 4.1), for instance through transpiration which depends on leaf activity. Water dynamics in the Amazon basin are largely influenced by forest cover (Chagnon and Bras 2005), and thus forest phenology.

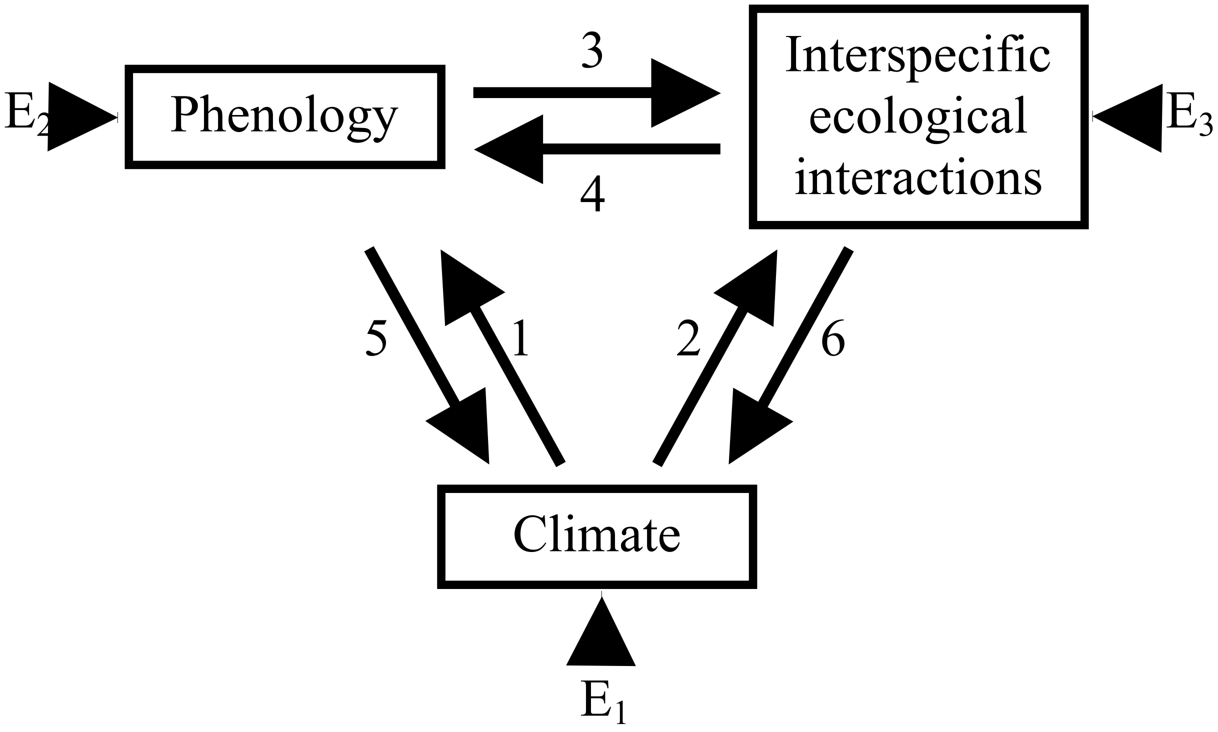

Figure 4.1. Graphical representation of a general structural equation model (Grace 2006) for the relationships among phenology, interspecific ecological interactions, and climate. Each box represents an observed variable related to phenology (e.g., flowering time), interspecific ecological interaction (e.g., frequency of visits to flowering plant by pollinators), and climate (e.g., monthly precipitation). Arrows between boxes represent causal relationships between the observed variables. E_1, E_2, and E_3 represent error terms subsuming all factors that affect the observed variables and are not explicitly considered.

Effects of Climate on the Phenology of Tropical Organisms

To examine how climate affects phenology we distinguish between "proximate" and "ultimate" causes (van Schaik et al. 1993). Proximate causes are the environmental stimuli as well as the genetic and physiological mechanisms that determine the function of a phenotype. Ultimate causes are the evolutionary forces that shape a phenotype, which is the physiology, morphology, and behavior of an individual organism. For example, the rapid flower closure in Andean plants of the genus *Gentianella* is proximately caused by climatic stimuli such as temperature and pressure changes that result in turgor loss and bending of plant organs (Claus 1926, Sibaoka 1991). The ultimate cause of this rapid flower closure may be evolution by natural selection as plants with rapid flower closure may better protect floral organs and pollen from damage by rain and other factors (He et al. 2006).

The ultimate causes of tropical plant phenology may be related directly to climate (arrow 1, Figure 4.1) in two ways. First, climate can limit plant production by lack of water and sunlight (van Schaik et al. 1993). For instance, many tropical woody plants lose their leaves during the dry season (Sanchez-Azofeifa et al. 2003) and show peaks of foliage production and flowering at the onset of the rains (Reich and Borchert 1982, Morellato 2003). Water availability may also regulate leaf production in some understory plants of a lowland Neotropical forest (Aide and Angulo-Sandoval 1997). Second, climate can determine the abiotic conditions for dispersal or survival of particular phenophases (van Schaik et al. 1993). Plants pollinated and dispersed by wind tend to produce flowers and seeds during the windiest part of the year (Foster 1982, Charles-Dominique et al. 1981, Stevenson 2004). In areas with strongly seasonal water availability, the fruiting time of species may coincide with the onset of the rains (Foster 1982, Garwood 1983), presumably timing seed germination to the season with adequate moisture.

The ultimate causes of plant phenology may also be related indirectly to climate through its effects on interspecific interactions (arrows 2 and 4 in Figure 4.1). Climate can determine seasonality in the abundance of pollinators, seed dispersers, and other mutualists which, in turn, may support selection for a particular phenological schedule (van Schaik et al. 1993). Determining cause and effect is often difficult because the reverse direction of causality is possible: the abundance of animal mutualists may be determined by the availability of plant resources. For example, the Amazonian ant species *Allomerus octoarticulatus* breeds at the time of highest availability of nests provided by the hollow stem chambers (domatia) in the plant *Cordia nodosa*, which in turn seems to be determined by insolation (Frederickson 2006). Climate may also determine the seasonal abundance of natural enemies, selecting for plants that time their phenology to avoid herbivores (van Schaik et al. 1993). For instance, herbivores in seasonal forests may be less abundant during the dry season, and plants producing new leaves at that time may experience reduced herbivory (Aide 1988).

Proximate causes of tropical plant phenology sometimes also relate to climate. Trees with shallow roots occurring in forest with strongly seasonal rainfall patterns drop their leaves and arrest growth in response to water stress during the dry season, and flush leaves, flower and resume growth in response to the rainy season (Borchert 2004). However, some deciduous species drop their leaves before water stress occurs and start producing new leaves before the onset of rains, suggesting that water availability may not be the proximate cause of vegetative phenology, although it may well be its ultimate cause (van Schaik et al. 1993). Severe dry seasons during El Niño years may serve as proximate cues for tropical plants to increase reproductive efforts in anticipation of abiotic environments conducive to seedling establishment (the ultimate cause) during a milder dry season the following year (Wright et al. 1999). Supra-annual climatic oscillations such as El Niño may provide cues for supra-annual phenological patterns, synchronized across single or multiple species, which may serve to satiate predators or attract pollinators (Wright et al. 1999, Kelly and Sork 2002, Sakai et al. 2006, Brearley et al. 2007). In those cases the proximate cause is climatic, but the ultimate cause is related to biotic effects. Bamboo species of the genus *Chusquea* are conspicuous elements of several habitats across the tropical Andes and have supra-annual flowering phenology (Judziewicz et al. 1999), which may be triggered by cues related to El Niño (Jaksic and Lima 2003). High inter-annual variance in the phenology of tree species may be more common in the Neotropics than previously thought and could be associated to climatic cues (Norden et al. 2007).

Other factors than rainfall also provide ultimate and proximate causes of tropical plant phenology (Figure 4.1; Ratchcke and Lacey 1985, Borchert 2004). Drought tolerant plants with deep root systems, small leaf area, or low xylem resistance to water flow, for instance, may not be limited by seasonal water availability. For such species, and in areas with little seasonality in water availability, insolation may be a more important ultimate cause of phenology (Wright and van Schaik 1994). This is because young leaves are most efficient at photosynthesis and plants may maximize fitness by producing them during times of highest insolation. Flowers may also be produced at this time because it is more efficient to transfer the products of photosynthesis directly to growing organs than to store and mobilize them later. Consistent with this idea, leaf flush and flowering in forests with weak rainfall seasonality reach a maximum during months with little cloud cover and highest insolation (Wright and van Schaik 1994, Huete et al. 2006). Similarly, leaf flush and flowering of drought tolerant species in strongly seasonal forests is timed for maximal insolation (Wright and van Schaik 1994). Seasonal variation in solar radiation is thought to be an important proximate cause for synchronized flowering in tropical plants that allows cross pollination (Rivera et al. 2002, Borchert et al. 2005, Yeang 2007, Rivera and Cozza 2008). Although variation in solar radiation is small in the tropics relative to temperate areas, plants are able to use it as a cue. The mechanism of this sensitivity to photoperiod is not well-understood (Renner 2007).

Inter-specific staggering of phenologies may evolve as a response to non-climatic factors such as competition for pollinators and dispersers, or to avoid interspecific pollination and hybridization (van Schaik et al. 1993, Morin 1999). Competition for pollinators was indicated in a study showing that fertilization of plant ovules in diverse tropical communities is limited by pollen availability (Vamosi et al. 2006). Thus it may play a role in the flowering times of *Bombacaceae* species (Lobo et al. 2003) or the temporal patterns of fruit production in *Piper* species (Thies and Kalko 2004). Phenological studies of trees in the tropical Andes (Bendix et al. 2006, Gunter et al. 2008) and elsewhere in the tropics (Stevenson 2004, Chapman et al. 2005) illustrate the wide range of phenological patterns exhibited by different species, and indicate that multiple proximate and ultimate causes are at play at any single site.

Strong seasonal variation in activities like reproduction and migration is well known for birds in temperate regions, where variations in climate are pronounced. By contrast, Neotropical birds generally exhibit much less seasonality in their phenology (review by Stutchbury and Morton 2001). Within a given community, Neotropical birds may breed at all times of the year, frugivores often in the dry, insectivores in the wet season. The breeding seasons of individual species are 2-3 times longer than those of temperate zones. However, one cannot conclude that aseasonal breeding patterns are typical for the tropics based on a few single-species studies from lowland rain forest localities (see Stutchbury and Morton 2001). Detailed studies of the spotted antbird (*Hylophylax n. naevioides*) in a lowland forest of Panama, for instance, have documented strongly seasonal breeding, starting at the beginning of the rainy season (Wikelski et al. 2000). Gonad enlargement in this species responds to small variations in photoperiod, allowing spotted antbirds to anticipate the rainy season (Hau et al. 1998). Further experimental work showed that these birds fine-tune the timing of gonad growth and reproductive behavior using additional proximate cues, including the opportunity to "handle" or see live insect prey (Hau et al. 2000). These studies documented proximate causes of breeding phenology, but the ultimate causes remain largely unknown. Such synchronous breeding at the onset of the rainy season may be explained by selective pressures associated with food availability, reduced predation risk, and the need to avoid molting and breeding simultaneously (Wikelski et al. 2000). In contrast, breeding activities of birds that live in unpredictable habitats, such as small ground finches (*Geospiza fuliginosa*) in the Galapagos archipelago, may not be triggered by photoperiod, but rather by cues that are more directly related to reproductive success, such as rainfall or barometric pressure (Hau et al. 2004). These detailed studies on selected species illustrate what might be common proximate causes of bird phenology, and hint at possible ultimate causes as well.

Very little has been published on the phenology of bird reproduction in the tropical Andes. A study in the Andes of Colombia (Miller 1963), where rainfall is bimodal with peaks of precipitation in March-May and October-November, revealed a reproductive peak at the community level during the first rainy season of the year, but some species bred throughout the year independent of rainfall, and a few species bred during the dry season. Some thrushes (Turdidae) breed during the first and molt during the second rainy season of the year (Beltrán and Kattan 2001). A recent study (S.K. Herzog, unpubl.) in inter-Andean dry valleys in Bolivia showed that avian reproduction is highly seasonal and largely restricted to the austral spring and summer, showing similar degrees of synchronization as temperate bird communities. The overriding factors for the timing of breeding are precipitation and insect biomass, which itself is highly correlated with precipitation. This makes sense intuitively, because inter-Andean dry forests have a more seasonal climate than lowland rainforests. Therefore, avian phenology in the tropical Andes can be expected to become increasingly seasonal with increasing seasonality in climatic parameters, especially in drier habitats where greater seasonal variation in precipitation can be expected to have a pronounced impact.

Even less is known about migration in Andean birds. Species in the Andes can generally be divided into three categories of migration systems: (1) Long-distance Nearctic-Neotropical migrants that spend the northern-hemisphere winter in the tropics; (2) Austral migrants that breed in the southern temperate zone and spend the Austral winter in the tropical Andes; and (3) intratropical migrants that are either year-round residents migrating altitudinally or latitudinally within the tropical Andes, or breeding Austral summer residents that migrate to lowland areas at the end of the Austral summer. Several species also perform more nomadic long-range movements to track patchy food resources such as mass-seeding bamboo. Intra-Andean migrants, especially altitudinal migrants, are perhaps the most relevant group in the present context. The extent and magnitude of altitudinal migration in Andean birds is largely unknown, and so are the environmental cues that determine migration timing. As with reproductive phenology, climatic factors such as precipitation may play an important role. In some cases, avoidance of temporal overlap and resulting competition for food resources between Nearctic-Neotropical and intra-Andean migrants (e.g., *Catharus ustulatus* and *Turdus nigriceps*, respectively) may be important.

Climate, particularly precipitation, is related to the phenology in many other vertebrates. The phenology of bats in montane forests between 1300-1750 m of the eastern Andean slopes in Bolivia (Montaño 2007) showed various seasonal reproductive peaks per year. This was related to resource availability which, in turn, was linked to precipitation, so that most females are pregnant at the time of maximum rainfall. During the dry season Andean amphibians are exceedingly hard to find, but with the first rains they burst out into an impressive chorus that ranks among the most spectacular biological phenomena in the Andes. Reproductive activity of *Agalychnis* tree frogs and microhylids are known to be extremely seasonal related to rainfall patterns (Gottsberger and Gruber 2004; Stuart et al. 2008). Ground-dwelling amphibians and reptiles may respond to seasonal variations in soil humidity. Reproductive cycles of tropical freshwater fishes, particularly in mountain streams, remain poorly understood, but are likely to be tightly linked to stream flow and rainfall changes. Whereas lowland fish species inhabiting floodplain rivers are thought to primarily spawn during the wet season (reviewed by Munro et al. 1990), several fish species inhabiting mountain streams have been shown to spawn during dry periods (Torres-Mejia and Ramírez-Pinilla 2008 and references therein). Climate-induced variations in river flow, in terms of timing, duration, and magnitude of high and low flow events, could provide cues to migratory species that live, feed, or spawn in Andean piedmont rivers (e.g., *Prochilodus magdalenae*, *P. reticulatus*, *P. nigricans*, *Salminus affinis*).

The abundance and diversity of several Neotropical insect groups show marked seasonal variation, often low during the dry season and increasing at the onset of the rainy season (Wolda 1978, 1983, 1992; Smythe 1982; Janzen 1984; Wolda and Wong 1988; Brown

1991; DeVries et al. 1997). For instance, ant breeding flights peak at the onset of the rainy season in a lowland forest in Panama (Kaspari et al. 2001). The beginning of the rainy season may be the proximate cause of this pattern if it serves as a cue to synchronize breeding within species, and may also relate to ultimate causes because rainfall is thought to provide higher food availability and more suitable microclimates for breeding and colony foundation (Kaspari et al. 2001). Climate events such as rainfall also trigger the synchronized and extremely short-lived swarming events of termites in Atlantic rainforest of Brazil (Medeiros et al. 1999). Likewise, insect biomass and abundance closely correlate with precipitation in an inter-Andean dry forest of Bolivia (A.C. Hamel-Leigue and S.K. Herzog, unpubl.). Dung beetles (Scarabaeidae: Scarabaeinae) also show significant seasonal variations in species richness at the same site (A.C. Hamel-Leigue, D.J. Mann and S.K. Herzog, unpubl.). This indicates that reproductive cycles of many insects may be closely tied to climatic variables.

However, not all insect species respond to the same environmental cues or share similar ultimate causes of phenology. Some Panamanian ants perform breeding flights throughout the year (Kaspari et al. 2001). While most Atlantic rainforest termites swarm during the rainy season, dry-wood termites (Kalotermitidae) swarm in the dry season (Medeiros et al. 1999). Some species of dung beetles in the Bolivian Andes show patterns that contrast with the overall trend of minimum abundance during the height of the dry season. Compared to the Bolivian seasonal deciduous forest, dung beetle abundance and species richness varies little over the year in more tropical, evergreen forests in Peru (T. Larsen, pers. comm.). Thus, analogous to the timing of breeding in tropical Andean birds, insects can be expected to become increasingly seasonal with increasing seasonality in one or more climatic parameters.

Temporal variation in the life cycle stages of Neotropical fungi relates to variation in precipitation. Mycelial activity and abundance of fruiting bodies of leaf litter fungi in tropical forests is related to seasonal variation in water availability (Hedger 1985). High temporal turnover in species suggests that different fungi species in lowland tropical forests show strong seasonality related to rainfall (Lodge and Cantrell 1995). Variation in mycorrhiza spore abundance is also correlated to rainfall seasonality (Janos et al. 1995, Guadarrama and Álvarez-Sánchez 1999). At shorter time scales, the cumulative rain during three days was positively related to the diversity of fungal fruiting bodies in leaf litter of a central Amazonian forest (Braga-Neto et al. 2008). Deposition of endophyte hyphal fragments and spores on lowland tropical understory leaves is high just after rainfall events and decreases markedly as hours pass (Arnold 2008). In general, the temporal and spatial distribution of tropical forest fungi suggests that different species are adapted to different climate or weather conditions (Lodge and Cantrell 1995), but rigorous studies aimed to understand proximate and ultimate causes of the phenology are scarce.

Cycles of macroinvertebrate abundance in forest leaf-litter vary with precipitation and moisture content of the litter (Kattan et al. 2006, Levings and Windsor 1996). Abundance of bacteria in tropical forest leaf-litter is affected by water availability (Cornejo et al. 1994, Lodge et al. 1994, Yavitt et al. 2004). The life cycles of many parasites are affected by climate. Temperature affects the emergence of free swimming stages of trematode parasites from their snail hosts (Poulin 2006), and determines development and survival of Apicomplexan protistan organisms such as *Cryptosporidium parvum* (Fayer et al. 1998), a parasite of mammalian intestines causing cryptosporidiosis. Abundance of the causative agent of human malaria, *Plasmodium falciparum,* is similarly climate dependent (Paaijmans et al. 2009). A complete review of these patterns across taxonomic groups is outside the scope of this chapter, but it is clear that the phenology of Neotropical organisms is linked to climate, and to precipitation in particular.

Effect of Climate on Interspecific Interactions of (Neo)tropical Organisms

Climate may determine the nature of interspecific interactions in multiple ways and at a variety of temporal and spatial scales, as seen in the examples in previous paragraphs. Here we examine just a few ways that seem particularly important in the context of future climate change in the tropical Andes. Spatial variation in climate can affect the outcome of ecological interactions. For instance, climate often determines the geographic range of species (Gaston 2003, Sexton et al. 2009; see also Larsen et al. Chapter 3, this volume) and thus where species overlap geographically and interact. Altitudinal species turnover in the tropical Andes has been argued to result from interactions in which some species are excluded from particular elevations by competitively superior species, while the elevational range of the latter species is limited by climatic factors (Terborgh and Weske 1975, Remsen and Cardiff 1990, Remsen and Graves 1995). Recent empirical support for this hypothesis derives from studies of Andean birds and mammals (Anderson et al. 2002, Cadena and Loiselle 2007, Herzog et al. 2009). Likewise, inter-annual variation in precipitation may determine the geographic range of specialized parasitoid wasps, creating a spatial gradient of parasitism in caterpillars (Stireman et al. 2005). Even within the geographic range of a species climate can alter ecological interactions through its effects on phenotypes. Flight performance of Andean hummingbirds is influenced by climatic factors that change with elevation, with consequences for territorial behavior and competitive interactions (Altshuler 2006).

Temporal variation in climate can also have major effects on ecological interactions. Temporal variation in incidence of diseases such as malaria, influenza, and West Nile virus has been correlated to climate, although the causal structure underlying these correlations can be complex (Lafferty 2009). Prolonged drought can reduce habitat size in tropical forest streams, potentially increasing the strength of interspecific interactions due to crowding (Covich et al. 2003). El Niño southern oscillation has affected plant phenology in a Neotropical forest (see above) and thereby the population dynamics of fruit and seed eating animals (Wright et al. 1999). Pronounced drought during an El Niño year in a Borneo lowland rainforest lead to failure in the production of flowers by fig trees (*Ficus* spp.), resulting in local extinction of their Agaoninae wasp pollinators (Harrison 2000). Species of these wasps require fig trees to reproduce and vice versa, and fruits of fig trees are important resources for many vertebrates (Herre et al. 2008). Thus, local extinction of fig-pollinating wasps could potentially trigger changes in the composition of vertebrate frugivore communities (Harrison 2000).

The effect of climate on interspecific interactions played over long evolutionary time may have had a major impact on the nature of tropical ecosystems, including those in the tropical Andes. For instance, the contrast between tropical dry and rain forest in rainfall seasonality results in major differences in temporal patterns of foliage availability for herbivores and may have resulted in stronger selection pressures for increased plant defense in rain forest plants (Dirzo and Boege 2008). Moreover, little variation in temperature at seasonal (Vazquez and Stevens 2004) and geological (Imbrie et al. 1993, Weaver et al. 1998) time scales may have allowed interspecific ecological interactions to be more important selective pressures in the tropics than in temperate regions. Evidence supporting this idea derives from a variety of sources (Schemske et al. 2009). For instance, the effects of herbivores on plants (Coley and Aide 1991, Dyer and Coley 2002), effects of predators and parasitoids on herbivores (Dyer and Coley 2002), predation pressure from ants on other insects (Novotny et al. 2006), and bird nest predation rates (Schemske et al. 2009) appear to be higher in the tropics than in temperate latitudes. The frequency of animal pollinated (Regal 1982) and animal dispersed (Moles et al. 2007) plants is much higher in the tropics than in temperate regions. About 90% of tropical plants depend on animals for pollination or seed dispersal (Jordano 2000; see Krömer et al. 2006 for a tropical Andean example). Interactions in which symbiotic ants live in specialized plant structures are far more common in the tropics (Davidson and McKey 1993). Endophitic fungi can provide plants with herbivore defenses (Herre et al. 2007) and their incidence is higher in the tropics (Arnold and Lutzoni 2007). These patterns suggest that interspecific ecological interactions are particularly important for the structure and function of tropical ecosystems, and that disruption of such interactions due to climate change may have far-ranging consequences.

Potential Effects of Future Climate Change on Phenology and Interspecific Interactions of Andean Organisms

Scenarios of Future Change in Climatic Parameters Correlated to Phenology of Andean (or Neotropical) Organisms

The studies mentioned in previous sections suggest that proximate and ultimate causes of the phenology of many Andean organisms relate to the spatial and temporal distribution of precipitation. This is consistent with studies showing that precipitation drives general phenology in several Neotropical biomes (Reich 1995, Asner et al. 2000, Morellato 2003, Sanchez–Azofeifa et al. 2003). A prominent exception is the effect of temporal variation in solar insolation on plant phenology (see above). But even in this case, in many (but not all) sites temporal variation in insolation is associated with cloud cover and thus related to temporal variation in precipitation (Wright and van Schaik 1994, da Rocha 2004). Thus we focus on temporal and spatial patterns of precipitation as key abiotic drivers of phenology in the tropical Andes, while acknowledging that other abiotic factors may also be important. Ideally, we would like to know which particular parameters of the distribution of precipitation (e.g., amplitude of rainfall peaks, length of the dry and rainy seasons) determine phenological patterns of Andean organisms overall, and the future trends of such parameters. Some of the climatic data available allow the estimation of many detailed descriptors of rainfall seasonality (Figure 4.2) that would allow to test different possibilities, but phenological data for the tropical Andes are scant (Morellato 2003, see above). To overcome this limitation, below we point out three kinds of future changes in climate that might have important impacts on the phenology of tropical Andean organisms.

First, total annual precipitation may change, with increasing trends in some regions and decreasing in others such as inter-Andean valleys (Marengo et al. Chapter 7, this volume). Effects on phenology are likely to be non-linear and depend on relative rather than absolute change. For instance, a 200 mm decrease from currently 1,000 mm of annual precipitation (Figure 4.3) may result in a shift from moist forest to dry forest life zones (Holdridge 1947) while a change of the same magnitude in a place receiving 3,000 mm would maintain a wet forest. A similar case could be made for areas that currently receive around 100 mm of monthly precipitation during the driest month (Figure 4.4). Second, although there are no studies in the tropical Andes, in the south of the continent the amplitude of the annual precipitation cycle may be increasing (IPCC 2007). This may cause increased seasonality in phenology (see above). Third, warming trends will affect elevation profiles of relative humidity, shifting the location of orographic cloud banks that supply significant amounts of water to Neotropical mountain forest (Pounds et al. 2005; Ruiz et al. Chapter 12, this volume). In some areas these shifts may increase the number of dry days per year, lengthening the dry season or interrupting the wet season (Pounds et al. 2005). This would likely create seasonally stressful environments and a more seasonal phenology (Ruiz et al. Chapter 12, this volume).

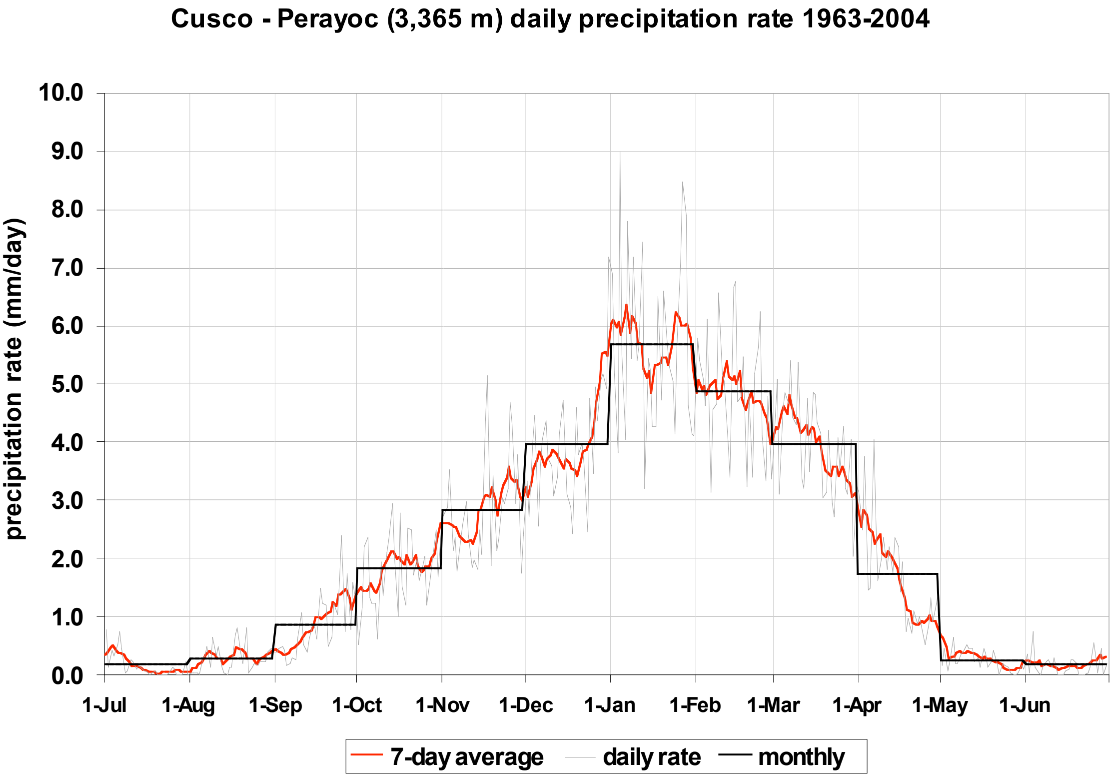

Figure 4.2. The daily mean precipitation rate over the July-June hydrological year at Cusco over the 42-year period 1963-2004 shown as daily values, 7-day running averages and monthly means. The abrupt intensification of wet season rainfall is a common characteristic for many locales in the central Andean region, yet is unrecognized in the scientific literature where monthly statistics are mostly presented to characterize rainfall, rather than the daily resolution required to capture such high-frequency behavior. The ecological significance of such behavior is unknown, though it may act to trigger phenological responses in and among species. (Data analysis by A. Seimon).

Beyond the three changes highlighted above, other future climatic changes are likely (Anderson et al. Chapter 1 and Marengo et al. Chapter 7, this volume), primarily associated with the behavior of the Pacific High, the Bolivian High, and the Intertropical Convergence Zone (see Martínez et al. Chapter 6, this volume). Although some trends can be suggested based on extrapolation of already observed changes in temperature and precipitation, it would be useful to develop studies specifically on variables likely to affect the phenology of tropical Andean organisms, including descriptors for the seasonality and inter-annual variation of precipitation.

Figure 4.3. Geographic distribution of areas with annual precipitation <900 mm (gray), 900 mm – 1,000 mm (red), and >1,000 mm (blue). From Worldclim (http://www.worldclim.org/methods.htm).

Figure 4.4. Geographic distribution of areas with precipitation of the driest month <90 mm (gray), 90 mm – 100 mm (red), and >100 mm (blue). From Worldclim (http://www.worldclim.org/methods.htm).

Potential Impacts of Climate Change on Phenology of Andean Organisms

We are unaware of studies on the effect of ongoing climate change on the phenology of tropical Andean organisms, so we use examples from elsewhere to explore possible scenarios. Responses to climate change depend on how climate relates to proximate and ultimate causes of phenological patterns. When climate is closely related to both the proximate and ultimate causes of phenological patterns, climate change may be expected to have immediate effects on phenology. Likely examples of such instances are seasonally deciduous trees (Borchert 2004, see above) or birds that time their breeding using climatic cues (Hau et al. 2004, see above). In these cases phenological adaptation may ameliorate negative impacts of climate change on fitness (Parmesan 2006).

When climate is closely related to ultimate but not proximate causes of phenological patterns, climate change may decrease fitness due to a mismatch between the cues triggering phenological events and the factors determining survival and reproduction. For instance, plants that drop leaves anticipating the water stress characteristic of the dry season may be using non-climatic cues (van Schaik et al. 1993, see above). Likewise, spotted antbirds use changes in photoperiod to gradually enlarge gonads in preparation for breeding during the rainy season (Hau et al. 2000, see above), when high availability of invertebrate prey is conducive for successful reproduction (Wikelski et al. 2000). If climate change alters the correlation between cues such as photoperiod and the factors that determine fitness such as water or prey availability, a decrease in fitness may result. Temperate plants and birds provide examples of this. In eastern North America, plants' ability to shift flowering time with climate change affects abundance, with species that have not shifted their phenology decreasing in abundance (Willis et al. 2008). Migratory bird species that have not shifted their arrival time at their breeding grounds in response to climate change appear to be declining in abundance too (Both et al. 2006, Miller-Rushing et al. 2008, Møller et al. 2008). Decreasing fitness, however, creates selective pressures that may result in evolution of responses to environmental cues, as documented for organisms as diverse as insects, birds, and mammals (Bradshaw and Holzapfel 2006). Such evolutionary responses may or may not be enough to halt population decline.

When climate is closely related to proximate but not ultimate causes of phenological patterns, climate change will likely result in phenological change, but the impact on fitness may be particularly difficult to predict. For instance, climatic cues may synchronize flowering or fruiting across one or several species. Such synchrony may increase fitness by increasing pollinator attraction or predator satiation (van Schaik et al. 1993, see above). As long as the climatic cue still occurs, organisms may still be able to synchronize their phenology and climate change may have little impact on their fitness. On the other hand, if different climatic cues are used by different species to stagger their phenologies and avoid interspecific competition for pollinators and seed dispersers (see above), climate change may result in more overlapping phenologies and decreased fitness. Species may then evolve responses to the changes in cues and thus adjust their life cycles according to the fitness consequences. We emphasize that this section is only an exploration of possible scenarios, and that predicting consequences of climate change for phenology and fitness is notoriously difficult due to the complexity of the relationships between climate, phenological patterns, and ecological interactions (Figure 4.1).

Potential Effects of Climate Change on Interspecific Interactions of Andean Organisms

Responses to climate change are species-specific because species differ in their ecological tolerances, life-history strategies, and dispersal and evolutionary abilities (Parmesan 2006). If species differ in their responses to a changing climate, ecological interactions may be affected in several ways. Here we discuss three potential outcomes: alteration of the timing of the interaction (temporal mismatch), shifts in geographic ranges (spatial mismatch), and changes in phenotypes or abundances of interacting species.

First, interacting species may differ in their phenological responses to new environmental conditions, altering the timing of the interactions. We know of no examples from the tropical Andes, but there are many examples elsewhere. Effects of climate on plant phenology (Cleland et al. 2007) can temporally decouple mutualistic interactions with animal pollinators (Memmott et al. 2007), as mentioned above for fig trees and wasps (Harrison 2000). Changes in phenology can also alter mutualistic relationships between plants and seed dispersers (Jordano 2000, Ness and Bresmer 2005), and antagonistic interactions between plants and insect herbivores (Visser and Holleman 2001, Visser and Both 2005, Musolin 2007, van Asch and Visser 2007). The latter can further propagate through trophic levels resulting in bird reproduction that is no longer synchronous with the abundance of their herbivore insect prey (Visser et al. 2004) as well as reproduction of top predators that does not match the abundance of their bird prey (Both et al. 2009). Effects of climate on phenology can alter the timing of interspecific interactions through the so called "priority effects" in which the order of species arrival to a local community inhibits or facilitates the arrival of other species (Morin 1999). For example, winter warming in Britain resulted in earlier breeding in newts (*Triturus* spp.) but no similar response occurred in frogs *(Rana temporaria*), so that early developmental stages of the latter species are exposed to higher predation pressure by newts (Beebee 1995). Climate can play a role in priority effects that seem common in the infection of tree roots by mychorrhizal fungi, with implications for the performance of both symbionts (Kennedy et al. 2009).

Second, species may respond to climate change by shifting their geographic ranges (Jackson and Overpek 2000, Parmesan 2006, Moritz et al. 2008), thereby affecting interactions. For instance, ongoing climate change is likely to contract the geographic range of leaf spurge (*Euphorbia esula*), an invasive plant now dominating ecosystems west of the Mississippi River, thus potentially releasing many species from a negative interspecific interaction and creating opportunities for the recovery of ecosystems (Bradley et al. 2009). Climate change is likely to expand the range of other introduced species resulting in opposite effects, as illustrated by experimental work on native (*Eriopis connexa*) and exotic (*Hippodamia variegate*) ladybird beetles in the Andes of central Chile (Molina-Montenegro et al. 2009). Climate change is also likely to result in spatial mismatch between a monophagous butterfly species (*Boloria titania*) and its larval plant host (*Polygonum bistorta*) in some European regions (Schweiger et al. 2008). Just as shifts in geographic ranges may interrupt interactions, they may result in new interactions among species. Avian malaria in Hawaii restricts native bird species to higher elevations (van Riper et al. 2003) where temperature halts appropriate development of the malaria pathogen inside its mosquito vector (*Culex quinquesfasciatus*, LaPointe et al. 2005). Yet, the incidence of avian malaria at higher elevations has increased over the last decade in association with increasing temperatures (Freed et al. 2005). High elevation Andean avifaunas may be similarly at risk from expansion of the geographic ranges of pathogens due to climate change (LaPointe et al. 2005). Vampire bats, *Desmodus rotundus*, are recognized reservoirs for the rabies virus, and their distribution is generally restricted to areas of warmer climates (McNab 1973, Greenhall et al. 1983). They seem to have moved upslope in Costa Rica during the last decades (LaVal 2004), extending the altitudinal range of their interaction with hosts and the rabies virus.

Third, species may remain in place and synchronized, but climate change can alter the phenotype (physiology, behavior, and morphology) or abundance of interacting species, thereby changing the outcome of the interaction. Temperature and humidity affect nectar concentration and secretion rate, which in turn affect pollinator behavior and, potentially, plant and pollinator fitness (Petanidou 2007). Climatic variation can directly affect the behavior of top predators, with repercussions through trophic cascades. Changes in winter climate related to the North Atlantic Oscillation caused Isle Royal wolves (*Canis lupus*) to hunt in larger packs, resulting in higher predation of moose (*Alces alces*) and consequent decreased hervibory and increased growth of balsam fir (*Abies balsamea*, Post et al. 1999). Climate variation directly affects the population dynamics at each tropic level in Isle Royal (wolves, moose, and fir), most strongly at the top and bottom trophic levels, and has the potential to threaten the persistence of the ecological community (Post and Forchhammer 2001). The negative impact of decreased water availability on the abundance of herbivore parasitoids and subsequent increase in herbivory rates may be one of the major effects of future climate change on tropical forests (Coley 1998). The effect of climate on species abundance can affect species interactions as diverse as mutualisms between plants and their pollinators or plants and ants, as well as antagonistic interactions between fish and metazoan parasites or mammals and fleas (Vásquez et al. 2007), because abundance determines the frequency of encounters among individuals of the different species which determines the strength of interactions.

Although there seems to be little documentation of the impacts of climate change on ecological interactions in the tropical Andes, there are reasons to believe that these impacts may be at least as important as in temperate regions. First, experimental studies of Neotropical organisms show the existence of strong effects of biotic interactions, such as the effect of herbivory on species distribution across habitats (Fine et al. 2004) and strong tritrophic interactions (Boege and Marquis 2006). Likewise, other studies of Neotropical organisms demonstrate that disrupting interspecific ecological interactions results in major impacts on the abundance and distribution of organisms. Studies of forest fragments that have lost predators of vertebrates document decreased availability of pollinators and seed dispersers, increased density of invertebrate predators, rodents, and herbivores, higher tree sapling mortality, and lower sapling recruitment (Terborgh et al. 2001, Terborgh and Feeley 2008). Local extinction of large vertebrates affects tree regeneration in other Neotropical forests as well (Dirzo and Miranda 1990, Terborgh et al. 2008). Indeed, ecological interactions may be particularly important in the structure and function of tropical ecosystems over both ecological and evolutionary time scales (Schemske et al. 2009, see above).

Second, specialization in ecological interactions may be more common in Neotropical than temperate ecosystems, as exemplified by the number of host plant species used by herbivore insects (Dyer et al. 2007, but see Novotny et al. 2006, Ollerton and Cranmer 2002). Specialization, however, is a major constraint that hinders response to temporal environmental change and thus contributes to extinction risk (Colles et al. 2009). In contrast to specialized ecological interactions, interactions may occur in diffuse networks involving multiple species. For example, the fruits of trees and shrubs are consumed by many different species of birds which disperse their seeds, and conversely, each bird species will feed on many different fruits (Figure 4.5). While bird species may differ in their role in seed dispersion due to differences in both the consumption and subsequent deposition of viable seeds (Schupp 1993), the multiple interacting species provide a redundancy of ecological roles that make the system robust to the extinction of individual seed dispersers (Loiselle and Blake 2002).

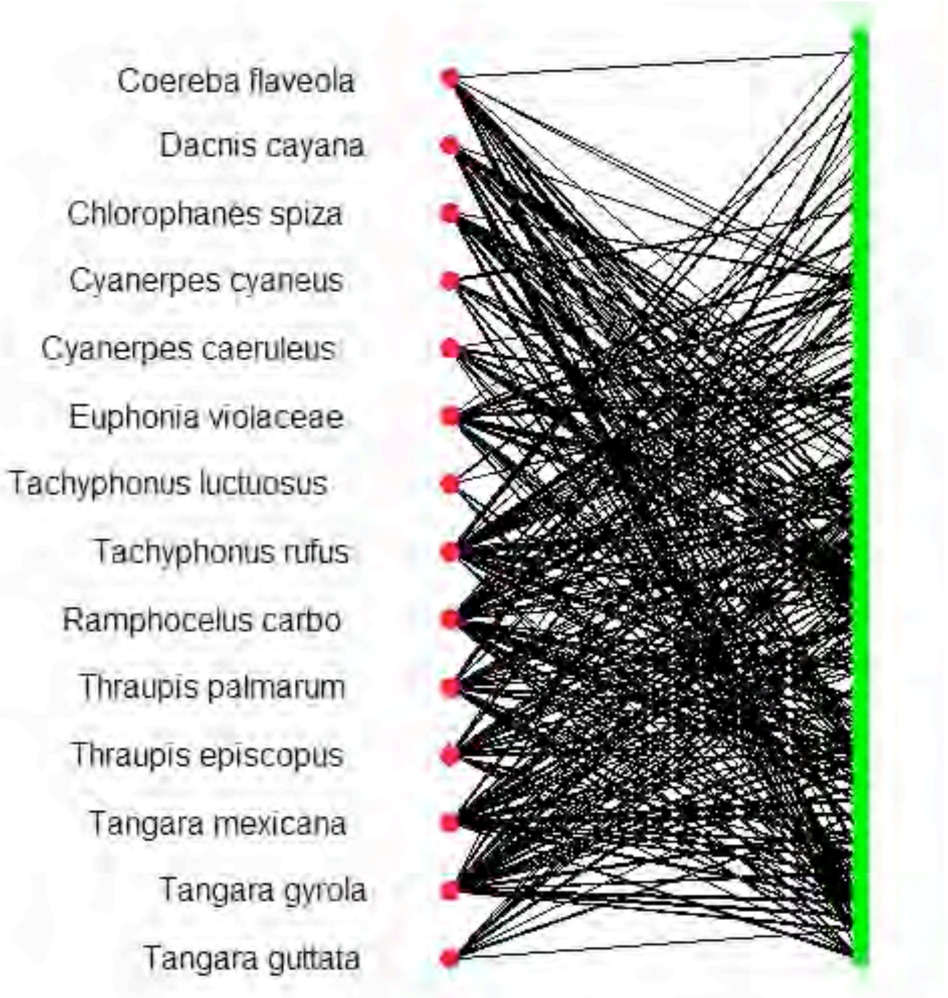

Figure 4.5. Network describing interactions between 65 plant species (green points) and 14 bird species (red points) that fed on their fruits in Trinidad from August 1960 through September 1961 (Snow and Snow 1971). Data available at the Interaction Web Database (http://www.nceas.ucsb.edu/interactionweb/index.html), hosted by the National Center for Ecological Analysis and Synthesis.

Conclusions

Further work to understand impacts of climate change on phenology should examine alternative hypotheses about how abiotic factors (e.g., precipitation and insolation) and ecological interactions determine phenological patterns. Examining such hypotheses for the tropical Andes may be hampered by the paucity of phenological data for the region (Morellato 2003), although climate data available for some areas may allow estimation of relevant parameters in some detail (Figure 4.2). Future phenological studies can draw from a wide range of tools to challenge the predictions of different hypotheses, including “phenological networks” aiming to gather long-term observations of phenophases of wild species across regions (see chapters in part 2 of Schwartz 2003a), remote sensing, airborne pollen data, manipulative experiments, and spatial models to predict phenology (Cleland et al. 2007). The distinction between ultimate and proximate causes, as emphasized in this chapter, is crucial to the understanding of phenological patterns (van Schaik et al. 1993) and the prediction of the impacts of climate change (Bradshaw and Holzapfel 2006). Studies regarding not only the relationship between phenology, climate, and other possible causal factors, but also regarding spatial and temporal variation in fitness will be helpful. Where ultimate and proximate causes of phenology are reasonably well understood, it would be useful to examine how climatic parameters related to both kinds of causes are likely to change. Analysis of observed tendencies and future scenarios, and predictive models of phenology and fitness under climate change are needed. Finally, the study of ecological interaction networks (Bascompte 2009) seems particularly useful because it focuses on properties describing the overall structure of networks of interacting species (e.g., Figure 4.5), such as the distribution of the number of interactions per species and the degree to which the network is nested (Figure 4.6). These characteristics of the overall structure of networks can be used to estimate the importance of different species for the persistence of ecological communities (Allesina and Pascual 2009), and to forecast the impact of multiple drivers of global change on biodiversity (Rezende et al. 2007, Tylianakis et al. 2008).

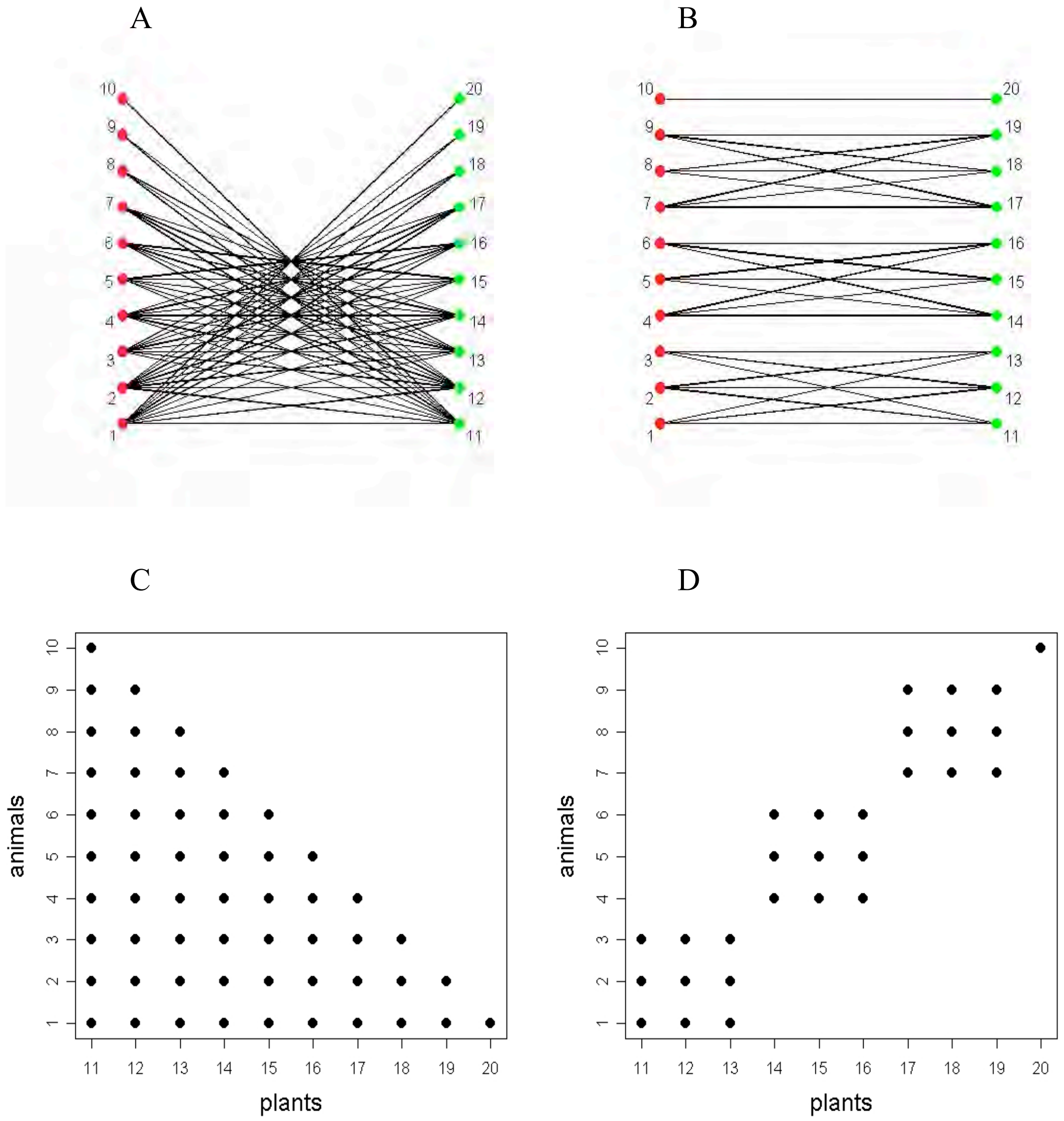

Figure 4.6. Illustration of interaction networks between plant (green dots) and animal (red dots) species with nested (A) and compartmentalized (B) structures. These networks are shown in plot form in C and D, respectively. This illustration is not based on real data. The robustness of networks of interacting species to temporal environmental change may depend on whether they are nested (Tylianakis et al. 2008). In nested networks generalist species interact with each other and with specialized species, while specialized species interact mostly with generalist species (A, C). Nested networks are relatively robust to disturbance because they depend on generalist species that can limit the effects of random species loss. In contrast, compartmentalized networks are composed of groups of species that interact strongly among them and only weakly with others (B, D), and are more susceptible to random species extinction. Mutualistic networks describing plant-pollinator or plant-seed disperser interactions may generally be nested and characterized by weak and asymmetric links (Jordano et al. 2003, Vázquez and Aizen 2004, Bascompte et al. 2003, 2006), while antagonistic interactions may be more compartmentalized and characterized by stronger links (Lewinsohn et al. 2006). Yet, networks of more intimate (i.e., symbiotic) interactions such as those between ants and myrmecophytes can also be highly compartmentalized (Guimaraes et al. 2007) and thus potentially more vulnerable.

Literature cited

Aide, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. *Nature* 336:574-575.

Aide, T. M., and P. Angulo-Sandoval. 1997. The effect of dry season irrigation on leaf phenology and the implications for herbivory in a tropical understory community. *Caribbean Journal of Science* 33:142-149.

Allesina, S., and M. Pascual. 2009. Googling food webs: can an eigenvector measure species' importance for coextinctions? *PLoS Computational Biology* 5:E1000494.

Altshuler, D. L. 2006. Flight performance and competitive displacement of hummingbirds across elevational gradients. *American Naturalist* 167:216-229.

Anderson, R. P., A. T. Peterson, and M. Gomez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98:3-16.

Arnold, A. E. 2008. Endophytic fungi: hidden components of tropical community ecology. Pp. 254-272 in *Tropical forest community ecology*, edited by W. P. Carson and S. A. Schnitzer. Oxford: Wiley-Blackwell.

Arnold, A. E., and F. Lutzoni. 2007. Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? *Ecology* 88:541-49.

Asner, G. P., A. R. Townsend, and B. H. Braswell. 2000. Satellite observation of El Niño effects on Amazon forest phenology and productivity. *Geophysical Research Letters* 27:981-984.

Bascompte, J. 2009. Mutualistic networks. *Frontiers in Ecology and the Environment* 7:429-436.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312:431-433.

Bascompte, J., P. Jordano, C. J. Melian, and J. M. Olesen. 2003. The nested assembly of plant animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America* 100:9383-9387.

Beebee, T. J. C. 1995. Amphibian breeding and climate change. *Nature* 374:219-220.

Beltrán, J. W., and G. H. Kattan. 2001. First record of the Slaty-backed Nightingale-Thrush in the Central Andes of Colombia, with notes on its ecology and geographical variation. *Wilson Bulletin* 113:134-139.

Bendix, J., J. Homeier, E. Cueva Ortiz, P. Emck, S.-W. Breckle, M. Richter, and E. Beck. 2006. Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *International Journal of Biometeorology* 50:370-384.

Boege, K., and R. J. Marquis. 2006. Bottom-up and top-down forces mediated by plant ontogeny: consequences for herbivores and plants. *Oikos* 115:559-592.

Borchert, R. 2004. The phenology of tropical trees and its environmental control. Available at: http://www.biology.ku.edu/tropical_tree_phenology/.

Borchert, R., S. S. Renner, Z. Calle, D. Navarrete, A. Tye, L. Gautier, R. Spichiger, and P. von Hildebrand. 2005. Photoperiodic induction of synchronous flowering near the equator. *Nature* 433:627-629.

Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78:73-83.

Both, C., S. Bouwhuis, C. M. Lessells, M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 44:81-83.

Bradley, B., M. Oppenheimer, and D. Wilcove. 2009. Climate change and plant invasions: restoration opportunities ahead? *Global Change Biology* 15:1511-1521.

Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. *Science* 312:1477-1478.

Braga-Neto, R., R. C. C. Luizao, W. E. Magnusson, G. Zuquim, and C. V. de Castilho. 2008. Leaf litter fungi in a central Amazonian forest: the influence of rainfall, soil and topography on the distribution of fruiting bodies. *Biodiversity and Conservation* 17:2701-2712.

Brearley, F. Q., J. Proctor, N. L. Suriantata, G. Dalrymple, and B. C. Voysey. 2007. Reproductive phenology over a 10-year period in a lowland evergreen rain forest of central Borneo. *Journal of Ecology* 95:828-839.

Brown Jr., K. S. 1991. Conservation of Neotropical environments: insects as indicators. Pp. 449-504 in *The conservation of insects and their habitats*, edited by N. M. Collins and J. A. Thomas. London: Academic Press.

Cadena, C. D., and B. A. Loiselle. 2007. Limits to elevational distributions in two species of emberizine finches: disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography* 30:491-504.

Chapman, C. A., L. J. Chapman, T. T. Struhsaker, A. E. Zanne, C. J. Clark, and J. R. Poulsen. 2005. A long-term evaluation of fruiting phenology: importance of climate change. *Journal of Tropical Ecology* 21:31-45.

Charles-Dominique, P., M. Atramentowicz, M. Charles-Dominique, H. Gerard, C. M. Hladick, and M. F. Prevost. 1981. Les mamiferes frugivores arboricoles nocturnes d'une foret Guyanaise: interrelations plantes-animaux. *Revue d'écologie (La terre et la vie)* 35:341-345.

Claus, G. 1926. Die Blütenbewegungen der Gentianaceen. *Flora* 120:198-226.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* 22:357-365.

Coley, P. D. 1998. Possible effects of climate change on plant-herbivore interactions in moist tropical forest. *Climate Change* 39:455-472.

Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broadleaved forests. Pp. 25-49 in *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*, edited by P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson. New York: JohnWiley & Sons.

Colles, A., L. H. Liow, and A. Prizing. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters* 12:849-863.

Cornejo, F. J., A. Varela, and S. J. Wright. 1994. Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. *Oikos* 70:183-190.

Covich, A. P., T. A. Crowl, and F. N. Scatena. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Fresh Water Biology* 48:1199-1206.

da Rocha, H. R., M. L. Goulden, S. D. Miller, M. C. Menton, L. D. V. O. Pinto, H. C. de Freitas, and A. M. S. Figueira. 2004. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecological Applications* 14:S22-S32.

Davidson, D. W., and D. McKey. 1993. Ant-plant symbioses: stalking the Chuyachaqui. *Trends in Ecology & Evolution* 8:326-332.

DeVries, P. J., D. Murray, and R. Lande. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62:343-364.

Dirzo, R., and K. Boege. 2008. Patterns of herbivory and defense in tropical dry and rain forest. Pp. 63-78 in *Tropical forest community ecology*, edited by W. P. Carson and S. A. Schnitzer. Oxford: Wiley-Blackwell.

Dirzo, R., and A. Miranda. 1990. Contemporary Neotropical defaunation and forest structure, function, and diversity – a sequel to John Terborgh. *Conservation Biology* 4:444-447.

Dyer, L. A., and P. D. Coley. 2002. Tritrophic interactions in tropical and temperate communities. Pp. 67-88 in *Multitrophic level interactions*, edited by T. Tscharntke and B. Hawkins. Cambridge: Cambridge University Press.

Dyer, L. A., M. S. Singer, J. T. Lill, J. O. Stireman, G. L. Gentry, R. J. Marquis, R. E. Ricklefs, H. F. Greeney, D. L. Wagner, H. C. Morais, I. R. Diniz, T. A. Kursar, and P. D. Coley. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696-699.

Fayer, R. J., M. Trout, and M. C. Jenkins. 1998. Infectivity of *Cryptosporidium parvum* oocysts stored in water at environmental temperatures. *Journal of Parasitology* 84:1165-1169.

Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305:663-665.

Foster, R. B. 1982. The seasonal rhythm of fruitfall in Barro Colorado Island. Pp. 151-172 in *The ecology of a Neotropcial forest*, edited by E. G. Leigh, A. S. Rand, and D. M. Windsor. Washington, DC: Smithsonian Institution.

Frederickson, M. E. 2006. The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. *Oecologia* 149:418-427.

Freed, L. A., R. L. Cann, M. L. Goff, W. A. Kuntz, and G. R. Bodner. 2005. Increase in avian malaria at upper elevation in Hawaii. *Condor* 107:753-764.

Futuyma, D. J. 1998. *Evolutionary Biology*. Third edition. Sunderland, MA: Sinauer Associates, Inc.

Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gottsberger, B., and E. Gruber. 2004. Temporal partitioning of reproductive activity in a Neotropical anuran community. *Journal of Tropical Ecology* 20:271-280.

Grace, J. B. 2006. *Structural equation modeling in natural systems.* Cambridge: Cambridge University Press.

Greenhall, A. M., G. Joermann, and U. Schmidt. 1983. *Desmodus rotundus*. *Mammalian Species* 202:1-6.

Guadarrama, P., and F. J. Alvarez-Sanchez. 1999. Abundance of arbuscular mycorrhizal fungi spores in different environments in a tropical rain forest, Veracruz, Mexico. *Mycorrhiza* 8:267-270.

Guimaraes Jr., P. R., V. Rico-Gray, P. S. Oliveira, T. J. Izzo, S. F. dos Reis, and J. N. Thompson. 2007. Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Current Biology* 17:1797-1803.

Günter, S., M. Cabrera, M. L. Diaz, M. Lojan, E. Ordoñez, M. Richter, and M. Weber. 2008. Tree phenology in montane forests of southern Ecuador can be explained by precipitation, radiation and photoperiodic control. *Journal of Tropical Ecology* 24:247-258.

Harrison, R. D. 2000. Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London B, Biological Sciences* 267:911-915.

Hau, M., M. Wikelski, H. Gwinner, and E. Gwinner. 2004. Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* 106:489-500.

Hau, M., M. Wikelski, and J. C. Wingfield. 1998. A Neotropical forest bird can measure the light changes in tropical photoperiod. *Proceedings of the Royal Society of London B, Biological Sciences* 265:89-95.

Hau, M., M. Wikelski, and J. C. Wingfield. 2000. Visual and nutritional cues stimulate reproduction in a Neotropical bird. *Journal of Experimental Zoology*:286:494-504.

He, Y.-P., Y.-W. Duan, J.-Q. Liu, and W. K. Smith. 2006. Floral closure in response to temperature and pollination in *Gentiana straminea* Maxim. (Gentianaceae), an alpine perennial in the Qinghai-Tibetan Plateau. *Plant Systematics and Evolution* 256:17-33.

Hedger, J. 1985. Tropical agarics, resource relations and fruiting periodicity. Pp. 41-86 in *Developmental biology of higher plants*, edited by D. Moore, L. A. Casselton, D. A. Wood, and J. C. Frankland. Cambridge: Cambridge University Press.

Herre, E. A., L. C. Mejía, D. A. Kyllo, E. Rojas, Z. Maynard, A. Butler, and S. A. Van Bael. 2007. Ecological implications of anti-pathogen effects of tropical fungal endophytes and mycorrhizae. *Ecology* 88:550-558.

Herre, E. A., K. C. Jander, and C. A. Machado. 2008. Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annual Review of Ecology and Systematics* 39:439-458.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.

Huete, A. R., K. Didan, Y. E. Shimabukuro, P. Ratana, S. R. Saleska, L. R. Hutyra, W. Yang, R. R. Nemani, and R. Myneni. 2006. Amazon rain forest green-up with sunlight in dry season. *Geophysical Research Letters* 33:L06405.

Imbrie, J., A. Berger, E. A. Boyle, S. C. Clemens, A. Duffy, W. R. Howard, G. Kukla, J. Kutzbach, D. G. Martinson, A. McIntyre, A. C. Mix, B. Molfino, J. J. Morley, L. C. Peterson, N. G. Pisias, W. L. Prell, M. E. Raymo, N. J. Shackleton, and J. R. Toggweiler. 1993. On the structure and origin of major glaciation cycles 2. The 100,000-year cycle. *Paleoceanography* 8:699-735.

IPCC. 2007. Climate change 2007: the physical science basis. Pp. 1-996 in *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26:194-220.

Jaksic, F. M., and M. Lima. 2003. Myths and facts on ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. *Austral Ecology* 28:237-251.

Janos, D. P., C. T. Sahley, and L. H. Emmons. 1995. Rodent dispersal of vesicular-arbuscular mycorrhizal fungi in Amazonian Peru. *Ecology* 76:1852-1858.

Janzen, D. H. 1984. Two ways of being a tropical big moth: Santa Rosa saturniids and sphingids. *Oxford Surveys in Evolutionary Biology* 1:85-140.

Jordano, P. 2000. Fruits and frugivory. Pp. 125-66 in *Seeds: the ecology of regeneration in natural plant communities*, edited by M. Fenner. Oxon, UK: CABI Publications.

Jordano, P., J. Bascompte, and J. M. Olesen. 2003. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters* 6:69-81.

Judziewicz, E. J., L. G. Clark, X. Londoño, and M. J. Stern. 1999. *American bamboos*. Washington, DC: Smithsonian Institution Press.

Kattan, G. H., D. Correa, F. Escobar, and C. A. Medina. 2006. Leaf-litter arthropods in restored forests in the Colombian Andes: a comparison between secondary forest and tree plantations. *Restoration Ecology* 14:95-102.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* 33:427-447.

Kennedy, P. G., K. G. Peay, and T. D. Bruns. 2009. Root tip competition among ectomycorrhizal fungi: are priority effects a rule or an exception? *Ecology* 90:2098-2107.

Lafferty, K. D. 2009. The ecology of climate change and infectious diseases. *Ecology* 90:888-900.

LaPointe, D., T. L. Benning, and C. Atkinson. 2005. Case study: avian malaria, climate change, native birds of Hawaii. Pp 317-324 in *Climate change and biodiversity*, edited by T. E. Lovejoy and L. Hannah. New Haven, CT: Yale University Press.

LaVal, R. K. 2004. Impact of global warming and locally changing climate on tropical cloud forest bats. *Journal of Mammalogy* 85:237-244.

Levings, S. C., and D. M. Windsor. 1996. Seasonal and annual variation in litter arthropod populations. Pp. 355-388 in *The ecology of a tropical forest: seasonal rhythms and long-term changes*, edited by E. G. Leigh, A. S. Rand, and D. M. Windsor. Washington, DC: Smithsonian Institution Press.

Lewinsohn, T. M., P. I. Prado, P. Jordano, J. Bascompte, and J. M. Olesen. 2006. Structure in plant–animal interaction assemblages. *Oikos* 113:174-184.

Lobo, J. A., M. Quesada, K. E. Stoner, E. J. Fuchs, Y. Herrerías-Diego, J. Rojas, and G. Saborío. 2003. Factors affecting phenological patterns of bombacaceous trees in seasonal Costa Rica and Mexico. *American Journal of Botany* 90:1054-1063.

Lodge, D. J., W. H. McDowell, and C. P. McSwiney. 1994. The importance of nutrient pulses in tropical forests. *Trends in Ecology and Evolution* 9:384-387.

Lodge, D. J., and S. Cantrell. 1995. Fungal communities in wet tropical forest: variation in time and space. *Canadian Journal of Botany* 73:S1391-S1398.

Loiselle, B. A., and J. G. Blake. 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Pp. 397-405 in *Seed dispersal and frugivory: ecology, evolution and conservation*, edited by D. J. Levey, W. R. Silva, and M. Galetti. Wallingford, U.K.: CABI Publishing.

McNab, B. K. 1973. Energetics and the distribution of vampires. *Journal of Mammalogy* 54:131-144.

Medeiros, L. G. S., A. G. Bandeira, and C. Martius 1999. Termite swarming in the northeastern Atlantic rain forest of Brazil. *Studies of Neotropical Fauna and Environment* 34:76-87.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. *Ecology Letters* 10:710-717.

Miller, A. H. 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. *University of California Publications in Zoology* 66:1-74.

Miller-Rushing, A. J., T. L. Lloyd-Evans, R. B. Primack, and P. Satzinger. 2008. Bird migration times, climate change, and changing population sizes. *Global Change Biology* 14:1959-1972.

Moles, A. T., D. D. Ackerly, J. C. Tweddle, J. B. Dickie, R. Smith, M. R. Leishman, M. M. Mayfield, A. Pitman, J. T. Wood, and M. Westoby. 2007. Global patterns in seed size. *Global Ecology and Biogeography* 16:109-116.

Molina-Montenegro, M. A., R. Briones, and L. A. Cavieres. 2009. Does global warming induce segregation among alien and native beetle species in a mountain-top? *Ecological Research* 24:31-36.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America* 105:16195-16200.

Montaño, F. A. 2007. Fenología reproductiva de murciélagos tropicales en Bolivia. Pp. 23-27 in *Historia natural, distribución y conservación de los murciélagos de Bolivia*, edited by L. F. Aguirre. Santa Cruz de la Sierra: Editorial Centro de Ecología y Difusión Simón I. Patiño.

Morellato, L. P. 2003. South America. Pp. 75-92 in *Phenology: an integrative environmental science*, edited by M. D. Schwartz. Dordrecht: Kluwer Academic Publishers.

Morin, P. J. 1999. *Community ecology*. Malden, MA: Blackwell Science, Inc.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261-264.

Munro, A. D., A. P. Scott, and T. J. Lam. 1990. *Reproductive seasonality in teleosts: environmental influences*. Boca Raton, FL: CRC Press, Inc.

Musolin, D. L. 2007. Insects in a warmer world: ecological, physiological and lifehistory responses of true bugs (Heteroptera) to climate change. *Global Change Biology* 13:1565-1585.

Ness, J. H., and K. Bressmer. 2005. Abiotic influences on the behaviour of rodents, ants, and plants affect an ant-seed mutualism. *Ecoscience* 12:76-81.

Norden, N., J. Chave, P. Belbenoit, A. Caubère, P. Châtelet, P.-M. Forget, and C. Thébaud. 2007. Mast fruiting is a frequent strategy in woody species of eastern South America. *PLoS ONE* 2:e1079.

Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313:1115-1118.

Ollerton, J., and L. Cranmer. 2002. Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos* 98:340-350.

Paaijmans, K. P., A. F. Read, and M. B. Thomas. 2009. Understanding the link between malaria risk and climate. *Proceedings of the National Academy of Sciences of the United States of America* 106:13844-13849.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37:637-669.

Pendall, E., S. Bridgham, P. J. Hanson, B. Hungate, D. W. Kicklighter, D. W. Johnson, B. E. Law, Y. Luo, J. P. Megonigal, M. Olsrud, M. G. Ryan, and S. Wan. 2004. Below-ground process responses to elevated CO_2 and temperature: a discussion of observations, measurement methods, and models. *New Phytologist* 162:311-322.

Petanidou, T. 2007. Ecological and evolutionary aspects of floral nectars in Mediterranean habitats. Pp. 343-376 in *Nectaries and nectar*, edited by S. W. Nicolson, M. Nepi, and E. Pacini. Dordrecht: Springer Verlag.

Post, E., and M. C. Forchhammer. 2001. Pervasive influence of large-scale climate in the dynamics of a terrestrial vertebrate community. *BMC Ecology* 1:5.

Post, E., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioral response to climate. *Nature* 401:905-907.

Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology* 132:143-51.

Pounds, J. A., M. P. L. Fogden, and K. L. Masters. 2005. Responses of natural communities to climate change in a highland tropical forest. Pp. 70-74 in *Climate change and biodiversity*, edited by T. E. Lovejoy and L. Hannah. New Haven, CT: Yale University Press.

Rathcke, B., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179-214.

Regal, P. J. 1982. Pollination by wind and animals: ecology of geographic patterns. *Annual Review of Ecology and Systematics* 13:497-524.

Reich, P. B. 1995. Phenology of tropical forests – patterns, causes, and consequences. *Canadian Journal of Botany* 73:164-174.

Reich, P., and R. Borchert. 1982. Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* 63:294-299.

Remsen Jr., J. V., and S. W. Cardiff. 1990. Patterns of elevational and latitudinal distribution, including a “niche switch” in some guans (Cracidae) of the Andes. *Condor* 92:970-81.

Remsen Jr., J. V., and W. S. Graves. 1995. Distribution patterns of *Buarremon* brush-finches (Emberizinae) and interspecific competition in Andean birds. *Auk* 112:225-36.

Renner, S. S. 2007. Synchronous flowering linked to changes in solar radiation intensity. *New Phytologist* 175:195-97.

Rezende, E. L., J. E. Lavabre, P. R. Guimaraes Jr., P. Jordano, and J. Bascompte. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448:925-28.

Ricklefs, R. E., and G. L. Miller. 2000. *Ecology*. Fourth edition. New York: W. H. Freeman and Company.

Rivera, J., and J. Cozza. 2008. Reduced photoperiod induces partially synchronous flowering time in an understory forest herb, *Begonia urophylla*, in Costa Rica. *Biotropica* 40:363-65.

Rivera, G., S. Elliot, L. S. Caldas, G. Nicolossi, V. T. R. Coradín, and R. Borchert. 2002. Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees – Structure and Function* 16:445-456.

Sakai, S., R. D. Harrison, K. Momose, K. Kuraji, H. Nagamasu, T. Yasunari, L. Chong, and T. Nakashizuka. 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany* 93:1134-1139.

Sanchez-Azofeifa, A., E. Kalacska, M. Quesada, K. E. Stoner, J. A. Lobo, and P. Arroyo-Mora. 2003. Tropical dry climates. Pp. 121-138 in *Phenology: an integrative environmental science*, edited by M. D. Schwartz. Dordrecht: Kluwer Academic Publishers.

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology and Systematics* 40:245-269.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108:15-29.

Schwartz, M. D. (ed.). 2003a. *Phenology: an integrative environmental science*. Dordrecht: Kluwer Academic Publishers.

Schwartz, M. D. 2003b. Phenoclimatic measures. Pp. 331-345 in *Phenology: an integrative environmental science*, edited by M. D. Schwartz. Dordrecht: Kluwer Academic Publishers.

Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kühn. 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89:3472-3479.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species limits. *Annual Review of Ecology and Systematics* 40:415-436.

Sibaoka, T. 1991. Rapid plant movements triggered by action potentials. *Journal of Plant Research* 104:73-95.

Smythe, N. 1982. The seasonal abundance of night-flying insects in a Neotropical forest. Pp. 309-318 in *The ecology of a tropical forest*, edited by E. G. Leigh Jr., A. S. Rand, and D. M. Windsor. Washington, DC: Smithsonian Institution Press.

Snow, B. K., and D. W. Snow. 1971. The feeding ecology of tanagers and honeycreeperes in Trinidad. *Auk* 88:291-322.

Stevenson, P. 2004. Phenological patterns of woody vegetation at Tinigua National Park, Colombia: methodological comparisons with emphasis on fruit production. *Caldasia* 26:125-150.

Stireman III, J. O., L. A. Dyer, D. H. Janzen, M. S. Singer, J. T. Lill, R. J. Marquis, R. E. Ricklefs, G. L. Gentry, W. Hallwachs, P. D. Coley, J. A. Barone, H. F. Greeney, H. Connahs, P. Barbosa, H. C. Morais, and I. R. Diniz. 2005. Climatic unpredictability and caterpillar parasitism: implications of global warming. *Proceedings of the National Academy of Sciences of the United States of America* 102:17384-17387.

Stuart, S. N., M. Hoffmann, J. S. Chanson, N. A. Cox, R. Berridge, P. Ramani, and B. E. Young. 2008. *Threatened amphibians of the world*. Barcelona: Lynx Ediciones.

Stutchbury, B. J. M., and E. S. Morton. 2001. *Behavioral ecology of tropical songbirds*. London: Academic Press.

Terborgh, J. and K. Feeley. 2008. Ecosystem decay in closed forest fragments. Pp. 308-321 in *Tropical forest community ecology*, edited by W. P. Carson and S. A. Schnitzer. Oxford: Wiley-Blackwell.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923-1926.

Terborgh, J., G. Nuñez-Iturri, N. C. A. Pitman, F. H. C. Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. E. T. Paine. 2008. Tree recruitment in an empty forest. *Ecology* 89:1757-1768.

Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562-576.

Thies, W., and E. K. V. Kalko. 2004. Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos* 104:362-376.

Thompson, J. N. 2009. The coevolving web of life. *American Naturalist* 173:125-150.

Torres-Mejia, M., and M. P. Ramírez-Pinilla. 2008. Dry-season breeding of a characin in a Neotropical mountain river. *Copeia* 2008:99-104.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363.

Vamosi, J. C., T. M. Knight, J. A. Steets, S. J. Mazer, M. Burd, and T. Ashman. 2006. Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences of the United States of America* 103:956-961.

van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology* 52:37-55.

van Riper, C., S. G. van Riper, M. L. Goff, and M. Laird. 2003. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* 56:327-344.

van Schaik, C. P., J. W. Terborgh, and S. J. Wright 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353-377

Vázquez, D. P., and M. A. Aizen. 2004. Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology* 85:1251-1257.

Vázquez, D. P., and R. D. Stevens. 2004. The latitudinal gradient in niche breadth: concepts and evidence. *American Naturalist* 164:E1–E19.

Vázquez, D. P., C. J. Melián, N. M. Williams, N. Bluthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120-1127.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for yardstick. *Proceedings of the Royal Society of London B, Biological Sciences* 272:2561-2560.

Visser M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35:89-110.

Visser, M. E., and L. J. M. Holleman. 2001. Warmer spring disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B, Biological Sciences* 268:289-294.

Weaver, A. J., M. Eby, A. F. Fanning, and E. C. Wiebe. 1998. Simulated influence of carbon dioxide, orbital forcing and ice sheets on the climate of the last glacial maximum. *Nature* 394:847-853.

Wikelski, M., M. Hau, and J. C. Wingfield. 2000. Seasonality of reproduction in a Neotropical rain forest bird. *Ecology* 81:2458-2472.

Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davies. 2008. Phylogenetic patterns of species loss in Thoreau’s woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105:17029-17033.

Wolda, H. 1978. Fluctuations in abundance of tropical insects. *American Naturalist* 112:1017-1045.

Wolda H. 1983. Spatial and temporal variation in abundance in tropical animals. Pp. 93-105 in *Tropical rain forest: ecology and management*, edited by S. L. Sutton, T. C. Whitmore, and A. C. Chadwick. Oxford: Blackwell.

Wolda, H. 1992. Trends in abundance of tropical forest insects. *Oecologia* 89:47-52.

Wolda, H., and M. Wong. 1988. Tropical insect diversity and seasonality. Sweep samples versus lighttraps. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series C* 91:203-216.

Wright, S. J., and C. P. van Schaik. 1994. Light and the phenology of tropical trees. *American Naturalist* 143:192-199.

Wright, S. J., C. Carrasco, O. Calderón, and S. Paton. 1999. The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632-1647.

Yavitt, J. B., S. J. Wright, and R. K. Wieder. 2004. Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. *Austral Ecology* 29:177-188.

Yeang, H.-Y. 2007. Synchronous flowering of the rubber tree (*Hevea brasiliensis*) induced by solar radiation intensity. *New Phytologist* 175:283-289.

5

A note on paleo-climate

This note was prepared by Holm Tiessen in an attempt to provide a brief overview. It is based on contributions by Jaime Argollo and Edsón Ramírez with help from Rodney Martinez, and inclusion of recent literature.

Past climate variations can provide valuable lessons for understanding climate change and its potential impacts on landscapes and ecosystems. In the tropical Andes knowledge on climates for periods of several thousands of years ago has been derived principally from a small number of studies of ice cores from Andean glaciers and of sediment cores from lacustrine sites. For the past 700 years, some additional detail is available from dendrochronologies using mostly Polylepis trees whose annual rings reflect seasonal moisture patterns. In summary, information on past climate in the tropical Andes is relatively scarce. What is known can be summarized in the context of the principal climate components.

Data on paleo-climate are derived from geomorphology and sedimentology in combination with carbon dating, and from detailed isotopic analyses of ice cores. Geomorphology of glacial valleys and moraine positions show that during the past 2.5 million years, glacial extent in the Andes has changed frequently, probably as a result of changes in precipitation, rather than temperature. Sedimentology has established chronologies of lake extents and these have been shown to co-vary with glacial extent. For instance, low glacial and lake extents coincided around 18,000 ybp, while glacial advances coincided with a larger extent of lake Titicaca around 15,400 ybp, and around 11,000 ybp for the Uyuni-Coipasa watershed. It is therefore likely that glacier and lake extents are controlled by a common cause, wet and dry periods, and that glaciers will buffer water availability during warmer or drier periods only for relatively short times. These conclusions are tentative because isotope records and dating for the past ice age are still plagued by uncertainties, making it difficult to show synchronies between ice, sediment and geomorphological records. Radiocarbon dates of peats near end moraines provide ages that vary greatly between individual valleys. It is likely that future climate change will similarly show great variation between locations, and that adaptation measures need to be fine-tuned to local needs.

Moraines from the last ice age have mostly been dated between 33 - 43,000 ybp (Schubert and Clapperton 1990) but some are as young as 15,000 ybp. Snow lines during the ice ages descended to below 4000m in several regions and below 3000m in some places. A common hypothesis is that during much of the last ice age humid and cold conditions prevailed over the tropical Andes.

Van der Hammen (1992) developed a synopsis of paleoclimate in the northern part of the tropical Andes: during the last interglacial (from 130,000-80,000 ybp), lake levels and extents were reduced, but rainfall was still sufficient to build up high elevation bogs and peat deposits. During the shift to the following ice age, forests retreated and the Andes were covered by savannas and páramo. During the peak of the ice age, maximum glacier extent was reached around 45-25,000 ybp, when glaciers may have reached far enough down to contact remaining forests. The late ice age from 25-13,000 ybp was cold and dry with a steeper thermal lapse rate of possibly 0.8°C per 100m elevation than today's 0.6°C. Dust layers in ice cores support the hypothesis of a drier period, as does Clapperton's (1993) hypothesis of savannization of part of the Amazon basin at the time. During this cold, dry period, the páramos of the Eastern Cordillera of Colombia expanded to allow separate patches of páramo to fuse. In the context of biodiversity such connectivities may have influenced species exchange and endemism.

The oxygen isotopic signatures between different ice cores in the region are similar, indicating that the water had a common origin. This holds even when comparing humid equatorial (9° South) with drier subtropical (20° South) regions (Hoffman et al. 2003). The source of rain or snow in the tropical Andes is the Amazon basin, and therefore ultimately the Atlantic. Some climate records from ice cores show coherence with European (Atlantic) events, while others appear to be more influenced by local conditions such as the formation of large lakes during humid periods (Thompson et al. 2000). Detailed interpretation of isotope records is hampered by uncertainties over the relative effects of precipitation amounts and temperatures on isotopic signatures (Ramirez et al. 2003), and the two may be linked through recycling of water by evapotranspiration.

Currently, rainfall in the Chilean Andes is supplied by the Pacific ocean while the Pacific is not a significant source of moisture for the Altiplano and the tropical Andes. There is a possibility that a northward displacement of the Southern-Hemisphere westerlies during the coldest periods of the last glacial maximum may have brought Pacific moisture to the western slopes of the tropical Andes in the past (Heusser 1989), possibly complicating isotope records.

The complication of reconciling the different proxy-data for the region with the sources and drivers of precipitation has been summarized by Vimeux et al. (2009): "It may seem counterintuitive that the robust regional inter-annual control on isotopic values in the tropical and subtropical Andes be driven by tropical Pacific sea surface temperatures since the moisture source for these ice core sites lies ... ultimately (in) the tropical Atlantic. It is, however, consistent with the dominant influence of the tropical Pacific on inter-annual climate variability in this part of the world". They conclude that "merging all these parameters into a multi-proxy data set is important to advance the paleoclimatic value of Andean ice cores". This will be needed not only to establish a more reliable climate record, but also to link that record to the history of Andean ecosystems.

For the understanding of Andean climate and its potential future changes it is therefore important to take into account both the role of the Atlantic ocean as a source of precipitation and that of the Pacific as a control over precipitation in the tropical Andes. The many systems that contribute to the Pacific influences on Andean climate were summarized, as part of an analysis of climate along the entire American Cordillera supported by the IAI, by Villalba et al. (2011): "Inter-annual climatic variations in the tropics and subtropics of the Western Americas are largely regulated by El Niño-Southern Oscillation (ENSO), whereas decadal-scale variations are induced by long-term Pacific modes of climate variability such as the Pacific Decadal Oscillation (PDO). At higher latitudes, climate variations are dominated by oscillations in the Annular Modes (the Arctic and Antarctic Oscillations) which show both inter-annual and longer-scale temporal oscillations." This complexity will require careful combinations of regional climate and weather observations, an understanding of teleconnections to distant oceanic systems and the use global circulation models to structure the knowledge. In the context of biodiversity and adaptation, it will be particularly important to understand local and regional trends based on an improved network of meteorological observing stations, because factors critical for ecosystem function such as the elevation at which clouds form are not easily deduced from more global models. Paleo studies are showing that current climate trends in the tropical Andes are outside the range of past patterns. This means that well-informed extrapolations of observed patterns and in-depth understanding are needed to plan adaptation and conservation measures.

Literature Cited

Clapertton, C. M. 1993. *The Quaternary geology and geomorphology of South America*. Amsterdam: Elsevier.

Heusser, C. J. 1989. Southern westerlies during the Last Glacial Maximum. *Quaternary Research* 31:423-425.

Hoffmann, G., E. Ramirez, J. D. Taupin, B. Francou, P. Ribstein, R. Delmas, H. Dürr, R. Gallaire, J. Simões, U. Schotterer, M. Stievenard, and M. Werner. 2003. Coherent isotope history of Andean ice cores over the last century. *Geophysical Research Letters* 30:1179-1182.

Ramirez, E., G. Hoffman, J. D. Taupin, B. Francou, P. Ribstein, N. Caillon, F. A. Ferron, A. Landais, J. R. Petit, B. Pouyaud, U. Schotterer, J. Simoes, and M. Stievenard. 2003. A new Andean deep ice core from Nevado Illimani (6350 m), Bolivia. *Earth and Planetary Science Letters* 212:337-350.

Schubert, C., and C. M. Clapertton. 1990. Quaternary glaciations on the northern Andes (Venezuela, Colombia and Ecuador). *Quaternary Science Reviews* 9:123-135.

Thompson, G. L., E. Mosley-Thompson, and K. A. Henderson. 2000. Ice-core paleoclimate records in tropical South America since the Last Glacial Maximum. *Journal of Quaternary Science* 15: 377-394.

Van der Hammen, T. 1992. *Historia ecológica y vegetación.* Bogotá: FEN, Corporación colombiana para la Amazonia. 411 pp.

Villalba, R., B. H. Luckman, J. Boninsegna, R. D. D’Arrigo, A. Lara, J. Villanueva-Diaz, M. Masiokas, J. Argollo, C. Soliz, C. LeQuesne, D. W. Stahle, F. Roig, J.-C. Aravena, M. K. Hughes, G. Wiles, G. Jacoby, P. Hartsough, R. J. S. Wilson, E. Watson, E. R. Cook, J. Cerano-Paredes, M. Therrell, M. Cleaveland, M. S. Morales, N. E. Graham, J. Moya, J. Pacajes, G. Massacchesi, F. Biondi, R. Urrutia, and G. Martinez Pastur. 2011. Dendroclimatology from regional to continental scales: understanding regional processes to reconstruct large-scale climatic variations across the western Americas. Pp. 175-227 in *Dendroclimatology: progress and prospects*, edited by M. K. Hughes, T. W. Swetnam, and H. F. Diaz. Dordrecht: Springer.

Vimeux, F., P. Ginot, M. Schwikowski, M. Vuille, G. Hoffmann, L. G. Thompson, and U. Schotterer. 2009. Climate variability during the last 1000 years inferred from Andean ice cores: a review of methodology and recent results. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281:229-241.

6

Synthesis of the Climate of the Tropical Andes

Rodney Martínez, Daniel Ruiz, Marcos Andrade, Luis Blacutt, Daniel Pabón, Ena Jaimes, Gloria León, Marcos Villacís, Juan Quintana, Edgard Montealegre, and Christian Euscátegui

The atmospheric systems of the tropical Andes (between 25ºS and 10ºN) are affected by orography (see Josse et al., Chapter 10, this volume), the main regional circulation systems, and by oceanic currents. The main factors that influence the Andean climate are the presence of the Amazon forest to the east, the displacement of the Inter-Tropical Convergence Zone (ITCZ), and the presence of the trade winds to the north. At high elevations, the subtropical jet stream and the permanent high pressure system of the South Pacific and South Atlantic are important. The topography of the tropical Andean range itself with its two main branches, the Cordillera Oriental and the Cordillera Occidental also modulate the formation of precipitation systems and temperature variations.

This chapter provides an overview of our current understanding of the climatology of the tropical Andes avoiding complex details on the physical mechanisms behind climate processes. For the purpose of this chapter, the tropical Andes have been separated into two regions: the northern (Colombia and Ecuador) and southern (Peru and Bolivia). For both we will describe decadal, interannual, seasonal and diurnal variabilities. The objective is to provide a comprehensive and understandable synthesis of the main factors influencing climate variability and change and also to present observed climate trends in the region. We hope this synthesis will provide informative context of the present and future role of a changing climate in the complex dynamics of biodiversity distribution, altitudinal gradients, range shifts, and other ecological processes, examined in different chapters of this book.

Climate Variability of the Northern Tropical Andes (Colombia-Ecuador)

The northern Andes are characterized by a very moist climate, low thermal seasonality, and marked diurnal temperature variations. Temperature variability is driven by elevational gradients and air humidity, both determined by local conditions (Buytaert et al. 2006). The near-surface environmental lapse rates (i.e., the decrease in air temperature with elevation) produce strong ecological elevational zonation. These lapse rates show significant differences between the eastern and western slopes of the Andes and between different flanks of inter-Andean valleys (Chaves and Jaramillo 1998; Ruiz et al. 2009). Frost and snow occur regularly at elevations above 4,000 m. Precipitation patterns are influenced by the tropical Atlantic Ocean, the Pacific Ocean and the Amazon basin. Although rainfall is highly variable, pluviometric optimum maxima are observed at elevations around 1,800-2,400 m (Oster 1979; Velez et al. 2000), the elevational belt that harbors dense cloud forests.

Decadal Variability

Climate variability at decadal or interdecadal timescales is mostly represented by the Pacific Decadal Oscillation (PDO). The PDO is a pattern exhibited by the surface waters of the Pacific Ocean north of 20°N. The PDO shifts between warm and cool phases at inter-decadal timescales (Mantua et al. 1997; Hare et al. 1999). During a warm (or positive) phase, the west Pacific cools and part of the eastern Pacific warms; during a negative phase, the opposite pattern takes place. Despite this signal being most evident in the North Pacific, there is increasing evidence of its influence in South America (Mantua and Hare 2002).

In particular, the observed climatic shift that occurred in the Pacific in 1976-77 (phase change in the PDO from negative to positive) was associated with significant changes in the El Niño-Southern Oscillation (ENSO, discussed below) (Trenberth and Stepaniak 2001) and with changes in ENSO teleconnections and links to precipitation and surface temperatures over South America (Trenberth 1991; Trenberth and Hurrell 1994; Mantua and Hare 2002; Minobe and Nakanowatari 2002; Marengo 2004). The causes of PDO and the dynamic linkage with ENSO remain unclear (Newman et al. 2003; Schneider and Cornuelle 2005). According to Garreaud et al. (2008), PDO-related anomalies of precipitation and temperature over South America are spatially similar to ENSO, but their amplitude is about half of that of their ENSO counterparts. The overlapping of different phases of ENSO and PDO could partially explain recent changes in temporal and spatial ENSO effects over the Andes.

The PDO has apparently been in its cold phase since the last strong El Niño in 1997-1998. Since 1999, in particular, there has been an increased frequency of occurrence of La Niña events in the Pacific basin, accompanied by few weak to moderate El Niño events. The typical time and spatial patterns of development of El Niño/La Niña events have been different from past ENSO impacts in the Andean region experienced in the 1990s. This suggests slight shifts in the start and declining phases (Garreaud et al. 2008).

Interannual Variability

The main mode of interannual variability over the northern Andes is ENSO. The Equatorial Pacific has a region of relatively cool waters in the eastern Pacific referred to as the “cold tongue” and a wide area of very warm sea surface temperatures (SST) in the west referred to as the “warm pool” (Rasmusson and Carpentier 1982; Philander 1990; Larkin and Harrison 2001). In general terms, an El Niño event is characterized by a warming of the cold tongue, an eastward shift of the warm pool, a weakening of the equatorial easterly winds and a flattening of the zonal thermocline slope (pronounced vertical variation of sea temperatures) (Rasmusson and Carpentier 1982; Neelin et al. 1998). La Niña is the opposite of El Niño and is associated with stronger zonal SST differences, stronger easterly winds, and a steeper thermocline (Larkin and Harrison 2001; Philander 1990).

El Niño and La Niña events are the major source of interannual variability in much of tropical South America (Ropelewsky and Halpert 1987; Aceituno 1988; Kiladis and Diaz 1989; Marengo 1992; Dettinger and Diaz 2000). Owing to its regional importance, ENSO has been widely examined. The hydro-climatic effects of ENSO in the region have been investigated by Hastenrath (1976, 1990), Waylen and Caviedes (1986), Hastenrath et al. (1987), Ropelewski and Halpert (1987), Aceituno (1988, 1989), and Kiladis and Diaz (1989), among others. The effects of ENSO over Colombia have been discussed by Poveda and Mesa (1997), Gutiérrez and Dracup (2001), Poveda et al. (2001, 2003, 2006), Waylen and Poveda (2002), Poveda (2004), and Tootle et al. (2008). The effects of ENSO over Ecuador have been described by Vuille (2000) and Villacís et al. (2003). Physical mechanisms of ENSO-related hydro-climatic anomalies over the region are reviewed in Vuille et al. (2000a), Garreaud et al. (2003), and Poveda et al. (2006).

Both the El Niño and La Niña phases of ENSO influence the temporal and spatial distributions of precipitation in much of South America. In the northern tropical Andes, El Niño events are associated with below-normal precipitation, whereas the opposite holds true for La Niña events over the Colombian Andes (Poveda et al. 2001). A bit further south, the relationship between precipitation and the ENSO phenomenon over the Ecuadorian Andes is not uniform. However, it has been suggested that more variability occurs during the rainy period October-May compared to the dry period June-August (Villacís et al. 2003).

Seasonal Variability

One of the main factors driving seasonal variability across the northern tropical Andes is the ITCZ. This low pressure band encircling the Earth near the equator is where the trade winds from both hemispheres converge. Its activity generates tropical perturbations, dense cloudiness, and rainfall of variable intensity. The ITCZ is not stationary and migrates latitudinally during the year (Mitchell and Wallace 1992). The Earth's axial tilt determines the level of solar radiation reaching different latitudes and is the main driver for the displacement of the ITCZ from south to north in the first half of the calendar year and in the opposite direction in the second half. Over tropical South America the average width of the ITZC fluctuates between 300 and 500 km. While the mean position of the ITCZ axis is around 5ºN, the annual range of displacement is from 6ºS to 12ºN (Mitchell and Wallace 1992).

The ITCZ passes through the central and northern Andes twice annually, determining a bimodal annual cycle of precipitation. The Colombian Andes experience marked rainy seasons (April-May and September-November) and relatively dry seasons (December-February and June-August) (Eslava 1993; Mejía et al. 1999; León et al. 2000; Poveda et al. 2007). The March-May and September-November quarters are thus characterized by considerable cloud cover (about 80-85% during these periods), whereas the December-February and June-August periods tend to have less cloud cover, with values as low as 75% in the month of January (Ruiz et al. 2009). Between December and March, the ITCZ migrates southward causing rainfall over Ecuador and reaching the northern coast of Peru. During intense ENSO events, the ITCZ can extend anomalously as far as 10°S, bringing heavy rains to the coastal desert of northern Peru (Horel and Cornejo-Garrido 1986; Goldberg et al. 1988).

Diurnal Cycle

In the northern tropical Andes the diurnal behavior of the precipitation systems can be classified into two different regimes: those systems found in the western and northeastern regions, and those systems found in the southeastern region. The daily cycle for the first group shows a single rainfall peak around midday. In contrast, the daily cycle for the systems formed in the southeastern region has typically two maxima of convective activity, one at midnight and the other around nine in the morning (Poveda et al. 2005).

These rainfall peaks are driven by local atmospheric instabilities, which in turn are affected by local circulation patterns. On a diurnal timescale, conditions of atmospheric stability in high-elevation environments at the Andean region tend to be affected by the following factors: (a) cloud and fog formation in down-slope cloud forests; (b) moisture advection occurring during day-time uplifting thermodynamic processes; and (c) cooling and drying processes driven by nocturnal dynamics (Vernekar et al. 2003; Ruiz et al. 2009). Local differences in temperature and humidity between higher and lower levels control the diurnal dynamics and will likely continue to drive future climate conditions in Andean environments.

Climate Variability of the Southern Tropical Andes (Peru-Bolivia)

A comprehensive review of the climatology of the southern tropical Andes can be found in Garreaud et al. (2003). Roughly speaking, the climate in the southern tropical Andes is dryer than the one observed in Colombia and Ecuador. Precipitation systems in this region are mainly controlled by the availability and transport of water vapor from the Amazon basin, the behavior of the Pacific Ocean, and the presence of Lake Titicaca (Garreaud 2000a; Falvey and Garreaud 2005).

Decadal Variability

The main influence of decadal variability is seen in the modulation of ENSO over the Western Altiplano and is probably related to PDO (Vuille and Bradley 2003). More research is needed at this time scale in other zones of the Southern Andes.

Interannual Variability

ENSO variability over the Bolivia-Peru Altiplano is summarized in Garreaud et al. (2003). The relationship between ENSO and interannual rainfall variability is inconsistent over the Altiplano, with El Niño events often (but not always) associated with droughts and La Niña events with above normal precipitation. However, this relationship is not always evident; if the ENSO peak phase occurs early (or late) in relation to the austral summer wet season on the Altiplano, its influence will be limited (Vuille et al. 2000b). More research must be conducted to improve our limited understanding of the decadal and interannual climate variability in the southern tropical Andes. The great importance of ENSO events seems to be related to its influence on the Andean glaciers ice volume. The 1997-1998 El Niño was an example that produced a large loss of ice volume at the Chacaltaya glacier near the city of La Paz, Bolivia (Francou et al. 2003). The timing of the ENSO seems to be crucial to the possible effects on the Andean glaciers.

Seasonal Variability

The dominant climatic features of the southern tropical Andes on an intra-annual timescale are the prolonged wet and dry periods of the annual cycle. They are influenced by the fluctuations of two prominent circulation systems: the South Pacific Anticyclone (SPAC) and the Bolivian High (BH). The SPAC is a global-scale circulation with a dominant influence on the climate of western South America, mainly from May to October over coastal Ecuador, Peru, and the subtropical portions of Chile. It produces very stable conditions in the lower troposphere (subsidence and thermal inversion), surface divergence associated with relatively low SST, predominant southerly winds, and an extensive stratus cover. The strong static stability of the SPAC traps moisture in a relatively shallow layer near the surface, preventing convection and inhibiting the transport of moisture into the Andean interior from the west. The SPAC center is located approximately at 32ºS-88ºW in January and 24ºS-90ºW in July: it moves slightly poleward during the austral summer and equatorward during winter (Garreaud and Aceituno 2007). The occurrence of El Niño and La Niña phases has been linked to the intensity and position of the SPAC (Aceituno 1988).

In contrast, the BH is the dominant mechanism for seasonally introducing moisture that ultimately falls as precipitation in the Andean interior, and is thus of primary importance to regional ecology. The BH is an upper troposphere circulation that forms seasonally above the Bolivian Altiplano. It is generated through the combination of sensible heat from the Andean cordillera in Bolivia and latent heat release from intense convection over the western Amazon basin (Lenters and Cook 1997; Vuille 1999). It appears in December and remains significant until March. Normally it weakens by early April as the ITCZ displaces northward. At its annual peak of development around January, the center of the BH is located over the Bolivian Amazon (Lenters and Cook 1997). The combination of the BH and the subtropical jet stream favors the occurrence of thunderstorms over the Altiplano.

Rainfall across the southern tropical Andes takes place almost exclusively from October through April, with fifty percent or more of the annual precipitation occurring in only three of those months (Mota 2003). The available water vapor in the Amazon rain forest is frequently transported to the southern tropical Andes during austral summer (December-February), and this is the the most important source of water vapor for the altiplano (Garreaud and Aceituno 2001). The release of latent heat in the northern part of the Amazon changes the position of the BH (Lenters and Cook 1997; Lenters and Cook 1999), causing moisture advection over the Andes that, due to orography, contributes to the formation of clouds and precipitation (Vuille 1999; Vuille and Keimig 2004). Lake Titicaca generates enough humidity by evaporation to produce precipitating systems in its immediate vicinity throughout the year. However, the maximum activity here also occurs during austral summer due to the transport of humidity from the Amazon (Falvey and Garreaud 2005). Precipitation on the Altiplano is highly episodic rather than continuous. Multiday dry and wet periods alternate depending on water vapor availability, easterly winds and the position of the BH (Garreaud and Aceituno 2001).

Diurnal Cycles

Diurnal cycles are very complex and cannot be generalized for the southern tropical Andes. Their understanding would require a discussion of complex physical processes that vary spatially within the region which is beyond the scope of this chapter.

Cold Fronts and Polar Influence

During the cooler season (austral winter) in the Southern Hemisphere, surges of cold polar air originating at high latitudes over the southern South Pacific tend to be channeled northward to the eastern side of the Andes (called *surasos* in Bolivia and *friajes* in Peru). These move cold polar air masses to subtropical latitudes and sometimes into near-equatorial regions (5°S). In contrast, active cold fronts rarely reach subtropical latitudes (north of 30°S) west of the Andes (Garreaud 1999; Garreaud 2000b). Several times each winter, migratory jet-stream disturbances associated with cold fronts east of the Andes also bring anomalously cold and unseasonably moist conditions to the Altiplano region, causing mountain snowfalls and very low daytime temperatures.

Climate Trends over the Tropical Andes

Precipitation and Temperature

Historical trends in precipitation and temperature have been explored by, among others, Vuille et al. (2000b), Vuille et al. (2003), Pabón (2003, 2004), and Ruiz et al. (2009). Based on daily precipitation and temperature data from 24 meteorological stations operated by regional met services (IDEAM-Colombia, INAMHI, SENAMHI-Peru and SENAMHI-Bolivia) for the period 1964-2008, an estimation of indexes was performed using the RClimdex methodology (Wang et al. 2007; Wang 2008). All data were previously error-checked and, when necessary, homogenized. Statistical significance of calculated trends was over 80%, but not all reached 95%. The trend of annual precipitation during the observation period is shown in Figure 6.1a. In general, annual precipitation shows a decreasing trend with the exception of stations in the Western Cordillera of the Colombian Andes, in the southern Andes of Ecuador, and a few stations in the southern highlands of Peru. Estimated trends in annual maximum and minimum temperatures are shown in Figures 6.1b and 6.1c, respectively. Of all 24 stations only three indicated a decreasing trend in annual maximum temperature. In the case of annual minimum temperature, trends are also positive with the exception of two stations. These trends are in agreement with previous estimations reported in Vuille et al. (2000b) and Vuille et al. (2003). In this limited data set, annual precipitation is decreasing and annual maximum and minimum temperatures are increasing region-wide. It will be important to consider the variation of these variables over the past 45 years to find correlations with biological and other ecological parameters.

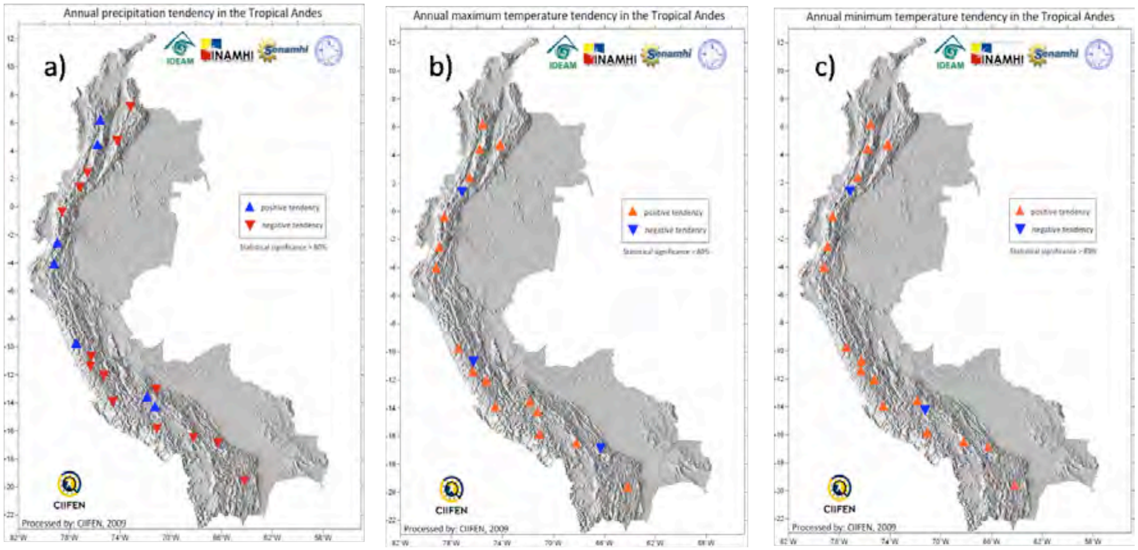

Figure 6.1. Historical trends in annual rainfall (a), annual maximum temperatures (b), and annual minimum temperatures (c). Stations with statistical significance >80%. Data from National Meteorological Services from Bolivia, Colombia, Ecuador, and Peru, processed by CIIFEN.

Cloud Cover and Humidity

Analyses of outgoing long-wave radiation data to determine cloud cover and estimate historical cloud cover trends have been conducted by Chu et al. (1994), Chen and Dudhia (2001), Chen et al. (2002), Wielicki et al. (2002), and Vuille et al. (2003). Their results suggest that a positive cloud cover trend exists in the northern tropical Andes, especially during the December-February period. In contrast, over the southern tropical Andes the trend has been negative.

Detailed analysis of near surface and tropospheric humidity has been done by Gutzler (1992) and Curtis and Hastenrath (1999a, b), whereas Vuille and Keimig (2004) examined interannual variability in cloudiness across the southern tropical Andes and the Altiplano. A specific trend analysis was made by Vuille et al. (2003) based on CRU05 data sets (New et al. 2000). Their results suggest a positive trend of relative humidity in northern Ecuador and southern Colombia, whereas in southern Peru and western Bolivia the increase is more moderate.

Final Remarks and Future Research Lines

Much of the previously published research describes the complexity of the Andean climate. However, remarkable progress has recently been made in understanding the main physical mechanisms which interact over the tropical Andes. At present, there is improved understanding of the role that ENSO and the PDO play in the northern tropical Andes, but more effort is needed to improve the understanding of decadal and interannual variabilities in the southern Andes. Despite the difficulties in accessing high quality data and the scattered and often lacking weather stations, especially in high-Andean regions, valuable climate trends obtained in different ways and with different data sets and methodologies are now available. Most agree with a rapid and sustained increasing trend of the temperature (minimum and maximum) over the Andes with a faster rate the last two decades. In contrast, precipitation trends are not conclusive and exhibit differences between the northern and southern tropical Andes. However, in the case of southern Peru and western Bolivia it seems to be a consistent trend to slightly drier conditions (Vuille et al. 2003).

There is increasing evidence of changes in hydrological regimes in the tropical Andes and an apparent upward shift in the orographic cloud band (Barry and Seimon 2000). However, considerable effort needs to be done to study the vertical processes on the slopes of the Andes, and analyze important data in stations in the highlands. The importance of this vertical cloud shift is relevant for the cloud forest and subsequent impacts in the páramo ecosystem and their associated environmental services (see Ruiz et al., Chapter 12, this volume).

Even though there are significant gaps in the understanding of Andean climate, some priorities must be established in order to improve our knowledge of Andean ecosystems under a changing climate. Physical processes involved in ocean-atmosphere-land interactions, occurring at regional-, subregional- and meso-scales, should be better understood. Also, our knowledge of the inter-basins connection and its role on the regional climate should be improved. The understanding of the interaction of decadal and interannual variability within a globally warming climate must be enhanced with a regional focus on the Andes. In other timescales, more effort must be done to improve the comprehension of deep convection processes in the Andean region in order to enhance our current capacities to model and predict the future climate with higher resolution.

Despite the sparse hydro-meteorological network in the Andean region, it is important to consider the significant amounts of data collected that are not available for analysis because they are still in analog format and/or have not been quality controlled. These data, along with other sources of information such as remote sensing or palaeoclimate records, could help reconstruct past Andean climates and better understand the complex climate variability of the region.

Acknowledgments

The authors express their thanks to Anton Seimon for his valuable guidance and many suggestions to improve this chapter; to Affonso Mascarenhas and an anonymous referee for their review and suggestions. We are grateful to IDEAM, INAMHI, SENAMHI-Peru, and SENAMHI-Bolivia for providing climate change indexes for each country.

Literature Cited

Aceituno, P. 1988. On the functioning of the Southern Oscillation in the South American sector. Part I: surface climate. *Monthly Weather Review* 116:505-524.

Aceituno, P. 1989. On the functioning of the Southern Oscillation in the South American sector. Part II: upper-air circulation. *Journal of Climate* 2:341-355.

Barry, R., and A. Seimon. 2000. Research for mountain area development: climatic fluctuations in the mountains of the Americas and their significance. *Ambio* 29:364-370.

Buytaert, W., R. Celleri, B. De Bievre, F. Cisneros, G. Wyseure, J. Deckers, and R. Hofstede. 2006. Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews* 79:53-72.

Chaves C., B., and A. Jaramillo R. 1998. Regionalización de la temperatura del aire en Colombia. *CENICAFE* 49:224-230.

Chen, F., and J. Dudhia. 2001. Coupling an advanced land surface-hydrology model with the Penn State-NCAR MM5 modeling system. Part I: model implementation and sensitivity. *Monthly Weather Review* 129:569-585.

Chen, J., B. E. Carlson, and A. D. Del Genio. 2002. Evidence for strengthening of the tropical general circulation in the 1990s. *Science* 295:838-841.

Chu, P. S., Z. P. Yu, and S. Hastenrath. 1994. Detecting climate change concurrent with deforestation in the Amazon basin: which way has it gone? *Bulletin of the American Meteorological Society* 75:579-583.

Curtis, S., and S. Hastenrath. 1999a. Trends of upper-air circulation and water vapour over equatorial South America and adjacent oceans. *International Journal of Climatology* 19:863-876.

Curtis, S., and S. Hastenrath. 1999b. Long-term trends and forcing mechanisms of circulation and climate in the Equatorial Pacific. *Journal of Climate* 12:1134-1144.

Dettinger, M. D., and H. F. Diaz. 2000. Global characteristics of stream flow seasonality and variability. *Journal of Hydrometeorology* 1:289-310.

Eslava, J. 1993. Algunas particularidades de la región del Pacífico colombiano. *Atmósfera* 17:45-63.

Falvey, M., and R. D. Garreaud 2005. Moisture variability over the South American Altiplano during the South American Low Level Jet Experiment (SALLJEX) observing season. *Journal of Geophysical Research* 110(D2):2105.

Francou, B., M. Vuille, P. Wagnon, J. Mendoza, and J.-E. Sicart. 2003. Tropical climate change recorded by a glacier in the central Andes during the last decades of the twentieth century: Chacaltaya, Bolivia, 16°S. *Journal of Geophysical Research* 108(D5):4154.

Garreaud, R. D. 1999. Cold air incursions over subtropical and tropical South America: a numerical case study. *Monthly Weather Review* 127:2823-2853.

Garreaud, R. D. 2000a. Intraseasonal variability of moisture and rainfall over the South American Altiplano. *Monthly Weather Review* 128:3337-3346.

Garreaud, R. D. 2000b. Cold air incursions over subtropical South America: mean structure and dynamics. *Monthly Weather Review* 128:2544-2559

Garreaud, R. D., and P. Aceituno. 2001. Interannual rainfall variability over the South American Altiplano. *Journal of Climate* 14:2779-2789.

Garreaud, R. D., M. Vuille, and A. C. Clement. 2003. The climate of the Altiplano: observed current conditions and mechanisms of past changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 194:5-22.

Garreaud, R. D., and P. Aceituno. 2007. Atmospheric circulation over South America: mean features and variability. Pp. 45-59 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Garreaud, R., M. Vuille, R. Compagnucci and J. Marengo. 2008. Present-day South American climate. *PALAEO3 Special Issue (LOTRED South America)* 281:180-195.

Goldberg, R., F. Tisnado, and R. Scofield. 1988. Characteristics of extreme rainfall events in northwestern Peru during the 1982-1983 El Niño period. *Journal of Geophysical Research* 92:14225-14241.

Gutierrez, F., and J. A. Dracup. 2001. An analysis of the feasibility of long-range streamflow forecasting for Colombia using El Niño-Southern Oscillation indicators. *Journal of Hydrology* 246:181-196.

Gutzler, D. S. 1992. Climatic variability of temperature and humidity over the tropical western Pacific. *Geophysical Research Letters* 19:1595-1598.

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaskan and west coast salmon. *Fisheries* 24:6-14.

Hastenrath, S. 1976. Variations in low-latitude circulations and extreme climatic events in the tropical Americas. *Journal of Atmospheric Science* 33:202-215.

Hastenrath, S., L. C. de Castro, and P. Aceituno. 1987. The Southern Oscillation in the tropical Atlantic sector. *Contributions to Atmospheric Physics* 60:447-464.

Hastenrath, S. 1990. Diagnostic and prediction of anomalous river discharges in northern South America. *Journal of Climate* 3:1080-1096.

Horel, J. D., and A. Cornejo-Garrido. 1986. Convection along the coast of northern Peru 1983: spatial and temporal variations of clouds and rainfall. *Monthly Weather Review* 114:2091-2105.

Kiladis, G., and H. F. Diaz. 1989. Global climatic anomalies associated with extremes in the Southern Oscillation. *Journal of Climate* 2:1069-1090.

Larkin, N. K., and D. E. Harrison. 2001. ENSO warm (El Niño) and cold (La Niña) event life cycles: ocean surface anomaly patterns, their symmetries, asymmetries, and implications. *Journal of Climate* 15:1118-1140.

Lenters, J. D., and K. H. Cook. 1997. On the origin of the Bolivian High and related circulation features of the South American climate. *Journal of Atmospheric Science* 54:656-678.

Lenters, J. D., and K. H. Cook. 1999. Summertime precipitation variability over South America: role of the large-scale circulation. *Monthly Weather Review* 127:409-431.

León, G. E., J. A. Zea, and J. A. Eslava. 2000. Circulación general del trópico y la Zona de Confluencia Intertropical en Colombia. *Meteorología Colombiana* 1:31-38.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069-1079.

Mantua, N. J., and S. J. Hare. 2002. The Pacific Decadal Oscillation. *Journal of Oceanography* 58:35-44.

Marengo, J. 1992. Interannual variability of surface climate in the Amazon basin. *International Journal of Climatology* 12:853-863.

Marengo, J. 2004. Interdecadal variability and trends of rainfall across the Amazon basin. *Theoretical and Applied Climatology* 78:79-96.

Mejía, F., O. Mesa, G. Poveda, J. Vélez, C. Hoyos, R. Mantilla, J. Barco, A. Cuartas, M. Montoya, and B. Botero. 1999. Distribución espacial y ciclos anual y semianual de la precipitación en Colombia. *DYNA* 127:7-26

Minobe, S., and T. Nakanowatari. 2002. Global structure of bidecadal precipitation variability in boreal winter. *Geophysical Research Letters* 29:1396-1399.

Mitchell, T. P., and J. M. Wallace. 1992. The annual cycle in the equatorial convection and sea surface temperature. *Journal of Climate* 5:1140-1156

Mota, G. 2003. *Characteristics of rainfall and precipitation features defined by the Tropical Rainfall Measuring Mission*. PhD thesis. University of Utah.

Neelin, J. D., D. S. Battisti, A. C. Hirst, F.-F. Jin, Y. Wakata, T. Yamagata, and S. E. Zebiak. 1998. ENSO theory. *Journal of Geophysical Research* 103:14261-14290.

New, M., M. Hulme, and P. D. Jones. 2000. Representing twentieth century space-time climate variability. Part 2: development of 1901-96 monthly grids of terrestrial surface climate. *Journal of Climate* 13:2217-2238.

Newman, M., G. P. Compo, and M. A. Alexander. 2003. ENSO-forced variability of the Pacific Decadal Oscillation. *Journal of Climate* 16:3853-3857.

Oster, R. 1979. Las precipitaciones en Colombia. *Revista Colombia Geográfica*, Vol. VI(2).

Pabón, J. D. 2003. El cambio climático global y su manifestación en Colombia. *Cuadernos de Geografía* 12(1-2): 111-119.

Pabón, J. D. 2004. El cambio climático y sus manifestaciones en Colombia. *Innovación y Ciencia* 11(3-4):68-73.

Philander, S. G. H. 1990. *El Niño, La Niña and the Southern Oscillation*. San Diego: Academic Press.

Poveda, G. 2004. La hidroclimatología de Colombia: una síntesis desde la escala inter-decadal hasta la escala diurna. *Revista de la Academia Colombiana de Ciencias* 28(107):201-222.

Poveda G., O. J. Mesa, L. F. Salazar, P. A. Arias, H. A. Moreno, S. C. Vieira, P. A. Agudelo, V. G. Toro, and J. F. Alvarez. 2005. The diurnal cycle of precipitation in the tropical Andes of Colombia. *Monthly Weather Review* 133:228-240.

Poveda, G., and O. J. Mesa. 1997. Feedbacks between hydrological processes in tropical South America and large-scale oceanic and atmospheric phenomena. *Journal of Climate* 10:2690-2702.

Poveda, G., A. Jaramillo, M. M. Gil, N. Quiceno, and R. Mantilla. 2001. Seasonality in ENSO related precipitation, river discharges, soil moisture, and vegetation index (NDVI) in Colombia. *Water Resources Research* 37:2169-2178.

Poveda, G., O. J. Mesa, and P. R. Waylen. 2003. Non-linear forecasting of river flows in Colombia based upon ENSO and its associated economic value for hydropower generation. Pp. 351-371 in *Climate and water: transboundary challenges in the Americas*, edited by H. Diaz and B. Morehouse. Dordrecht: Kluwer Academic Publishers.

Poveda, G., P. R. Waylen, and R. Pulwarty. 2006. Annual and inter-annual variability of the present climate in northern South America and southern Mesoamerica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 234:3-27.

Poveda, G., J. Velez, O. Mesa, A. Cuartas, J. Barco, R. Mantilla, J. Mejia, C. Hoyos, J. Ramirez, L. Ceballos, M. Zuluaga, P. Arias, B. Botero, M. Montoya, J. Giraldo, and D. Quevedo.

2007. Linking long-term water balances and statistical scaling to estimate river flows along the drainage network of Colombia. *Journal of Hydrologic Engeneering* 12:4-13.

Rassmuson, E. M., and T. C. Carpentier. 1982. Variations in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Niño. *Monthly Weather Review* 110:354-384.

Ropelewski, C., and M. Halpert. 1987. Global and regional scale precipitation patterns associated with the Southern Oscillation. *International Journal of Climatology* 11:63-76.

Ruiz, D., M. P. Arroyave, A. M. Molina, J. F. Barros, M. E. Gutierrez, and P. A. Zapata. 2009. *Signals of climate variability/change in surface water supply of high-mountain watersheds - case study: Claro River high mountain basin, Los Nevados Natural Park, Andean Central Mountain Range, Colombia*. World Bank Group. 207 pp.

Schneider, N., and B. D. Cornuelle. 2005. The forcing of the Pacific Decadal Oscillation. *Journal of Climate* 18:4355-4373.

Tootle, G. A., T. C. Piechota, and F. Gutierrez. 2008. The relationships between Pacific and Atlantic Ocean sea surface temperatures and Colombian streamflow variability. *Journal of Hydrology* 349:268-276.

Trenberth, K. E. 1991. General characteristics of El Niño-Southern Oscillation. Pp. 13-42 in *Teleconnections linking worldwide climate anomalies*, edited by R. M. Glantz, R. Katz, and N. Nicholls. Cambridge: Cambridge University Press.

Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere–ocean variations in the Pacific. *Climate Dynamics* 9:303-319.

Trenberth, K. E., and D. P. Stepaniak. 2001. Indices of El Niño evolution. *Journal of Climate* 14:1697-1701.

Vélez, J. I., G. Poveda, and O. J. Mesa. 2000. Balances hidrológicos de Colombia. *Serie del Posgrado en Recursos Hidráulicos* No. 16.

Vernekar, A. D., B. P. Kirtman, and M. J. Fennessy. 2003. Low-level jets and their effects on the South American summer climate as simulated by the NCEP Eta model. *Journal of Climate* 16:297-311.

Villacís, M., J. Taupin, E. Heredia, E. Palacios, and J. Palacios. 2003. Viariabilité climatique dans la sierra équatorienne en relation avec le phénoméne ENSO. Pp. 202-208 in *Hydrology of the Mediterranean and semi-arid regions*. *IAHS Publication 278*, edited by E. Servat, W. Najem, C. Leduc, and A. Shakeel. Wallingford, Oxfordshire: IAHS Press. 498 pp.

Vuille, M. 2000. Atmospheric circulation over the Bolivian Altiplano during dry and wet periods and extreme phases of the Southern Oscillation. *International Journal of Climatology* 19:1579-1600.

Vuille, M., R. S. Bradley, and F. Keimig. 2000a. Climate variability in the Andes of Ecuador and its relation to tropical Pacific and Atlantic sea surface temperature anomalies. *Journal of Climate* 13:2520-2535.

Vuille, M., R. S. Bradley, and F. Keimig. 2000b. Interannual climate variability in the central Andes and its relation to tropical Pacific and Atlantic forcing. *Journal of Geophysical Research* 105:12447-12460.

Vuille, M., R. Bradley, M. Werner, F. Keimig. 2003. 20th century climate change in the tropical Andes: observations and model results. *Climatic Change* 59:75-99.

Vuille, M., and F. Keimig. 2004. Interannual variability of summertime convective cloudiness and precipitation in the central Andes derived from ISCCP-B3 data. *Journal of Climate* 17:3334-3348.

Waylen, P. R., and C. Caviedes. 1986. El Niño and annual floods on the north Peruvian littoral. *Journal of Hydrology* 89:141-156.

Waylen, P. R., and G. Poveda. 2002. El Niño-Southern Oscillation and aspects of western South America hydro-climatology. *Hydrological Processes* 16:1247-1260.

Webster, P. J. 1995. The annual cycle and the predictability of the tropical coupled ocean-atmosphere system. *Meteorology and Atmospheric Physics* 56:33-55.

Wang, W., X. Chen, P. Shi, P. H. A. J. M. van Gelder, and G. Corzo. 2007. Extreme precipitation and extreme streamflow in the Dongjiang River Basin in southern China. *Hydrology and Earth Systems Sciences Discussions* 4:2323-2360.

Wang, W., X. Chen, P. Shi, and P. H. A. J. M. van Gelder. 2008. Detecting changes in extreme precipitation and extreme streamflow in the Dongjiang River Basin in southern China. *Hydrology and Earth Systems Sciences* 12:207-221.

Wielicki, B., T. Wong, R. Allan, A. Slingo, J. Kiehl, B. Soden, C. Gordon, J. Miller, S. Yang, D. Randall, F. Robertson, J. Susskind, and H. Jacobowitz. 2002. Evidence for large decadal variability in the tropical mean radiative energy budget. *Science* 295:841-844.

7

Climate Change: Evidence and Future Scenarios for the Andean Region

José A. Marengo, José D. Pabón, Amelia Díaz, Gabriela Rosas, Grinia Ávalos, Edgard Montealegre, Marcos Villacis, Silvina Solman, and Maisa Rojas

Climate change is one of the most relevant topics on the current international environmental agenda. It cuts across economies, trade, and political decisions in our globalized world. In South America, the countries of the Andean region will be the ones most affected by the consequences of climate change. This chapter is intended to provide an integrated overview of climate change in the Andean region based on observational studies and climate projections currently being discussed in the international and national literature on the tropical Andean countries.

Observational Evidence of Long-Term Climatic Variability and Climate Change in the Andes

Mean annual temperature in the countries of the northern Andes (Venezuela, Colombia, Ecuador, Peru) has increased by about +0.8 °C during the 20th century. Vuille and Bradley (2000) documented the tendencies of air temperature anomalies from 1939 to 1998 for the tropical Andes from 1°N to 23°S in relation to the 1961-1990 mean, and they found a positive tendency of +0.11 °C per decade for this period. This tendency tripled over the past 25 years of the 20th century (+0.34 °C per decade), although some variability is associated with the occurrence of the El Niño Southern Oscillation (ENSO). The magnitude of this warming tendency tends to be greater for climate stations at higher elevations.

Table 7.1 summarizes the tendencies observed in Andean climate and hydrometeorology in recent studies, indicating time periods, variables, and magnitude of change. The use of different time periods and analysis techniques by different studies hampers an integrated evaluation of the results. However, leaving aside problems related to differences in time-series length, it can be observed that air temperatures tend to increase. For precipitation it is difficult to obtain information that indicates any systematic tendency; nonetheless, both considerable interannual variability associated with ENSO and interdecadal variability can be observed. These tendencies are consistent with those detected by the IPCC Working Group I AR4 Report (Trenberth et al. 2007).

In the Peruvian Andes total annual and seasonal precipitation show regionally contrasting tendencies, and local factors condition differential behaviors with or without dependence on interannual variations (SENAMHI 2009a). Thus, observed tendencies show systematic increases in precipitation on the western flank and reductions in parts of the southern and central portion of the eastern flank of the Peruvian Andes (SENAMHI 2009a,c, SENAMHI 2007a,b). Evaluations of precipitation extremes have established the central Peruvian Andes as an increasingly homogeneous area with a clear tendency of reduced extreme rainfall events, whereas an increase in the number of days with extreme precipitation has been detected in the northern Peruvian Andes. A reduction in the number of cold days has primarily been observed in the south, whereas the number of warm days has increased throughout the Peruvian Andes. In the central portion of the western flank of the Peruvian Andes (Rio Santa watershed) a high-elevation warming trend of up to 0.07 °C per year has been detected, which is more pronounced than that at mid- and lower elevations (SENAMHI 2009c, SENAMHI 2005b).

On the western flank of the subtropical Andes in Chile and on the opposite flank in Argentina, lower mid-elevations (2000 m) experienced a significant warming trend of 0.28 °C and 0.23 °C, respectively, from 1979 to 2006. The northern Patagonian Andes between 37°S and 43°S have also experienced a significant warming trend of approximately 0.056 °C per decade from 1912 to 1990 on both the western and eastern flank. Throughout the subtropical Andean region in Argentina between 22°S and 28°S mean annual temperature increased by 0.62 °C during the 20th century. In the same region, based on analyses of cumulative annual precipitation series, significantly negative tendencies of -4.67% per decade have been observed, with the greatest decrease occurring during austral winter (Table 7.1).

The scarcity of continuous climatic records in large areas of the tropical Andes does not allow for conclusive evidence on mean tendencies and particularly on extremes.

Glacier Retreat

Recent studies have shown that most glaciers from Colombia to Chile and Argentina (to 25°S) have experienced drastic reductions in volume with an increased pace since the 1970s (Mark and Seltzer 2003, Leiva 2006, Vuille et al. 2008). In the central Andes glacier retreat is an indirect consequence of rising temperatures. These cause an increase in rain (rather than snow) on the lower sections of glaciers, thereby exposing the ice, increasing the glacier's capacity for absorbing solar energy and increasing melting of the ice (Favier et al. 2004). Between 35°S and 47°S in Chile, where a significant reduction in precipitation has been accompanied by increasing temperatures during the past 50 years (Carrasco et al. 2008), increased river discharge suggests that glaciers are melting. Table 7.2 summarizes results of studies on observed tendencies of glacial retreat and its impacts detected to date in some Andean countries.

Table 7.1. Summary of climatic tendencies observed in the Andean region.

Region	Period	Variable	Tendency	Reference
Cordillera Oriental-Colombia	1961-1990	Temperature	+0.1 °C to +0.2 °C	Pabon (2003)
Cordillera Occidental-Colombia	1961-1990	Precipitation	+4 %/30 years	Pabón (2003)
Cauca y Magdalena valleys-Colombia	1961-1909	Precipitation	-4%/30 years	Pabón (2003)
Inter-Andean valley-Ecuador	1905-2005	Temperature	+0.12 °C	Villacis (2008)
Inter-Andean valley-Ecuador	1980-2005	Temperature	+0.22 °C	Villacis (2008)
Inter-Andean valley-Ecuador	1891-1986	Precipitation	-10 mm/decade	Pourrut (1995)
Subtropical west Andes-Chile	1930-2000	Precipitation	-5 to -10% /decade	Quintana (2004)
Foothills-Chile	1979-2006	Temperature	+0.28 °C	Falvey and Garreaud (2009)
Eastern Andes-Chile	1979-2006	Temperature	+0.23 °C	Falvey and Garreaud (2009)
Patagonian Andes-Argentina	1912-1990	Temperature	+0.056°C/decade	Masiokas et al. (2008)
Patagonian Andes-Argentina	1912-1990	Temperature	+0.62°C/100 years	Masiokas et al. (2008)
Patagonian Andes-Argentina	1960-1990	Temperature	+0.4°C/decade	Villalba et al. (2003)
Subtropical Andes-Argentina	1950-1990	Precipitation	-12%/decade	Castañeda and Gonzalez (2008)
Subtropical Andes-Argentina	1912-1990	Precipitation	-4.67%/decade	Masiokas et al. (2008)
Piura watershed-northwestern Andes-Peru	1963-2003	Minimum temperature	+0.2 to 0.3°C/decade	SENAMHI (2005 a)
Piura watershed-northwestern Andes-Peru	1963-2003	Maximum temperature	+0.3 to 0.45°C/decade	SENAMHI (2005a)
Piura watershed-northwestern Andes-Peru	1963-2003	Precipitation	Summer, fall: +9 to 14 mm/year Winter: -0.5 mm/year Spring: +0.2 to 0.5 mm/year	SENAMHI (2005 a)
Santa watershed-central western Andes-Peru	1965-2006	Precipitation	Annual: 20-30% increase in the last 40 years	SENAMHI (2009 c)
Santa watershed-central western Andes-Peru	1965-2006	Minimum temperature	0.17ºC/decade in the upper part of the watershed	SENAMHI (2009 c)
Santa watershed-central western Andes-Peru	1965-2006	Maximum temperature	0.67ºC/decade in the upper part of the watershed	SENAMHI (2009 c)
Mantaro valley-central eastern Andes-Peru	1965-2006	Precipitation	Annual:-3 to -28 mm/year Summer: -4.5 to -7 mm/year Winter: -0.3 to -0.8 mm/year	SENAMHI (2007 a)
Mantaro valley-central eastern Andes-Peru	1965-2006	Maximum temperature	Annual: +0.03°C to +0.07°C/year Summer: +0.02 °C to +0.04/year Winter: +0.01 to +0.04 °C/year	SENAMHI (2007 a)
Mantaro valley-central eastern Andes-Peru	1965-2006	Minimum temperature	Annual: +0.01°C to +0.11°C/year Summer: +0.02 °C to +0.01/year Winter: -0.02 to +0.03 °C/year	SENAMHI (2007 a)
Arequipa-southern Andes-Peru	1964-2006	Maximum temperature	Annual: +0.06°C to +0.42°C/year Summer: -0.07 °C to +0.42/year Winter: +0.02 to +0.44 °C/year	Marengo et al. (2009)
Arequipa-southern Andes-Peru	1964-2006	Minimum temperature	Annual: +0.12°C to +0.57°C/year Summer: -0.07 °C to +0.56/year Winter: +0.26 to +0.5 °C/year	Marengo et al. (2009)

Arequipa-southern Andes-Peru	1964-2006	Precipitation	-2 to +1.5 mm/decade	Marengo et al. (2009)
Urubamba watershed-southeastern Andes-Peru	1965-2006	Precipitation	Annual:-0.7 a 8.5 mm/year (upper part of watershed) Annual 0.2 a -1.1 mm/year (lower part of watershed)	SENAMHI (2007 b)
Urubamba watershed-southeastern Andes-Peru	1965-2006	Maximum temperature	Annual: +0.01°C to +0.04°C/year	SENAMHI (2007 b)
Urubamba watershed-southeastern Andes-Peru	1965-2006	Minimum temperature	Annual: +0.02°C to +0.05°C/year	SENAMHI (2007 b)
Mayo watershed-northeastern Andes-Peru	1965-2006	Maximum temperature	Alto Mayo: -0.25°C/decade Bajo mayo:+0.43 °C/decade	SENAMHI (2009 b)
Mayo watershed-northeastern Andes-Peru	1965-2006	Temperature mínima	Alto Mayo: +0.48°C/decade Bajo Mayo: +0.22°C/decade	SENAMHI 2009 b)
Mayo watershed-northeastern Andes-Peru	1965-2006	Precipitation	Annual: -20 to +20% relative to the annual mean Summer : -10 to +40% relative to the trimester mean Winter : -10 to -40% relative to the trimester mean	SENAMHI (2009 b)

Table 7.2. Observed tendencies of Andean glacier retreat and detected impacts. This table is an updated version of table 13.3 of the IPCC AR4 GT2 report (Magrin et al. 2007).

Glacier/Period	**Tendencies/Impacts**
Peru[a, b] (1965-2002)	A 22% reduction in total glacier area; 12% reduction in supply of drinking water for the coastal region (where 60% of the population). The estimated lost water volume is about 7 billion m^3.
Peru[c] (1970-2002)	Up to 80% reduction in the extension of small glaciers; loss of 188 million m^3 in water reserves during the last 50 years.
Peru[d] (1998-2004)	In the Cordillera Blanca retreat of the Yanamarey glacier was 23% greater in 2001-2004 than in 1998-1999 and was responsible for a 58% increase in the mean annual discharge of the Rio Santa.
Peru[d] (1977-2004)	Melting of the Yanamarey glacier, retreating at a speed of 20 m/year (mean 1977-2003), four times faster than the 5 m/year observed between 1948 and 1977.
Peru[e] (1953-1997)	A 13% increase in the discharge of the Laguna Yanganuco in the Cordillera Blanca.
Peru[c] (1985-1996)	During the last 10 years the ice cap of the Pastoruri glacier was reduced by almost 40%.
Peru[f] (1950-2006)	Up to 50% reduction in the extension of the Coropuna glacier, generating irrigation problems in the Pampa de Majes.
Colombia[g] (1990-2000)	An 82% reduction in glacier area, an estimated retreat of 10-15 m/year corresponding to an approximately 70-80% reduction compared to 1850.
Ecuador[h] (1956-1998)	A 30% loss in glacier surface on the Cotopaxi volcano since 1956. Glacier area above 5000 m remained stable between 1956 and 1976. Subsequently an accelerated retreat was observed, with a small recovery in 2000, but without affecting the overall decreasing trend.
Bolivia[i] (1991-2002)	A 9.4% loss of the area covered by snow on the Zongo glacier, causing serious problems for agriculture, ecosystem sustainability, and causing socioeconomic impacts in the rural population.
Bolivia[i] (1940-2003)	A 47.4% loss of the area covered by snow on the Charquini glacier.
Bolivia[o] (1963-2006)	An analysis based on aerial photogrammetry of 21 glaciers in the Cordillera Real shows that on average glaciers have lost 43% of their volume between 1963 and 2006 (essentially between 1975 and 2006). Between 1975 and 2006 they lost 48% of their surface area.
Argentina[j,k] (1912-1990)	Numerous studies throughout the Patagonian Andes show a marked loss of glacier volume in the southern portion. Masiokas et al. (2008) documented strong retreat of six glaciers in the northern Patagonian Andes (between 39 and 43°S) based on an analysis of photographs. The concomitant increase in temperatures and reduction in precipitation observed during the 20th century could explain the glacial retreat.
Chile[l] (1952-2007)	Marked retreat of Patagonian glaciers during the 20th century. It is estimated that with each temperature increase of 1°C, the Andean snowline in Chile will rise by 120 elevational meters. The southern Patagonian Andes have suffered a marked loss in glacier volume.
Chile[m] (1950-2007)	Analysis of trends in flow volume in 13 Andean watersheds in Chile between 28 and 47°S that are partially fed by glaciers (between 1-23%) for the period 1950 to 2007. An increasing trend in flow volume was recorded at the end of austral summer, which the authors attributed to melting glaciers, but this trend was not significant.
Chile[n] (1970-2002)	Significant reductions in discharge of the Aconcagua and Blanco rivers in the central Chilean Andes.

[a]Chuquisengo Vásquez 2004; [b]Mark and Seltzer 2003; [c]CONAM 2001; [d]Mark et al. 2005; [e]Pouyaud et al. 2005; [f]Silverio 2004; [g]NC-Colombia 2001; [h]Jordan et al. 2005; [i]Francou et al. 2003; [j]Masiokas et al. 2008; [k]Coudrain et al. 2005; [l]Fuenzalida et al. 2006; [m]Pellicciotti et al. 2007; [n]Casassa et al. 2009; [o]Soruco et al. 2009.

Methods for Deriving Greenhouse Gas Emissions Scenarios and Future Climate Projections in the Andean Region

Revision of emissions scenarios considered in the production of future climate projections

To obtain future climate projections, climate models are run under different greenhouse gas emission scenarios and degrees of social and economic development consistent with those emissions. These socioeconomic and environmental scenarios used by the IPCC represent a framework for structured thinking about how the future could develop. All possible future climate projections depend on the range of emissions prospects. Scenarios of greenhouse gas emissions due to human activities depend on a variety of socioeconomic factors such as population and economic growth, technology, and energy use (Nakicenovic et al. 2000). By 2100, the concentration of atmospheric carbon dioxide will increase from the current (1999) 370 parts per million by volume (ppmv) to close to 550 ppmv under scenario B2 (low emissions) and to over 830 ppmv under scenario A2 (high emissions).

Use of Global and Regional Models for the Generation of Future Climate Projections in the Andean Countries

Global climate models are mathematic representations of nature, its components and their interactions, with such a degree of complexity that only powerful "supercomputers" are able to run these models. In these models the Earth's surface is divided into grid cells of equal size and shape, and the spatial resolution of the model decreases with increasing grid cell size and *vice versa*. Global models have low spatial resolution with grid cells of between 300 km and 500 km in latitudinal and longitudinal extension. This coarse resolution does not permit the detection of changes in certain areas such as coastlines and topographically complex mountain regions, nor of small-scale phenomena such as intense rainfalls. Thus, the high and steep Andean mountains are poorly covered by climate models with low spatial resolution, and linear interpolation is generally used to fill in missing regional detail. However, this procedure may introduce errors and uncertainties.

Therefore it is necessary to use climate models with greater spatial resolution (smaller grid cells of ca. 50x50 km) or regional climate models. The process of generating climate projections using regional models is called downscaling. In this method, which is frequently applied in the generation of future climate scenarios with high spatial resolution, regional climate models are run using boundary conditions of a global model. In the Andean region, future climate projections are generated with the HadRM3P regional model of the Hadley Centre for Climate Prediction and Research of the United Kingdom Met Office. This regional model has a spatial resolution of 50x50 km and it is run with the parameters of the global model HadAM3P until the end of the 21st century for scenarios A" and B2 of the IPCC. The HadRM3P model constitutes a component of the climate modeling system PRECIS (Providing Regional Climate Change Scenarios for Impact Studies).

Climate Change Scenarios: Projections for the Andean Countries

In recent years several Andean countries have developed climate change scenarios to evaluate vulnerability and impacts, either using the global models employed in the preparation of the IPCC reports, or regional models. In 2007 several South American countries analyzed climate projections for the period 2080-2099 relative to 1980-1999 based on the Japanese high-resolution (20x20 km) global atmospheric model JMA-MRI TL959L60 using the supercomputer Earth Simulator (Vergara et al. 2007). Table 7.3 provides a summary of these recent experiences from the Andean region with climate change projections until the middle or end of the 21st century, which will serve as a reference for projections of regional models to be presented and discussed subsequently.

Future climate projections for the Andean countries were generated using the only available regional simulation model HadRM3P for the periods 201-2040, 2041-2070, and 2071-2100 based on emissions scenarios A2 and B2 (Figures 7.1, 7.2; Table 7.4). These projections are coherent with those derived by the global and regional models from the IPCC´s Forth Assessment Report (Meehl et al. 2007, Christensen et al. 2007) for South America, and with the projections derived from the Japanese MRI-JMA T219L60 high resolution global model. The qualitative agreement between those models is considered as a "subjective" indicator of the confidence of the climate change projections described in Table 7.4.

Rainfall projections suggest an increase in mean precipitation for the tropical Andes region (5°N to 20°S) under the A2 scenario, with increases of up to 20-25% on the eastern and western flank of the Andes, whereas the western Andes of northern Peru may experience an increase of up to 70%, levels characteristic of El Niño years. The greatest uncertainties exist for the eastern flank and inter-Andean valleys between 5°S and 15°S. On the Altiplano, and in the subtropical Andes south to Patagonia, on the other hand, there is a tendency for a decrease in precipitation of up to 10%. The most pronounced pattern in temperature projections with a high level of confidence is a warming in near-surface air temperatures in the tropical Andes and south to Patagonia, which is greatest on the Altiplano, in the subtropical Andes, and on the eastern flank. Future warming also is predicted for inter-Andean valleys, but due to the steep topography of these regions HadRM3P projections differ in magnitude from those of the Japanese model and the IPCC's Fourth Assessment Report.

Vulnerability studies conducted in the region suggest that due to glacier retreat as a result of increasing temperatures, bottlenecks in water availability may come about in Colombia by 2015-2025, affecting water availability in the paramos (IDEAM 2000). In Peru 60% of the population will be affected by lower water availability (Chuquisengo Vásquez 2004), and the same applies to the generation of hydroelectric power. Among the affected rivers will be the Rio Mantaro, which currently generates 40% of Peruvian electricity and supplies 70% of the energy used in industry in Lima (Montoro Asencios 2004). For the Cordillera Blanca Pouyaud et al. (2005) suggested that based on a conservative 1°C warming estimate, river flow volumes will increase due to melting glaciers, with meltwater discharge reaching a peak between 2025 and 2050, followed by a progressive decrease until their disappearance between 2175 and 2250. Similar phenomena would be observed in Ecuador (Villacís 2008). In Ecuador, 7 of the country's 11 main watersheds would be affected by a reduction of river discharge by 2010 under a scenario of 2°C warming and a 15% reduction in precipitation (Cáceres in litt.). More recent studies, however, show that a slight increase may be observed in river discharge until 2030 as a result of a ca. 20% increase in precipitation according to the mean of the 21 global climatic models of the IPCC (Buytaert et al. 2009).

Andean ecosystems such as the paramos of the northern tropical Andes could be severely affected by the consequences of glacier retreat. These ecosystems hold a unique, endemic flora and provide resources and ecosystem services for nearby populations (Buytaert et al. 2006). Although our understanding of the processes involved in glacier retreat has improved greatly in recent years, the consequences for natural Andean ecosystems are still poorly known. In Ecuador, the loss of meltwater contribution to river discharge will not only affect watersheds with low (15%) glacier cover and the regulation capacity of rivers especially during the dry season (Villacís 2008), but it will also disrupt the water production capacity of paramos and existing aquifers, given that these are partly fed by glacial meltwater (Favier et al. 2008, Villacís et al. 2009).

Sources of Uncertainty and their Quantification

We are more confident about some aspects of climate change than others. For example, we have greater certainty about near-surface air temperature increases than we have about an increased occurrence of climatic extremes. The behavior of El Niño events is not well represented in climate models, and predicting how these events will be affected by global warming is therefore difficult. The uncertainties in climate projections are introduced by two factors. First, future greenhouse gas emissions are unknown, so that global warming scenarios have to project future changes in emissions based on the observed increase of emissions over the past 50 years, assuming certain behaviors of society. Second, representation of some physical processes and of interactions between components of the climatic system in climate models may be limited. This is the case, for example, for interactions between soil humidity and climate near the surface. Other sources of uncertainty also exist, such as those stemming from regionalization, specifically the type of regional model used and also the coupling of the regional and global model.

When comparing simulations of the regional HadRM3P model with those of the global models used by the IPCC's Fourth Assessment Report and those of the high-resolution Japanese model, it can be observed that these models predict drier future conditions for the southern Andes, especially during austral summer. However, this qualitative consensus could be related to systematic errors in the general circulation patterns established in current climatology, and such errors need to be corrected before building the climatology of the future. Due to the large uncertainties of climate projections, it is important to recognize the need for a greater number of regional simulations in order to reduce the inherent uncertainty associated with the formulation of models itself.

Despite the scarcity of studies on climate variability and change in the Andes, indisputable evidence exists of the severe impacts of climatic extremes that are happening or could happen in the region. Therefore, investment into climatological research is of crucial importance to evaluate with greater certainty the impacts of a changing climate on Andean and Amazonian ecosystems, biodiversity, agriculture, socioeconomic infrastructure, generation of hydroelectric power, tourism, and other sectors. The studies and climate projections presented in this chapter respond to a need to provide scientific information on climate change and glacier retreat in the Andean region, and their effects on the dynamics of montane ecosystems. This information can be helpful in the identification if necessary adaptation measures to cope with climate change and to protect Andean ecosystems.

Table 7.3. Summary of climate change experiences and projections in the Andean region using global or regional climate models. Projections are until 2001 in relation to the period 1961 to 1990 unless noted otherwise.

Region/Period/ Reference	**Projected changes**	**Models used**	**Expected impacts**
Northern Andes -Colombia Until 2100 *(Pabón 2006, 2007, 2008)*	Temperature: +2.0 °C to +4.0 °C Precipitation: -30 to +30% of annual amounts	Statistics of global models: ECHAM4 and CCM3 with 2xCO_2 Regional: HadRM3P	A reduction in annual precipitation is expected, in some regions over 30%; in the eastern foothills of the Cordillera Oriental and in the Pacific region increases would occur under scenario A2.
Colombian Andes Period 2080-89 *(Vergara et al. 2007)*	Temperature: +2.0°C to +3.0 °C Precipitation +2.5 to +3 mm/day	Global: JMA-MRI TL959L60	Future temperature increase in the Andes, greater than the mean temperature projected for the entire country. Increase in precipitation on the eastern and western flanks of the Andes.
Ecuadorian Andes Period 2071-2100 *(Centella and Bezanilla in litt.)*	Temperature: + 1.8 °C to +4.0 °C Precipitation: -20% to +20%	Global: HadCM3 and ECHAM4 Regional: HadRM3P	Ecuador is expected to experience a considerable increase in temperature that could reach magnitudes of between 2.7°C and 4.3°C, accompanied by a mean increase in precipitation between 18.5% and 63%, according to scenarios A2 and B2. Temperature increases will be most severe in the Amazonian region, while the western Andes will experience the lowest increases. Among future changes in precipitation high inter-annual variability figures prominently, with elevated maxima that appear to be associated with the occurrence of major precipitation events with similar effects as El Niño events.
Ecuadorian Andes Period 2080-89 *(Centella and Benzanilla 2008)*	Temperature: + 1.8 °C to +4.0 °C Precipitation: -20% to +20%	Global: JMA-MRI TL959L60	Under the intermediate scenario A1B predicted temperature increases range from 1.8°C to 4.0°C, whereas changes in precipitation vary between -20% and +20%. Minimum temperatures are expected to increase by between 2.0°C and 4°C, with most severe increases in Amazonia.
Northwestern Andes - Peru Until 2030 *(SENAMHI 2005 a)*	Temperature: +0.2 a +2.0 C Precipitation: +5% to 10%	Global: NCAR-CSM Regional: RAMS	The upper Rio Piura watershed is expected to experience a positive precipitation trend in all trimesters approximately 5% greater than the mean except in spring, for which no major changes are predicted. An increase in the frequency of warmer days and warmer nights in summer and fall is predicted. The highest temperatures would occur in spring.
Northeastern Andes - Peru Until 2030 *(SENAMHI 2009 b)*	Temperature: +0.7 to +1.2 C Precipitation -3% to -7 %	Global: NCAR–CSM Regional: RAMS	The Mayo watershed is expected experience the greatest temperature increases in spring, with an increased tendency for warmer days and warmer nights. Mean precipitation is expected to decrease slightly by 3% annually and by 7% in summer, and extreme precipitation events would occur with decreasing frequency.
Central western Andes - Peru Until 2030 *(SENAMHI 2009 c)*	Temperature +0.2 to + 0.9 ºC Precipitation: -3% to 5% (upper elevations) -10% to -3% (lower elevations)	Global: NCAR–CSM Regional: RAMS	The Santa watershed is expected to experience slight increases in precipitation at higher elevations and slight decreases at lower elevations, which fall within the area's natural variability. Extreme temperatures would become more frequent primarily in winter and spring.

Central and southern eastern Andes - Peru Until 2100 *(SENAMHI 2007a,b)*	Temperature Over +2.0 °C Precipitation -5 to -35% (Mantaro) +10 to +24% (Urubamba)	Global: MCGA TL959L60 MRI/JMA	The Mantaro and Urubamba watersheds are expected to experience increases in the frequency of extreme temperatures, which would be most severe at elevations above 3500 m. Precipitation would decrease to insufficient levels in large parts of the Mantaro watershed, while it would remain within natural variability in the Urubamba watershed, but with a slight increase.
Andes del Sur occidental Until 2100 *(Marengo et al. 2009)*	Temperature +2.0 to +5.0 °C Precipitation -2 to -3 mm/day	Global: IPCC AR4 Regional: HadRM3P	In Arequipa, the most severe increases in temperature are expected to occur at elevations above 3000-4000 m. Below 4000 m climate projections predict an increase in the frequency of warm nights, possibly heat waves, and a reduction in the frequency of cold nights and days. Above 4000 m there also is a trend for an increase in warm nights and days, with more heat waves, and a reduction in the frequency of cold days and nights, particularly of days with subzero temperatures. Precipitation scenarios indicate reductions at elevations above 4000 m (2-3 mm/day less than at present) and increases at lower elevations (1-2 mm/day more than at present). For elevations below 4000 m more extensive dry periods are predicted, combined with an increase in the frequency of extreme precipitation events.
Northwest Argentina and Bolivian Altiplano Until 2100 *(Solman et al. 2007, Nuñez et al. 2008)*	Temperature: +2.5 C to +3.5 °C Precipitation: -40%	Regional: MM5	Increases in temperature during summer months of 3.5°C and 2.5°C are projected under scenarios A2 and B2, respectively. Increases in temperature are expected to be greater for winter months (4.5°C for scenario A2 and 3.5°C for scenario B2). The region is characterized by humid summers and dry winters. For the end of the 21st century a reduction in precipitation of 40% is projected for summer months, which would lead to an increasing aridity in the region..
Subtropical Andes (28°S to 35°S), eastern flank - Argentina 2081-2090 *(Solman et al. 2007, Nuñez et al. 2008)*	Temperature: +2.5 °C to +4.0 °C Precipitation: -25% to +30%	Regional: MM5	Projected temperature changes during summer months are expected to reach 4°C under scenario A2, being slightly less pronounced during winter months. For the most optimistic scenario (B2), less severe increases of 2.5-3.0°C during summer and 2.0-2.5°C during winter are predicted. The region's precipitation regime is characterized by maxima during winter. For scenario A2 a 25% decrease in rainfall is predicted for the winter months, largely due to a reduction in the number of days with rain, whereas a 30% increase is predicted for summer months.
Patagonian Andes 2081-2090 *(Solman et al. 2007, Nuñez et al. 2008)*	Temperature: +1.5 °C to +2.5 °C Precipitation: -50% to +10%	Regional: MM5	Projected warming for the region is greatest at middle latitudes and decrease towards higher latitudes. Greatest increases are expected for summer months (3°C for scenario A, 1.5-2.0°C for scenario B2). During winter temperature increases are expected to be on the order of 2.5°C for scenario A2 and 1.5°C for scenario B2. The region is characterized by a winter precipitation regime. For the end of the 21st century A2 scenario projections indicate a reduction in winter precipitation on the order of 50% for the northern Patagonian Andes and an increase of 10% in the southern portion (south of 40°S), whereas summer precipitation is expected to increase by 30% in the north and decrease by 40% in the south. Under scenario B2 an approximately 30% increase in precipitation is expected for both summer and winter in the northern Patagonian Andes, while reductions of about 15% and 10% are expected for the southern portion in summer and winter, respectively.
Subtropicales Andes - Chile Until 2100 *(Fuenzalida et al. 2006)*	Temperature: +2.5 °C to +4.5 °C Precipitation: Reduction	Regional: HadRM3P	A warming of the central Chilean Andes in summer and of the Altiplano in winter are predicted. Important changes in the annual cycle of river discharges are expected in central Chile: increases in flow volume and inundation risk during winter as well as a decrease in flow volume during spring and summer (due to decreased meltwater discharge) are probable.

Table 7.4. Summary of expected climatic changes by the end of the 21st century under the extreme scenario A2. Qualitative indicators of reliability are defined based on consistencies in the direction of the tendencies (positive or negative) predicted by models HadRM3P, the mean of the IPCC AR4 models and the Japanese model: High = The three models present the same direction of tendencies; Medium = Two models show the same tendency, but the third model shows no or the opposite tendency; Low = Two models show opposite directions of tendencies and the third model shows no tendency, or only one of the three models predicts a tendency.

Region	**Projected changes: Temperature**	**Confidence**	**Projected changes: Precipitation**	**Confidence**
10°N-5°S Western flank	+2.0 °C to +3.0 °C	High	+15 to +20 %	High
10°N-5°S Eastern flank	+2.5°C to +4.0 °C	High	+7% to 10%	Medium
10°N-5°S Inter-Andean region	+2.0 °C to +4.0 °C	High	-4% to -15 %	Medium
5°S-10°S Western flank	+3.0 °C to +4.0 °C	High	+60 to +70 %	High
5°S-10°S Eastern flank	+4.0 °C to +5.0 °C	Medium	+16 to +25%	Low
5°S-10°S Inter-Andean region	+3.0 °C to +4.0 °C	Medium	+10% to +16%	Low
10°S-15°S Inter-Andean region – western flank	+3.0 °C to +4.0 °C	High	+6% to +11 %	Low
10°S-15°S Eastern flank	+4.0 °C to +5.0 °C	High	+16% to +22 %	Low
15°S-20°S Inter-Andean region	+3.0 °C to +5.0 °C	High	+10% to + 25%	Medium
15°S-20°S Altiplano	+4.0 °C to +5.0 °C °C	High	+4% to +10%	Low
20°S-35°S Subtropical Andes	+3.0 °C to +5.0 °C	High	-6% to -10%	Medium
South of 35°S Patagonia	+3.0 °C to +4.0 °C	High	-4% to -5%	Medium

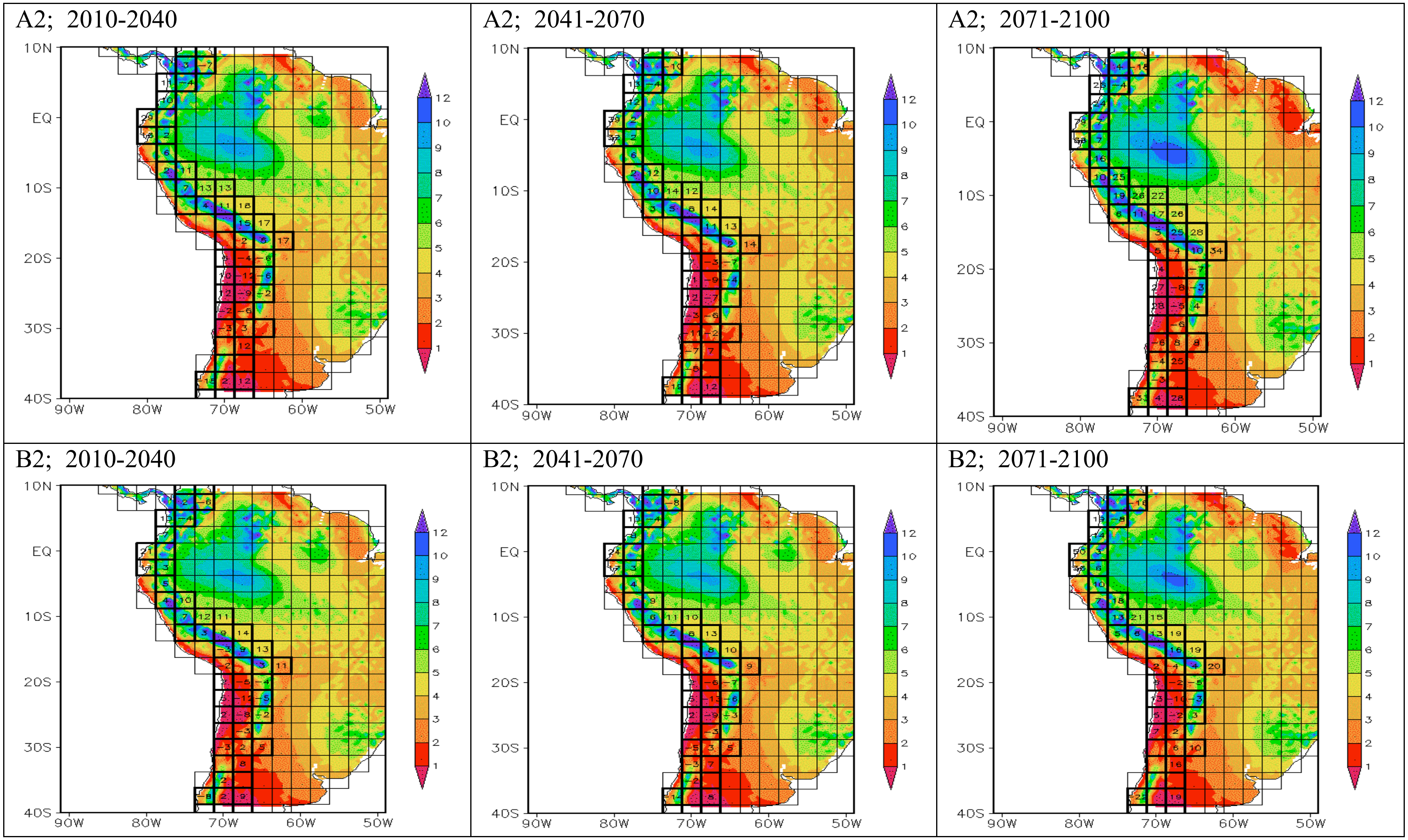

Figure 7.1. Future mean annual precipitation in mm per day (map colors) and relative changes in precipitation (numbers in grid cells; in relation to the period 1961-1990) under emissions scenarios A2 (high emission, upper row) and B2 (low emission, lower row) for the periods 2010-2040, 2041-2070, and 2071-2100 as projected by the model HadRM3P. Numbers in grid cells are only given for those cells where the projected difference is statistically significant in relation to the 30-year (1961-1990) natural variability.

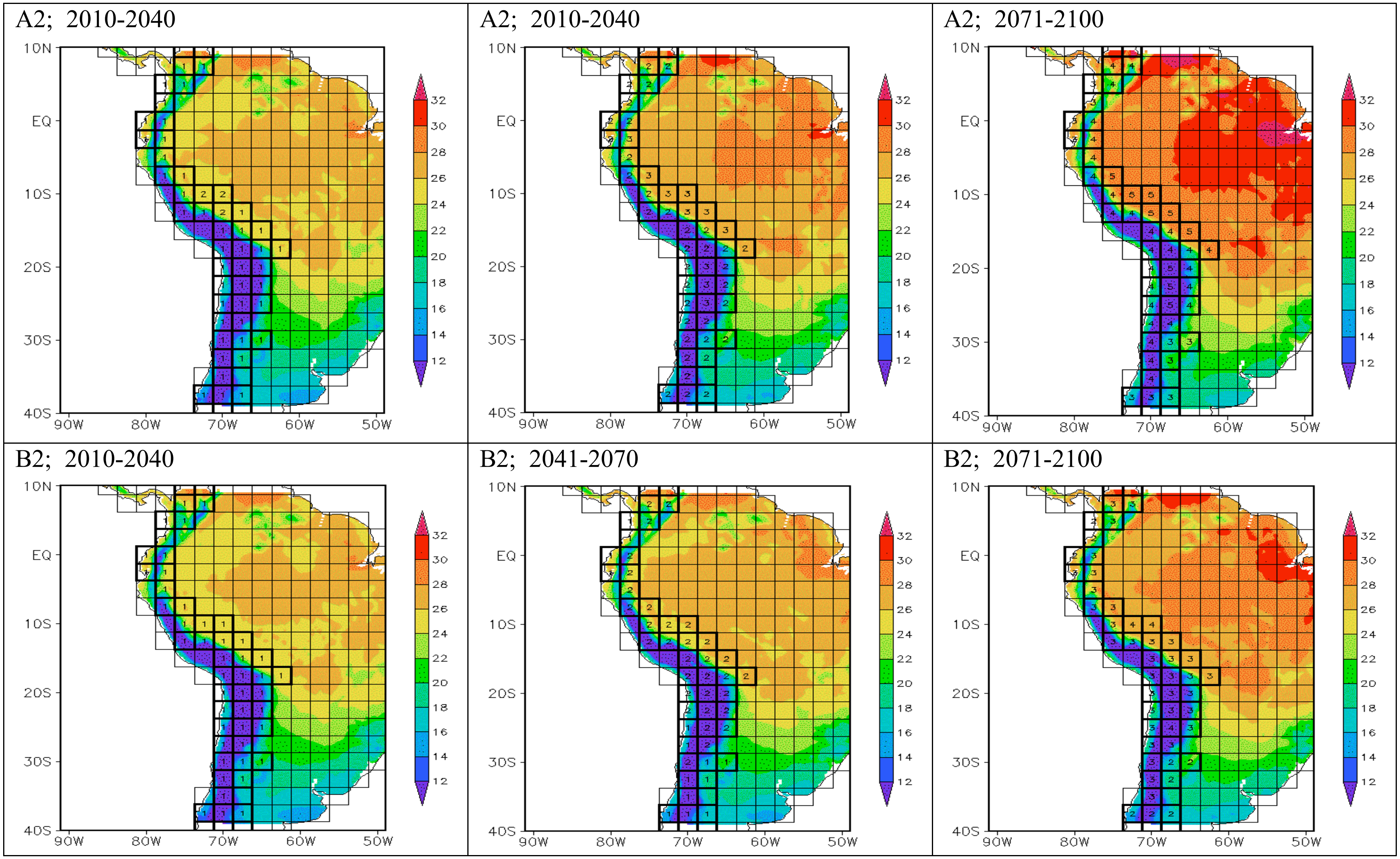

Figure 7.2. Future mean annual temperature in °C (map colors) and changes in temperature in °C (numbers in grid cells; in relation to the period 1961-1990) under emissions scenarios A2 (high emission, upper row) and B2 (low emission, lower row) for the periods 2010-2040, 2041-2070, and 2071-2100 as projected by the model HadRM3P. Numbers in grid cells are only given for those cells where the projected difference is statistically significant in relation to the 30-year (1961-1990) natural variability.

Literature Cited

Buytaert, W., R. Célleri, B. De Bièvre, R. Hofstede, F. Cisneros, G. Wyseure, and J. Deckers. 2006. Human impact on the hydrology of the Andean páramos. *Earth Science Reviews* 79:53-72.

Buytaert, W., C. Rolando, and L. Timbe. 2009. Predicting climate impacts on water resources in the tropical Andes: effects of GCM uncertainty. *Geophysical Research Letters* 36:L07406.

Carrasco, J., R. Osorio, and G. Cassasa. 2008. Secular trend of the equilibrium-line altitude on the western side of the southern Andes, derived from radiosonde and surface observations. *Journal of Glaciology* 54:538-550.

Casassa, G., P. López, B. Pouyaud, and F. Escobar. 2009. Detection of changes in glacial run-off in alpine basins: examples from North America, the Alps, central Asia and the Andes. *Hydrological Processes* 23:31-41.

Castañeda, M. E., and M. González. 2008. Statistical analysis of the precipitations trends in the Patagonian region in southern South America. *Atmósfera* 21:303-318.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W. T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C. G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections. Pp. 847-940 in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge: Cambridge University Press.

Chuquisengo Vásquez, O. (ed.). 2004. *El fenómeno El Niño en Perú y Bolivia: experiencias en participación local*. Lima: Intermediate Technology Development Group. 209 pp. Available at: http://www.crid.or.cr/digitalizacion/pdf/spa/doc16231/doc16231.htm.

CONAM. 2001. *Primera comunicación nacional del Perú a la convención de Naciones Unidas sobre cambio climático*. Lima: Consejo Nacional del Ambiente. 155 pp.

Coudrain, A., B. Francou, and Z. W. Kundzewicz. 2005. Glacier shrinkage in the Andes and consequences for water resources. *Hydrological Sciences Journal* 50:925-932.

Falvey, M., and R. D. Garreaud. 2009. Regional cooling in a warming world: recent temperature trends in the southeast Pacific and along the west coast of subtropical South America (1979–2006). *Journal of Geophysical Research* 114:D04102.

Favier, V., A. Coudrain, E. Cadier, B. Francou, E. Ayabaca, L. Maisincho, E. Pradeiro, M. Villacís, and P. Wagnon. 2008. Evidence of groundwater flow on Antizana ice-covered volcano, Ecuador. *Hydrological Sciences Journal* 53:278-291.

Favier, V., P. Wagnon, and P. Ribstein. 2004. Glaciers of the inner and outer tropics: a different behavior but a common response to climatic forcing. *Geophysical Research Letters* 31:L16403.

Francou, B., M. Vuille, P. Wagnon, J. Mendoza, and J.-E. Sicart. 2003. Tropical climate change recorded by a glacier in the central Andes during the last decades of the twentieth century: Chacaltaya, Bolivia, 16°S. *Journal of Geophysical Research* 108(D5):4154.

Fuenzalida, H., M. Falvey, M. Rojas, P. Aceituno, and R. Garreaud. 2006. *Estudio de la variabilidad climática en Chile para el siglo XXI*. Unpublished report. Comisión Nacional del Medio Ambiente. Available at: http://www.dgf.uchile.cl/PRECIS/articles-39442_pdf_Estudio_texto.pdf.

IDEAM. 2000. *Los glaciares colombianos, expresión del cambio climático global*. Bogotá: Instituto de Hidrología, Meteorología y Estudios Ambientales. 19 pp.

Jordan, E., L. Ungerechts, B. Cáceres, A. Peñafiel, and B. Francou. 2005. Estimation by photogrammetry of the glacier recession on the Cotopaxi Volcano (Ecuador) between 1956 and 1997. *Hydrological Sciences Journal* 50:949-961.

Leiva, J. C. 2006. Assessment of climate change impacts on the water resources at the northern oases of Mendoza province, Argentina. Pp. 81-83 in *Global change in mountain regions*, edited by M. F. Price. Kirkmahoe, Dumfriesshire: Sapiens Publishing.

Magrin, G., C. Gay García, D. Cruz Choque, J. C. Giménez, A. R. Moreno, G. J. Nagy, C. Nobre, and A. Villamizar. 2007. Latin America. Pp. 581-615 in *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson. Cambridge: Cambridge University Press.

Marengo, J. A., R. Jones, L. M. Alves, and M. C. Valverde. 2009. Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. *International Journal of Climatology* 29:2241-2255.

Mark, B. G., J. M. McKenzie, and J. Gomez. 2005. Hydrochemical evaluation of changing glacier meltwater contribution to stream discharge: Callejon de Huaylas, Peru. *Hydrological Sciences Journal* 50:975-987.

Mark, B. G., and G. O. Seltzer. 2003. Tropical glacier meltwater contribution to stream discharge: a case study in the Cordillera Blanca, Perú. *Journal of Glaciology* 49:271-281.

Masiokas, M. H., R. Villalba, B. H. Luckman, M. E. Lascano, S. Delgado, and P. Stepanek. 2008. 20th-century glacier recession and regional hydroclimatic changes in northwestern Patagonia. *Global and Planetary Change* 60:85-100.

Meehl, G., C. Covey, T. Delworth, M. Latif, B. McAvaney, J. F. B. Mitchell, R. J. Stouffer, and K. E. Taylor. 2007. The WCRP CMIP3 multimodel data set: a new era in climate change research. *Bulletin of the American Meteorological Society* 88:1383-1394.

Montoro Asencios, J. 2004. Calor intenso y largas sequías. In *Informes Especiales*. Lima: Universidad Nacional Mayor de San Marcos. Available at: http://www.unmsm.edu.pe/Destacados/contenido.php?mver=11.

Nakicenovic, N., J. Alcamo, G. Davis, B. De Vries, J. Fenhann, S. Gaffin, K. Gregory, A. Grubler, T. Y. Jung, T. Kram, E. L. La Rovere, L. Michaelis, S. Mori, T. Morita, W. Pepper, H. Pitcher, L. Price, K. Riahi, A. Roehrl, H. Rogner, A. Sankovski, M. Schlesinger, P. Shukla, S. Smith, R. Swart, S. Van Rooijen, N. Victor, and Z. Dadi. 2000. *Special report on emissions scenarios*. Cambridge: Cambridge University Press. 599 pp.

NC-Colombia. 2001. *1st national communication to the UNFCCC*. 267 pp. Available at: http://www.climate.org/CI/latam.shtml.

Nuñez, M., S. Solman, and S. Cabré. 2008. Regional climate change experiments over southern South America. II: climate change scenarios in the late twenty first century. *Climate Dynamics* 32:1081-1095.

Pabón, J. D. 2003. El cambio climático global y su manifestación en Colombia. *Cuadernos de Geografía* 12(1-2):111-119.

Pabón, J. D. 2006. Escenarios de cambio climático para Colombia. In *Memorias del IV Encuentro de la Red de Universidades del Pacífico Sur*, 8-10 de noviembre de 2006.

Available at: http://www.cisdaiv.unal.edu.co/ponencias/E2_Cambio_clima/E2_daniel_pabon.pdf

Pabón, J. D. 2007. El cambio climático en Colombia: tendencias actuales y proyecciones para el siglo XXI. Pp. 31-48 in *Memórias de la Primera Conferencia Internacional de Cambio Climático: impacto en los sistemas de alta montaña*. Bogotá: IDEAM and University of Zurich.

Pabón, J. D. 2008. Informe de evaluación del cambio climático en Colombia. Bogotá: Instituto de Hidrología, Meteorología y Estudios Ambientales, Integrated National Adaptation Pilot Program, and Departament of Geography, Universidad Nacional de Colombia.

Pellicciotti, F., P. Burlando, and K. Van Vliet. 2007. Recent trends in precipitation and streamflow in the Aconcagua River basin, central Chile. Pp. 17-38 in *Glacier mass balance changes and meltwater discharge*, edited by P. Ginot and J. Sicart. Wallingford: IAHS Publication 318.

Pouyaud, B., M. Zapata, J. Yerren, J. Gomez, G. Rosas, W. Suarez, and P. Ribstein. 2005. Avenir des ressources en eau glaciaire de la Cordillère Blanche. *Hydrological Sciences Journal* 50:999-1022.

Pourrut, P. 1995. *El agua en el Ecuador. Clima, precipitaciones, escorrentía*. Quito: ORSTOM, Colégio de Ingenieros Geógrafos del Ecuador, and Corporación Editora Andina. 118 pp.

Quintana, J. 2004. *Estudio de los factores que explican la variabilidad de la precipitacion en Chile en las escalas de tiempo interdecadal*. Magister thesis. Santiago de Chile: Universidad de Chile. 93 pp.

Ramírez, E., B. Francou, P. Ribstein, M. Descloitres, R. Guérin, J. Mendoza, R. Gallaire, B. Pouyaud, and E. Jordan. 2001. Small glaciers disappearing in the tropical Andes: a case study in Bolivia: the Chacaltaya glacier, 16°S. *Journal of Glaciology* 47:187-194.

SENAMHI. 2005a. *Escenarios del cambio climático en el Perú al 2050 - cuenca del río Piura*. Lima: Programa de Cambio Climático y Calidad de Aire, Servicio Nacional de Meteorología e Hidrología. 197 pp.

SENAMHI. 2005b. *Escenarios climáticos en la cuenca del río Santa para el año 2030*. Lima: Servicio Nacional de Meteorologia e Hidrologia, Ministerio de Ambiente. 139 pp.

SENAMHI. 2007a. *Escenarios de cambio climático en la cuenca del río Mantaro para el año 2100*. Lima: Servicio Nacional de Meteorologia e Hidrologia, Ministerio de Ambiente. 124 pp.

SENAMHI. 2007b. *Escenarios de cambio climático en la cuenca del río Urubamba para el año 2100*. Lima: Servicio Nacional de Meteorologia e Hidrologia, Ministerio de Ambiente. 120 pp.

SENAMHI. 2009a. *Escenarios climáticos en el Perú para el año 2030. Segunda Comunicación Nacional de Cambio Climático*. Lima: Servicio Nacional de Meteorología e Hidrología, Ministerio del Ambiente. 136 pp.

SENAMHI. 2009b. *Escenarios climáticos en la cuenca del rio Mayo para el año 2030. Segunda Comunicación Nacional de Cambio Climático*. Lima: Servicio Nacional de Meteorología e Hidrología, Ministerio del Ambiente. 133 pp.

SENAMHI. 2009c. *Escenarios climáticos en la cuenca del rio Santa para el año 2030. Segunda Comunicación Nacional de Cambio Climático*. Lima: Servicio Nacional de Meteorología e Hidrología, Ministerio del Ambiente. 139 pp.

Silverio, W. 2004. *Estudio de la evolucion de la cobertura glaciar del Nevado Coropuna entre 1955 y 2003*. Unpublished report. Geneva: Earth Sciences Section, University of Geneva. 289 pp.

Solman, S., M. Nuñez, and M. F. Cabré. 2007. Regional climate change experiments over southern South America. I: present climate. *Climate Dynamics* 30:533-552.

Soruco, A., C. Vincent, and B. Francou. 2009. Glacier decline between 1963 and 2006 in the Cordillera Real, Bolivia. *Geophysical Research Letters* 36:L03502.

Trenberth, K. E., P. D. Jones, P. Ambenje, R. Bojariu, D. Easterling, A. Klein Tank, D. Parker, F. Rahimzadeh, J. A. Renwick, M. Rusticucci, B. Soden, and P. Zhai. 2007. Observations: surface and atmosphere climatic change. In *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Soloman, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

Vergara, W., E. Perez, J. Méndez, V. Magaña, M. Martinez, F. Ruiz, G. Avalos, and E. Palacios. 2007. *Visualizing future climate in Latin America: results from the application of the Earth Simulator. Latin America and Caribbean Region Sustainable Development Working Paper 30*. Washington, DC: The World Bank. 90 pp.

Villacís, M. 2008. *Ressources en eau glaciaire dans les Andes d'Equateur en relation avec les variations du climat: le cas du volcan Antisana*. PhD thesis. Montpellier: Université Montpellier.

Villalba, R., A. Lara, J. A. Boninsegna, M. Masiokas, S. Delgado, J. Aravena, F. A. Roig, A. Schmelter, A. Wolodarsky, and A. Ripalta. 2003. Large-scale temperature changes across the southern Andes: 20th-century variations in the context of the past 400 years. *Climatic Change* 59:177-232.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers – past, present, future. *Earth Science Reviews* 89:79-96.

Vuille, M., and R. Bradley. 2000. Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophysical Research Letters* 27:3885-3888.

8

Introduction to Andean Geographies

Kenneth R. Young

The tropical Andes Mountains epitomize change and diversity. They soar to more than 6000 m elevation, and include many of the Earth's life zones. The topography includes geological structures so vast that they can influence air circulation and hydrological regimes across South America (Veblen et al. 2007). The varied ecological conditions due to changes in microclimates and soils, found from valley-to-valley and from mountain-to-mountain, create spatial heterogeneity in biophysical constraints, and can produce biogeographical barriers, that in turn act to control the distributions of species and of ecosystems (e.g., Rosenzweig 1995). The biota found among the cordilleras is diverse and often endemic, restricted to relatively small or narrow distributions (e.g., Myers et al. 2000; Weigend et al. 2005; Young 2007). This affects conservation goals for plant (Young et al. 2002) and animal species (Young et al. 2009).

Because of natural variability in temperature, precipitation, and winds, the Andes have created through time a shifting ecological mosaic, complete with changes in species ranges and environmental controls. It is important to consider the various ways Andean biodiversity will be affected by future change as a function of the innate dynamism of the natural environments, of the characteristics of native species, of the legacies of past change, and of the imprint of human land use upon Andean landscapes.

Oversimplifying this complexity can lead to premature generalizations and to inadequate biodiversity conservation strategies. With change as a constant, the important question is whether future biophysical changes are within the adaptive capacities of Andean organismal, ecological, and human systems. The data required to begin to answer this question include paleoclimatic reconstructions, in addition to an in-depth appreciation of water and nutrient cycles, and of population responses and other ecological processes following natural disturbances and or changes in land use. In addition, the Andean countries often have disparate means, goals, and perspectives concerning biodiversity conservation (Sierra 2006; Young and Rodriguez 2006). Responses will need to be adapted and implemented at local, national, regional, and global levels.

Advances in understanding human impacts on species and ecosystems come from the realization that those influences provide feedbacks (Liu et al. 2007), meaning that the results may be moderated, amplified, or sent into novel states, depending on the nature of the feedbacks. For example, the grazing of livestock and the burning of pasturelands alter plant species dominance (Gordon and Prins 2008). However, if climate change is simultaneously altering species dominance, then the resulting vegetation is a product of herbivory, different temperature and moisture regimes, and some unknown amount of interaction among those factors (Asner et al. 2004). While adding to the factors to consider, the connecting of land use and other socioeconomic factors to resulting land covers also potentially allows for determining the ultimate and proximate controls at work (e.g., Swinton and Quiroz 2003).

In this chapter, the tropical Andes are addressed in terms of areas above 500 m elevation in the countries of Colombia, Ecuador, Peru, and Bolivia. Multiple sources of spatial heterogeneity are identified, with the goal of facilitating future evaluations of the consequences of global change for plants, animals, and ecosystems.

Earth Surface Systems in the Andes

Bedrock formed in the Andes over many millions of years through deposition, compression, and various igneous processes (Meade and Conrad 2008). Uplift from movements of the Pacific plate created orogenies and the Pacific plate's subduction caused volcanism on the South American plate, with additional complexity in the northern Andes added by movements of the Caribbean plate (Taboada et al. 2000; Orme 2007). The Andean cordilleras formed at different times, with more recently uplifted bedrock on Pacific slopes, underlying the Peru-Bolivia Altiplano, and in the mountains overlooking the Caribbean (Taylor 1991; Gregory-Wodzicki 2000).

The relatively recent uplift of the highest peaks during the Pliocene and Pleistocene (Garzione et al. 2008) has led several high Andean groups to have some of the fastest speciation rates known (Hughes and Eastwood 2006). The rough topography and humid montane conditions combine to support numerous species, making the Andes regionally and globally biodiverse (Myers et al. 2000; Rahbek and Graves 2001). Both ecological and historical explanations for the speciation and maintenance of these species are important (Ricklefs 2004). For example, the distributions and diversity of some evolutionary lineages are best understood as relicts of much broader distributions in the distant past, or as affected by ancient biogeographical barriers, corridors, and vicariances (Pennington et al. 2000, 2004; Aleixo and Rossetti 2007; Antonelli et al. 2009).

Geological and topographic differences among tropical Andean countries influence ecoregions and landscapes. Colombia, with its three massive cordillera systems, often has unique species of the same evolutionary lineages on each cordillera (Luteyn 2002). Ecuador has active volcanoes and important intermontane valleys that have been greatly altered by land use, with much biodiversity concentrated in the forests located on the outer wet flanks of both sides of the Andes (Jørgensen and León-Yanez 1999). In turn, Peru has persistent arid-to-semiarid conditions along its Pacific slopes, making for a greater importance of drylands and shrublands across the highlands, with the wettest environments to be found on forested Amazon-facing versants (Young and León 2001). Tropical and subtropical Bolivia is characterized by a high flatland, the Altiplano, at about 4000 m, with steep topography to the east reaching down to Amazon lowlands, and intermontane valleys that stretch southward to Chaco woodlands (Navarro and Maldonado 2002).

Air circulation in the tropical Andes is influenced by the interaction of the Intertropical Convergence Zone (ITCZ) with local controls on climate due to the adiabatic cooling of rising air parcels and the reversal of winds with diurnal changes in temperature (Hastenrath 1982; Barry and Seimon 2000; Garreaud and Aceituno 2007). Tradewinds (tropical easterlies) tend to bring moist air masses to the piedmont of the eastern Andes during much of the year. Deep valleys may contain all variants in climate due to elevational differences and rain shadow effects (Kessler et al. 2001; Killeen et al. 2007). The mildly seasonal rhythms in precipitation found at the equator become increasingly seasonal at higher latitudes in the south (Espinoza et al. 2009), with a strong dry season in southern Peru and Bolivia amplified into a monsoonal air circulation system (Gan et al. 2004).

Spatial and temporal variability in precipitation characterize the tropical Andes. Colombia and northern Ecuador contain the Chocó region on the western Andes, famed for up to ten meters of annual precipitation, and especially high biodiversity (Gentry 1995). Southern Ecuador and northern Peru, in turn, are the Andean areas with the greatest subdecadal shifts in precipitation due to El Niño Southern Oscillation (ENSO) (see Martínez et al., Chapter 6, this volume). An oscillation in air pressure and the heavy rains of El Niño years are characteristic of the warm phase ENSO, caused by sea surface temperature increases in the tropical Pacific Ocean, which in turn teleconnect to altered air circulation worldwide (Caviedes 2001). These occasional years with relatively warm ocean temperatures bring rain to an otherwise dry environment in northwestern South America roughly every three to seven years. Species populations and ranges fluctuate in response (Caviedes 2007), as does glacier mass balance (Vuille et al. 2008). Additional climatic variability in the Andes occurs over decadal, centennial, and millennial timescales (Ekdahl et al. 2008).

The tropical Andes encompass the headwaters of some of the world's principal river systems, as well as important lentic environments. Heavy rains in the Chocó result in runoff in rivers flowing to the tropical Pacific or Caribbean, while the eastern Andes drain to the Amazon and Orinoco Rivers (Dunne and Mertes 2007). Most of the seasonality, chemistry, and ecosystem fluxes along the tributaries of the Amazon are ultimately driven by rainfall and erosion in the Andes (McClain and Naiman 2008): thus, Amazon biodiversity is in part a result of Andean Earth system processes. The Altiplano of southern Peru and western Bolivia contains the world's largest high elevation lake, Lake Titicaca, famed for its unique, isolated, and threatened freshwater biodiversity (Villwock 1986; Rodríguez 2001). Scattered across the middle to high elevations of the tropical Andes are lakes, most formed from depressions created by mountain glaciers and filled by runoff and groundwater.

Permanent ice in the form of mountain glaciers and ice caps is often found above 5300 m, although large ice masses send their lower lobes down to at least 4600 m and the high Andean areas in southern Peru and Bolivia can be too dry for glaciers to persist (Clapperton 1993; Smith et al. 2005). During the Quaternary, global Milankovitch cycles in solar radiation caused several repeated glacial-to-interglacial cycles of roughly 100,000 years duration (Alverson et al. 2003), and glaciers have extended further downslope at times in the past (Smith et al. 2008). The Holocene marks the start of the current interglacial, with many high elevation soils developing since that time. There is evidence of a generally warm and dry mid-Holocene (Abbott et al. 1997), and an atypical recent warming trend (Thompson et al. 2006), driven by a human-caused rise in greenhouse gases (Houghton et al. 2001).

Many Andean landscapes above 3000 m elevation have been directly affected by glaciers at some point in the Quaternary, or else have been indirectly affected by glacial melt or periglacial geomorphic processes (Young 1989; Clapperton 1993). As a result, Andean landscapes are composites, with landforms derived from geomorphic regimes operating under previous climate conditions. The glaciers of the Pleistocene carved U-shaped valleys into the high Andes. In lower and wetter environments, the valleys are often V-shaped, with steep slopes maintained by mass movements and fluvial dynamics (Trauth et al. 2000; Wilcke et al. 2003).

Eroded and weathered rocks form the mineral portion of Andean soils. Their edaphic characteristics are ultimately shaped by organic inputs and by mineral translocation with soil water movements, with an important set of controls associated with the respective temperature and moisture regimes (Birkeland 1999; Buol 2007). A given geological bedrock map provides some indication of the likely resulting spatial heterogeneity of soils for a particular part of the Andes. There are soil catenas, shifts in soil types from the deeper and often more organic soils in valley bottoms to shallow and coarser soils on steeper slopes (e.g., Miller and Birkeland 1992). Some soils that derived from volcanic ash are relatively fertile, as are those with much glacial loess or with a limestone bedrock. In general, plants are limited by the soils in which they grow, creating different vegetation types on different soils, along with changes imposed by elevation, aspect, and slope angle. Some of the plant diversity in the Andes undoubtedly comes from this edaphic and microclimatic diversity. In Colombia, botanists have recognized many dozens of vegetation types based on the names of locally dominant plant species (Rangel et al. 1997), with studies beginning to classify this high vegetation diversity in other Andean countries (Luteyn and Churchill 2000; Kappelle and Brown 2001; Navarro and Maldonado 2002).

Climatic change in the tropical Andes acts upon these Earth surface systems, altering atmospheric conditions and shifting the types of feedbacks among edaphic, geomorphic, weathering erosional and biological processes.

Ecological Transitions

Elevational change is associated with the most dramatic differences in species composition and ecosystem structure in the tropical Andes. However, elevational gradients are complex because there are multiple potentially controlling factors that vary and covary with altitude. Average temperature decreases with elevation, but the relative daily range can increase. Other factors shift nonlinearly and with thresholds, for example with frost becoming an important constraint only above mid to high elevations. Still other factors may change linearly with elevation, but be dramatically affected by local features. An example is slope aspect, which controls the number of hours of exposure to solar radiation (e.g., Kessler et al. 2007); slope angle affects not only solar radiation, but also stability and soil depth. Understanding the relationship of biodiversity to elevation requires: 1) sampling that stratifies for topographic and edaphic variation, and 2) acknowledgement that elevation operates as a complex environmental gradient.

Ecotones are both ecological boundaries and ecological transition zones (Crawford 2008). Their identification is useful for mapping land cover units, and for detecting change in those units over time (e.g., Kintz et al. 2006). They also are zones where responses to climate change are most likely to be identifiable (see Hole et al., Chapter 2, this volume), for example with the increased invasion of woody plants into herbaceous vegetation types. There are two kinds of forest-nonforest ecotones that are of particular interest in the tropical Andes: 1) an upper elevational limit to either tree growth forms (treeline) or to forest itself (timberline), and 2) lower elevational limits on trees and forests at around 2000 m on the arid western slopes of Peru, or those observed in many Andean intermontane valleys that are covered by shrublands or cultivated fields at lower altitudes (Young et al. 2007).

The upper treeline delimits the herbaceous vegetation of páramo in the north and puna in the south, although there are small woodlands of *Buddleia*, *Gynoxys*, and *Polylepis* that can be found almost to the level of permanent ice (e.g., Velez et al. 1998; Kessler et al. 2001). Andean forests are often on steep slopes, so they are affected by mass movements and by soil creep (Young and León 1990; Stern 1995; Restrepo et al. 2009). Andean forest fragments isolated by topography, climate, or by land use may be particularly important for some kinds of threatened biodiversity; recent studies include Köster et al. (2009) on epiphytic plants, Lloyd and Marsden (2008) and Mordecai et al. (2009) on birds, and Muriel and Kattan (2009) on butterflies.

One important source of future dynamism would be shifts in these ecotones, with the expectation that many warmer or more humid sites would be likely to change towards dominance by shrubs or trees, but fire or grazing may complicate such vegetation change processes. Newly exposed substrates at 5300 m that previously were covered by glacial ice now support a primary succession of forbs, lichens, mosses, and algae (Schmidt et al. 2008; Buffen et al. 2009). Lower downslope, large Andean wetlands form as more glacial melt temporarily increases ground- and surface water flows (Seimon et al. 2007).

These ecological transitions, from the spatial shifts across ecotones to the successional shifts following perturbation, are accompanied by alterations in associated animal, fungal, and microbial communities. Most plants in the tropical Andes have mycorrhizal mutualisms, and the majority is pollinated by insects or birds, and with seeds dispersed by birds or bats (Young et al. 2002). As a result, changes in vegetation due to shifts in biophysical constraints likely cause alterations in other trophic levels (see also Aguirre et al., Chapter 4, this volume). The soil-vegetation-animal couplings thus could be used to characterize the dynamic ecosystems to be found. This will continue to be a critical research need, as will the equivalent coupled systems in aquatic environments (e.g., Buisson et al. 2008).

Coupled Natural-Human Systems

Some of the dynamism of the Andes is due to human action over many millennia (Niemann and Behling 2009). Depending on the location, people have been farming and otherwise altering Andean landscapes for five to ten millennia (Denevan, 2001; Dillehay et al. 2007; see also Suárez et al., Chapter 9, this volume). Thus, the inhabited rural landscapes of the Andes often contain the native biota most resistant to land use activities, or those that are most facilitated by the relatively open habitats found amid the agricultural fields, pasturelands, and shrublands that are dominant land cover types (Young 1998, 2009). Future changes in species distributions will be limited by shifting land use patterns.

Biotic communities will alter as species shift along environmental gradients in an individualistic manner (Davis and Shaw 2001). Humans will continue to use many Andean landscapes for farming, grazing, and recreation, further altering species abundance and presence (e.g., Postigo et al. 2008) and hydrological regimes (Buytaert et al. 2006). Novel vegetation types likely will appear, and some future ecosystems may have no present-day analogue (Williams et al. 2007). Change will largely be gradual and incremental, but at times rapid and unpredictable as thresholds are crossed (Alley et al. 2003).

These predictions have important consequences for biodiversity conservation (Bush 2004; Darling and Côte 2008; Fitzpatrick and Hargrove 2009; see also Hole et al., Chapter 2, this volume) and they are also relevant for planning of economic development that includes sustainability goals. Many rural Andean residents depend upon access to land, water, and useful species (e.g., Thomas et al. 2009). Some natural hazards, such as catastrophic failure of lakes dammed by glacial moraines (Kaser and Osmaston 2002; Carey 2005; Vilimek et al. 2005) will increase. All of the cities of western South America are dependent to varying degrees on water originating in the high Andes, the electricity produced by hydropower, and the foodstuffs produced by their rural compatriots (Bradley et al. 2006). Human responses to climate change are ultimately connected both to biophysical change and to socioeconomic responses. They may be affected by the current limited capacity to predict either future temperature and precipitation regimes (Urrutia and Vuille 2009) or impacts on water resources in particular places in the Andes (Buytaert et al. 2009).

Implications for Biodiversity Conservation

If human goals and welfare are the ultimate drivers of transformation of Andean landscapes, then connecting the social, behavioral, and economic sciences to the study of landscape dynamism is essential. The realization that climate change impacts will often be mediated through coupled natural-human systems provides a means to make more nuanced predictions. The geographies of the tropical Andes must be understood in terms of their geological framework, their atmospheric connections to land surface processes, and their human histories.

If every place in the Andes is different in terms of topography, microclimate, soils, and biota, will detailed conservation planning need to be similarly place-specific? Must each species of concern be studied, protected, and managed? These questions and others provide the rationale for a series of comparative studies along the tropical Andes (Young and Lipton 2006). Robust generalizations may also require comparisons to other places in the world undergoing rapid change, for example in the high latitudes of North America and Eurasia (Moritz et al. 2002; Tape et al 2006) and other high elevation mountains (Foster 2001; Colwell et al. 2008; Willis et al. 2009). Places included in national protected area systems may need reassessments as environmental change proceeds (Kattan et al. 2006; Hole et al. 2009).

Species ranges will shift, and local abundances will change (e.g., Ron et al. 2003). In some cases, there will also be increases in pests and diseases (e.g., Seimon et al. 2007; Sánchez et al. 2008). Large fluctuations in temperature and moisture have characterized the Andes over many millennia across and along the cordilleras, and have shaped native biodiversity. The near ubiquity of human land use in the tropical Andes has acted to filter out some of the most sensitive species and to modify fragile ecosystems (Young 2009). Climate change taking place over the next decades will act upon species adapted to the Andes, but as constrained by human actions.

Literature Cited

Abbott, M., G. O. Seltzer, K. R. Kelts, and J. Southton. 1997. Holocene paleohydrology of the tropical Andes from lake records. *Quaternary Research* 47:70-80.

Aleixo, A., and D. de Fátima Rossetti. 2007. Avian gene trees, landscape evolution, and geology: towards a modern synthesis of Amazonian historical biogeography. *Journal of Ornithology* 148(Suppl. 2):S443-S453.

Alley, R. B., J. Marotzke, W. D. Nordhaus, J. T. Overpeck, D. M. Peteet, R. A. Pielke Jr., R. T. Pierrehumbert, P. B. Rhines, T. F. Stocker, L. D. Talley, and J. M. Wallace. 2003. Abrupt climate change. *Science* 299:2005-2010.

Alverson, K. D., R. S. Bradley, and T. F. Pederson. 2003. *Paleoclimate, global change and the future*. Berlin: Springer.

Antonelli, A., J. A. A. Nylander, C. Persson, and I. Sanmartín. 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Science of the United States of America* 106:9749-9754.

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29:261-299.

Barry, R. G., and A. Seimon. 2000. Research for mountain area development: climatic fluctuations in the mountains of the Americas and their significance. *Ambio* 29:364-370.

Birkeland, P. W. 1999. *Soils and geomorphology*. New York: Oxford University Press.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Climate change: threats to water supplies in the tropical Andes. *Science* 312:1755-1756.

Buffen, A. M., L. G. Thompson, E. Mosley-Thompson, and K. I. Huh. 2009. Recently exposed vegetation reveals Holocene changes in the extent of the Quelccaya Ice Cap, Peru. *Quaternary Research* 72:157-163.

Buisson, L., W. Thuiller, S. Lek, P. Lim, and G. Grenouillet. 2008. Climate change hastens the turnover of stream fish assemblages. *Global Change Biology* 14:2232-2248.

Buol, S. W. 2007. Soils. Pp. 101-111 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Bush, M. B. 2004. Distributional change and conservation on the Andean flank: a paleoecological perspective. *Global Ecology and Biogeography* 11:463-473.

Buytaert, W., R. Célleri, B. De Bièvre, F. Cisneros, G. Wyseure, J. Deckers, and R. Hofstede. 2006. Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews* 79:53-72.

Buytaert, W., R. Célleri, and L. Timbe. 2009. Predicting climate change impacts on water resources in the tropical Andes: effects of GCM uncertainty. *Geophysical Research Letters* 36:L07406.

Carey, M. 2005. Living and dying with glaciers: people's historical vulnerability to avalanches and outburst floods in Peru. *Global Planetary Change* 47:122-134.

Caviedes, C. N. 2001. *El Niño in history: storming through the ages*. Gainesville: University Press of Florida.

Caviedes, C. N. 2007. Impacts of El Niño-Southern Oscillation on natural and human systems. Pp. 305-321 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Clapperton, C. 1993. *Quaternary geology and geomorphology of South America*. Amsterdam: Elsevier – Academic Press.

Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261.

Crawford, R. M. M. 2008. *Plants at the margin: ecological limits and climate change*. Cambridge: Cambridge University Press.

Darling, E. S., and I. M. Côte. 2008. Quantifying the evidence for ecological synergies. *Ecology Letters* 11:1278-1286.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673-679

Denevan, W. M. 2001. *Cultivated landscapes of native Amazonia and the Andes*. New York: Oxford University Press.

Dillehay, T. D., J. Rossen, T. C. Andres, and D. E. Williams. 2007. Preceramic adoption of peanut, squash, and cotton in northern Peru. *Science* 316:1890-1893.

Dunne, T., and L. A. K. Mertes. 2007. Rivers. Pp. 76-90 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Ekdahl, E. J., S. C. Fritz, P. A. Baker, C. A. Rigsby, and K. Coley. 2008. Holocene multidecadal- to millennial-scale hydrologic variability on the South American Altiplano. *The Holocene* 18:867-876.

Espinoza Villar, J. C., J. Ronchail, J. L. Guyot, G. Cochonneau, F. Naziano, W. Lavado, E. De Oliveira, R. Pombosa, and P. Vauchel. 2009. Spatio-temporal rainfall variability in the Amazon basin countries (Brazil, Peru, Bolivia, Colombia, and Ecuador). *International Journal of Climatology* 29:1574-1594.

Fitzpatrick, M. C., and W. W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation* 18:2255-2261.

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Review* 55:73-106.

Gan, M. A., V. E. Kousky, and C. F. Ropelewski. 2004. The South American monsoon circulation and its relationship to rainfall over west-central Brazil. *Journal of Climate* 17:47-66.

Garreaud, R. D., and P. Aceituno. 2007. Atmospheric circulation and climatic variability. Pp. 45-59 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Garzione, C. N., G. D. Hoke, J. C. Libarkin, S. Withers, B. MacFadden, J. Eiler, P. Ghosh, and A. Mulch. 2008. Rise of the Andes. *Science* 320:1304-1307.

Gentry, A. H. 1995. Patterns of diversity and floristic composition in Neotropical montane forests. Pp. 103-126 in *Biodiversity and conservation of Neotropical montane forests*, edited by S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn. New York: New York Botanical Garden.

Gordon, I. J., and H. H. T. Prins (eds.). 2008. *The ecology of browsing and grazing*. Berlin: Springer.

Gregory-Wodzicki, K. M. 2000. Uplift history of the central and northern Andes: a review. *Geological Society of America Bulletin* 112:1091-1105.

Hastenrath, S. 1982. *Climate dynamics of the tropics*. New York: Kluwer.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* 12:420-431.

Houghton, T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu (eds.). 2001. *Climate change 2001: the scientific basis*. Cambridge: Cambridge University Press.

Hughes, C., and R. Eastwood. 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Science of the United States of America* 103:10334-10339.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211-1219.

Jørgensen, P. M., and S. León-Yanez (eds.). 1999. Catalogue of the vascular plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75. 1188 pp.

Kappelle, M., and A. D. Brown (eds.). 2001. *Bosques nublados del Neotrópico*. Santo Domingo de Heredia, Costa Rica: INBio.

Kaser, G., and H. Osmaston. 2002. *Tropical glaciers*. Cambridge: Cambridge University Press.

Kattan, G. H., P. Franco, C. A. Saavedra-Rodríguez, C. Valderrama, V. Rojas, D. Osorio, and J. Martínez. 2006. Spatial components of bird diversity in the Andes of Colombia: Implications for designing a regional reserve system. *Conservation Biology* 20:1203-1211.

Kessler, M., J. Böhner, and J. Kluge. 2007. Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. *Ecological Modelling* 207:223-233.

Kessler, M., S. K. Herzog, J. Fjeldså, and K. Bach. 2001. Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and Distribution* 7:61-77.

Killeen, T. J., M. Douglas, T. Consiglio, P. M. Jørgensen, and J. Mejia. 2007. Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography* 34:1357-1373.

Kintz, D. B., K. R. Young, and K. A. Crews-Meyer. 2006. Implications of land use/land cover change in the buffer zone of a national park in the tropical Andes. *Environmental Management* 38:238-252.

Köster, N., K. Friedrich, J. Nieder, and W. Barthlott. 2009. Conservation of epiphyte diversity in an Andean landscape transformed by human land use. *Conservation Biology* 23:911-919.

Liu, J., T. Dietz, S. R. Carpenter, M. Alberti, C. Folke, E. Moran, A. N. Pell, P. Deadman, T. Kratz, J. Lubchenco, E. Ostrom, Z. Ouyang, W. Provencher, C. L. Redman, S. H. Schneider, and W. W. Taylor. 2007. Complexity of coupled human and natural systems. *Science* 317:1513-1516.

Lloyd, H., and S. J. Marsden. 2008. Bird community variation across *Polylepis* woodland fragments and matrix habitats: implications for biodiversity conservation within a high Andean landscape. *Biodiversity and Conservation* 17:2645-2660.

Luteyn, J. L. 2002. Diversity, adaptation, and endemism in Neotropical Ericaceae: biogeographical patterns in the Vaccinieae. *Botanical Review* 68:55-99.

Luteyn, J. L., and S. P. Churchill. 2000. Vegetation of the tropical Andes: an overview. Pp. 281-310 in *Imperfect balance: landscape transformations in the Precolumbian Americas*, edited by D. L. Lentz. New York: Columbia University Press.

McClain, M. E., and R. J. Naiman. 2008. Andean influences on the biogeochemistry and ecology of the Amazon River. *BioScience* 58:325-338.

Meade, B. J., and C. P. Conrad. 2008. Andean growth and the deceleration of South American subduction: time evolution of a coupled orogen-subduction system. *Earth and Planetary Science Letters* 275:93-101.

Miller, D. C., and P. W. Birkeland. 1992. Soil catena variation along an alpine climatic transect, northern Peruvian Andes. *Geoderma* 55:211-223.

Mordecai, R. S., R. J. Cooper, and R. Justicia. 2009. A threshold response to habitat disturbance by forest birds in the Chocó Andean corridor, northwest Ecuador. *Biodiversity and Conservation* 18:2421-2431.

Moritz, R. E., C. M. Bitz, and E. J. Steig. 2002. Dynamics of recent climate change in the Arctic. *Science* 297:1497-1502.

Muriel, S. B., and G. H. Kattan. 2009. Effects of patch size and type of coffee matrix on ithomiine butterfly diversity and dispersal in cloud-forest fragments. *Conservation Biology* 23:948-956.

Myers, N., R. A. Mittermeier, C. G. da Fonseca, A. B. Gustavo, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

Navarro, G., and M. Maldonado. 2002. *Geografía ecológica de Bolivia: vegetación y ambientes acuáticos*. Cochabamba: Editorial Centro de Ecología y Difusión Simón I. Patiño.

Niemann, H., and H. Behling. 2009. Late Pleistocene and Holocene environmental change inferred from the Cocha Caranga sediment and soil records in the southeastern Ecuadorian Andes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 276:1-14.

Orme, A. R. 2007. The tectonic framework of South America. Pp. 3-22 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Pennington, T. R., M. Lavin, D. E. Prado, C. A. Pendry, S. K. Pell, and C. A. Butterworth. 2004. Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 359:515-537.

Pennington, T. R., D. E. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27:261-273.

Postigo, J., K. R. Young, and K. A. Crews. 2008. Change and continuity in a pastoralist community in the high Peruvian Andes. *Human Ecology* 36:535-551.

Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Science of the Umited States of America* 98:4534-4539.

Rangel, J. O., P. D. Lowry, and M. Aguilar (eds.). 1997. *Colombia diversidad biótica II: tipos de vegetación en Colombia*. Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

Restrepo, C., L. R. Walker, A. B. Shiels, R. Bussmann, L. Claessens, S. Fisch, P. Lozano, G. Negi, L. Paolini, G. Poveda, C. Ramos-Scharrón, M. Richter, and E. Velázquez. 2009. Landsliding and its multiscale influence on mountainscapes. *BioScience* 59:685-698.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1-15.

Rodríguez, J. P. 2001. Exotic species introductions into South America: an underestimated threat? *Biodiversity and Conservation* 10:1983-1996.

Ron, S. R., W. E. Duellman, L. A. Coloma, and M. R. Bustamente. 2003. Population decline of the Jambato toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *Journal of Herpetology* 37:116-126.

Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.

Sánchez, D., A. Chacón-Ortiz, F. León, B. A. Han, and M. Lampo. 2008. Widespread occurrence of an emerging pathogen in amphibian communities of the Venezuelan Andes. *Biological Conservation* 141:2898-2905.

Schmidt, S. K., S. C. Reed, D. R. Nemergut, A. S. Grandy, C. C. Cleveland, M. N. Weintraub, A. W. Hill, E. K. Costello, A. F. Meyer, J. C. Neff, and A. M. Martin. 2008. The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils. *Proceedings of the Royal Society of London B, Biological Sciences* 275:2793-2802.

Seimon, T. A., A. Seimon, P. Daszak, S. R. P. Halloy, L. M. Schloegel, C. A. Aguilar, P. Sowell, A. D. Hyatt, B. Konecky, and J. E. Simmons. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology* 13:288-299.

Sierra, R. 2006. A transnational perspective on national protected areas and ecoregions in the tropical Andean countries. Pp. 212-228 in *Globalization and new geographies of conservation*, edited by K. S. Zimmerer. Chicago: University of Chicago Press.

Smith, J. A., B. G. Mark, and D. T. Rodbell. 2008. The timing and magnitude of mountain glaciations in the tropical Andes. *Journal of Quaternary Science* 23:609-634.

Smith, J. A., G. O. Seltzer, D. T. Rodbell, and A. G. Klein. 2005. Regional synthesis of Last Glacial Maximum snowlines in the tropical Andes, South America. *Quaternary International* 138-139:145-167.

Stern, M. J. 1995. Vegetation recovery on earthquake-triggered landslide sites in the Ecuadorian Andes. Pp. 207-220 in *Biodiversity and conservation of Neotropical montane forests*, edited by S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn. New York: New York Botanical Garden.

Swinton, S. M., and R. Quiroz. 2003. Is poverty to blame for soil, pasture, and forest degradation in Peru's Altiplano*? World Development* 31:1903-1919.

Taboada, A., L. A. Rivera, A. Fuenzalida, A. Cistenas, H. Philip, H. Bijwaard, J. Olaya, and C. Rivera. 2000. Geodynamics of the northern Andes: subductions and intracontinental deformations (Colombia). *Tectonics* 19:787-813.

Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology* 12:868-702.

Taylor, D. W. 1991. Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Pliocene age. *Palaeogeography, Palaeoclimatology, Palaeoecology* 88:69-84.

Thomas, E., I. Vandebroek, P. Van Damme, P. Goetghebeur, D. Douterlungne, S. Sanca, and S. Arrazola. 2009. The relation between accessibility, diversity and indigenous valuation of vegetation in the Bolivian Andes. *Journal of Arid Environments* 73:854-861.

Thompson, L. G., E. Mosley-Thompson, H. Brecher, M. Davis, B. León, D. Les, P.-N. Lin, T. Mashiotta, and K. Mountain. 2006. Abrupt tropical climate change: past and present. *Proceedings of the National Academy of Science of the United States of America* 103:10536-10543.

Trauth, M. H., R. A. Alonso, K. R. Haselton, R. L. Hermanns, and M. R. Strecker. 2000. Climate change and mass movements in the NW Argentine Andes. *Earth and Planetary Science Letters* 179:243-256.

Urrutia, R., and M. Vuille. 2009. Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research* 114:D02108.

Veblen, T. T., K. R. Young, and A. R. Orme (eds.). 2007. *The physical geography of South America*. Oxford: Oxford University Press.

Velez, V., J. Cavelier, and B. Devia. 1998. Ecological traits of the tropical treeline species *Polylepis quadrijuga* (Rosaceae) in the Andes of Colombia. *Journal of Tropical Ecology* 14:771-787.

Vilimek, V., M. L. Zapata, J. Klimeš, Z. Patzelt, and N. Santillán. 2005. Influence of glacial retreat on natural hazards of the Palcacocha Lake area, Peru. *Landslides* 2:107-115.

Villwock, W. 1986. Speciation and adaptive radiation in Andean *Orestias* fishes. Pp. 387-403 in *High-altitude tropical biogeography*, edited by F. Vuilleumier and M. Monasterio. New York: Oxford University Press.

Vuille, M., G. Kaser, and I. Juen. 2008. Glacier mass balance variability in the Cordillera Blanca, Peru, and its relationship with climate and the large-scale circulation. *Global and Planetary Change* 62:14-28.

Weigend, M., A. Cano, and E. F. Rodríguez. 2005. New species and new records of the flora in Amotape-Huancabamba zone: endemics and biogeographic limits. *Revista Peruana de Biología* 12:249-274.

Wilcke, W., H. Valladarez, R. Stoyan, S. Yasin, C. Valarezo, and W. Zech. 2003. Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. *Catena* 53:79-95.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Science of the United States of America* 104:5738-5742.

Willis, S. G., D. G. Hole, Y. C. Collingham, G. Hilton, C. Rahbek, and B. Huntley. 2009. Assessing the impacts of future climate change on protected area networks: a method to simulate individual species' responses. *Environmental Management* 43:836-845.

Young, K. R. 2009. Andean land use and biodiversity: humanized landscapes in a time of change. *Annals of the Missouri Botanical Garden* 96:492-507.

Young, B. E. (ed.). 2007. *Distribución de las especies endémicas en la vertiente oriental de los Andes de Perú y Bolivia*. Arlington VA: NatureServe.

Young, K. R. 1989. The tropical Andes as a morphoclimatic zone. *Progress in Physical Geography* 13:13-22.

Young, B. E., I. Franke, P. A. Hernandez, S. K. Herzog, L. Paniagua, C. Tovar, and T. Valqui. 2009. Using spatial models to predict areas of endemism and gaps in the protection of Andean slope birds. *Auk* 126:554-565.

Young, K. R. 1998. Deforestation in landscapes with humid forests in the central Andes: patterns and processes. Pp. 75-99 in *Nature's geography: new lessons for conservation in developing countries*, edited by K. S. Zimmerer and K. R. Young. Madison: University of Wisconsin Press.

Young, K. R., and B. León. 2001. Perú. Pp. 549-580 in *Bosques nublados del Neotrópico*, edited by M. Kappelle and A. D. Brown. Heredia, Costa Rica: INBio.

Young, K. R., and B. León. 1990. Curvature of woody plants on the slopes of a timberline montane forest in Peru. *Physical Geography* 11:66-74.

Young, K. R., B. León, P. M. Jørgensen, and C. Ulloa Ulloa. 2007. Tropical and subtropical landscapes of the Andes Mountains. Pp. 200-216 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

Young, K. R., and J. K. Lipton. 2006. Adaptive governance and climate change in the tropical highlands of western South America. *Climatic Change* 78:63-102.

Young, K. R., and L. O. Rodríguez. 2006. Development of Peru's national protected area system: historical continuity in conservation goals. Pp. 229-254 in *Globalization and new geographies of conservation*, edited by K. S. Zimmerer. Chicago: University of Chicago Press.

Young, K. R., C. Ulloa Ulloa, J. L. Luteyn, and S. Knapp. 2002. Plant evolution and endemism in Andean South America: An introduction. *Botanical Review* 68:4-21.

9

Land Use Changes and their Synergies with Climate Change

César Freddy Suárez, Luis Germán Naranjo, Juan Carlos Espinosa, and Javier Sabogal

The tropical Andes have been a center of human development for over 10,000 years and are considered one of the world's 12 major centers of origin of plants cultivated for food, medicine, and industry (Saavedra and Freese 1986). The long presence of human cultures has caused variable impacts on the region's landscapes and biodiversity. Therefore, understanding the current responses of Andean ecosystems to climate change requires an examination of the processes responsible for these transformations.

In the wake of transformation and replacement of ancient cultures by western civilization, traditional land use systems have also changed, modifying soils, causing loss of plant and animal species, and removing much of the original land cover (Young 2008). Despite the long occupation of the tropical Andes by humans, most of the extensive alterations of natural habitats in the northern Andes have taken place since the beginning of the 20th century (Corrales 2001). Intensification of land and natural resource use continues today, resulting in further habitat loss, fragmentation, and degradation (Palminteri and Powell 2001).

In this chapter we present an overview of the transformation of Andean ecosystems through history and examine the relative importance of different land use change processes to ongoing ecosystem transformation, biodiversity and the possible interactions between these processes and regional climate change.

Historic Land Use Change in the Tropical Andes

When Europeans first arrived in the tropical Andes, they met different cultures along the mountains. Barié (2003) estimates that ca. 243 ethnic-linguistic groups occurred in the Andean region, several of them with influence over large distances. Before the arrival of the Spaniards, most of the Andes were ruled by two dominant nations: the Muisca culture in the northern Andes and the Inka empire, which extended from southern Colombia to northwestern Argentina (Lumbreras 1999, Mann 2005). Although the impact of the different cultures on their environments varied across the region, with the exception of snow peaks and natural barriers of the highlands, practically every type of ecosystem had some kind of occupation in pre-Columbian times (Fernández-Armesto 2002). Cultural activities were characterized by hunting, pottery, fishing, small-scale agriculture (quinua-*Chonopodium quinoa*, cañiwa-*Ch. Pallidicaule*, corn and potatoes-*Solanum tuberosum*), and the domestication of camelids (llama-*Lama glama* and alpaca-*Lama pacos*) and guinea pigs (*Cavia porcellus*).

This heterogeneous spatial pattern of land use was drastically modified during the XVI century, soon after the arrival of the Europeans. After the severe reduction of the indigenous population during the first decades of occupation (Crosby 1986, Denevan 1992), the progressive concentration of land ownership (Aramayo et al. 2004) due to the new social structures introduced by the invaders facilitated the expansion of livestock grazing, large concentrations of human settlements in some areas, and the relocation of entire ethnic groups, often into areas hitherto sparsely occupied (Corrales 2001).

These processes continued during the colonial period and the first republican stages of the Andean countries, and intensified as the young nations initiated their integration into international markets with the export of natural resources and intensified agricultural production to satisfy the needs of a growing population. Intensive production of sugar cane, cocoa, tobacco, and coffee and extensive ranching were among the first large-scale modifiers of the original landscapes of the inter-Andean valleys and the surrounding slopes, mainly in Colombia and Ecuador (Corrales 2001). In Bolivia, the increase in mining, the introduction of livestock (bovine, equine, sheep, and goat) and new crops, combined with new pasturing practices, caused an imbalance in the Andean ecology (Aramayo et al. 2004).

Anthropogenic disturbance and loss of *Polylepis* forests, formerly dominant across a large part of the high (>3500 m) central Andes, are held responsible for the population decreases in more than one half of the plant species (Kessler 2006) and ca. 26% of the bird fauna of the more humid habitats (Fjeldså 2002) mainly through fires and overgrazing of habitats (Ellenberg 1958; Kessler 2000, 2002).

During the first decades of the 20th century, the expansion of the agricultural frontier was responsible for significant transformation of some Andean landscapes. For instance, the colonization of large sectors of the Colombian Andes driven by the expansion of coffee cultivation caused the deforestation of vast landscapes between 1000 and 1500 m, and the introduction of exotic grasses favored the expansion of cattle ranching in many areas (Rivera et al. 2007). In Colombia alone, almost 500,000 ha of natural Andean ecosystems were transformed just between 1910 and 1925 (Corrales 2001).

Landscape Transformation of the 20th Century

The first developments of market driven agricultural systems in the Andean countries set the stage for the implementation of large scale transformations of entire landscapes during the second half of the 20th century. The implementation of the Green Revolution in the northern tropical Andes brought significant economic investments promoting the industrialization of agricultural sectors. As growing monocultures and extensive cattle ranching occupied the fertile inter-Andean valleys, smallholding subsistence farmers were displaced towards peripheral landscapes with the resulting replacement of the original mountain ecosystems (Rivera et al. 2007). Cattle grazing on the steep slopes of the tropical Andes and the intensification of monocultures of barley, potato, onion, and garlic also have taken a heavy toll on cloud forests and *páramos* of the northern Andes (Corrales 2001). In the southern tropical Andes, on the other hand, the 80's agricultural reforms in Bolivia have changed land tenure (Morales 1991) expanding croplands and pastures, and causing major degradation (Aramayo et al. 2004).

Early in the 20th century, the Colombian Andes had the highest percentage of area under agricultural uses among the countries of the tropical Andes, mostly cattle ranching, potatoes (especially in the páramo zones), and coffee, bananas, sugar cane, and flowers in the inter-Andean valleys. Although many of these uses have been in place for decades, there are regions with high land change dynamics such as the Andean-Amazon corridor (upper Putumayo and Caquetá watersheds and Macarena) and the southern Pacific piedmont, due to the deforestation initiated by coca production (Armenteras et al. 2006).

According to Arellano et al. (2000), the main causes of ongoing expansion of the agricultural frontier in Ecuador are demographic growth, social inequity, and the intensification of agriculture techniques. These same authors analyzed the relationship between poverty indices and deforested areas in Carchi Province (El Ángel basin, northern Ecuador) and found that the highest deforestation rates coincide with high poverty levels and population density.

In Peru, the primary Andean crops are potatoes, corn, wheat, and Andean cereals such as quinoa, maca, tarwi and kiwicha (Torres Lozada 2004). In the livestock sector, bovines, pigs and South American camelids (Alpaca, llama and vicuña) are characteristic of small productive units (less than 3 ha),. Studies carried out by Bussink and Hijmans (2000) and Frias (1995) in the Cajamarca province found that the area planted with tubers was decreasing and the area under pasture increasing.

In Bolivia, studies of land use changes in the Yungas and the Alto Beni region of La Paz show increases of 30% in agriculture lands and 20% in anthropogenic secondary vegetation during the period 1987-2001 (Killeen et al. 2005). The area planted with quinua increased until 1990, while since then this trend slowed and there is even evidence of a slight decrease (Crespo Valdivia 2000). As this same author points out, after the first half of the 1980's the amount of land planted with potatoes (the most important cash crop for Bolivian farmers) has also decreased in the Altiplano, while the production of cacao, coffee, cotton, and sugar has increased.

After the 1980's agricultural expansion in some areas of the tropical Andes slowed down due to the increase in agricultural imports in all countries of the region (Corrales 2001, Hervé and Ayangma 2000, Sarmiento et al. 2002). However, the rate of transformation of natural ecosystems in some areas continued unabated, as the less favored sectors of the population sought income alternatives. The expansion of illicit crops, mainly opium poppy and coca, has occurred in vast sectors of the tropical Andes, affecting some of the most fragile ecosystems. According to the United Nations Office on Drugs and Crime (2008a), coca plantations increased by 16% in Colombia, Peru, and Bolivia in 2007. In Colombia alone the increase of these crops caused the deforestation of 170,000 ha between 2001-2007 (United Nations Office on Drugs and Crime 2008b).

On the other hand, mining could be one of the most severe threats now faced by Andean ecosystems, as it represents a growing productive activity with high importance for public finances and corresponding support by governments. Current mining exploitation rights in Peru, Ecuador, and Colombia cover ca. 14% of the total paramo area in these countries, but an additional 14% of these ecosystems is subject to illegal mining (Guerrero 2009)

All of these landuse changes have produced ecosystem losses and degradation throughout the tropical Andes (Table 9.1), with the heaviest toll below 1000 m elevation.The connectivity between high-Andean ecosystems and the lowlands has been severely affected in many places, resulting in multiple threats to biodiversity and the loss of ecosystem services. An example of those effects is mentioned by Weigend et al. (2006) in their examination of the economic importance of ecosystem services provided by 23 relict forests in NW Peru.

Table 9.1. Ecosystem conversion by altitudinal range in the tropical Andes.

Elevational range	% area transformed
< 1000	34.0
1000-2000	28.4
2000-3000	23.8
>3000	11.4

Source: Vegetation map of South America. Eva, H.D et al. 2002

The IPCC's Fourth Assessment Report points out that global CO_2 emission from deforestation and agricultural development correspond to ca. 20% of the total anthropogenic emissions (IPCC 2007). In the Americas emissions from deforestation in Amazonia represent the most important percentage (Achard et al. 2004, DeFries 2002, Houghton 2003). A look at recent trends in the Andean countries reveals that Ecuador had the highest rate of deforestation during 2000 – 2005 (1.7%), and Venezuela the largest area deforested from 1990 to 2005 (4,313,000 ha) (Table 9.2, FAO 2005). Since the statistics of the FAO do not discriminate between types of forests, it is difficult to calculate the impact of deforestation of Andean forests. In Colombia, the most recent estimates indicate a deforestation rate of 118,000 ha/year of which 56,000 ha are in the Andes (Instituto de Hidrología, Meteorología y Estudios Ambientales 2008). This shows the importance of preserving the current natural cover to prevent greenhouse gas (GHGs) emissions due to deforestation and degradation.

Table 9.2. Changes in Forest Cover in Andean countries between 1990 and 2005.

	Area			**Annual Change**			
	1990	**2000**	**2005**	**1990-2000**		**2000-2005**	
	1000 ha			**1000 ha/year**	**%**	**1000 ha/year**	**%**
Bolivia	62.795	60.091	58.740	-270	-0,4	-270	-0,5
Colombia	61.439	60.963	60.728	-48	-0,1	-47	-0,1
Ecuador	13.817	11.841	10.853	-198	-1,5	-198	-1,7
Peru	70.156	69.213	68.742	-94	-0,1	-94	-0,1
Venezuela	52.026	49.151	47.713	-288	-0,6	-288	-0,6

Source: Evaluación de los Recursos Forestales Mundiales 2005: Tablas Mundiales 2005, Food and Agricultural Organization - FAO.

According to the northern and central Andes ecosystem map (Josse et al. 2009), 24% of the Andean region is anthropogenically altered land (agriculture, degraded vegetation), with Venezuela and Colombia being the countries with the highest percentage. Bolivia has the highest proportion of highland vegetation, whereas forest cover for all countries is between 35 and 41% (Table 9.3). Bolivia, Ecuador, and Peru emit three times more CO_2 through land use changes than by burning fossil fuels (Table 9.4) due to the demand for forest resources and the conversion of forest to agricultural and grazing lands (PNCC 2003).

Table 9.3. Land Use Cover Distribution (%) in the Andean Region.

Land cover classes	**Bolivia**	**Colombia**	**Venezuela**	**Ecuador**	**Peru**
Agriculture, degraded vegetation	3.26	59.05	50.98	43.23	12.60
Forest cover	37.29	35.11	35.99	41.25	36.72
Highland shrub, grass and bogs	51.10	4.38	16.66	35.35	6.38
Other montane vegetation	4.12	1.16	3.83	6.10	5.13
Glaciers	0.29	0.03	0.003	3.62	0
Lakes and others water bodies	3.93	0.37	0.25	1.08	0.07

Source: Adapted from Josse et al. (2009).

Table 9.4. Emissions of greenhouse gases (GHG) in the tropical Andean countries

Country	**Proportion of GHG in CO_2^e of Annex 1 countries**	**Proportion of GHG in CO_2^e of all countries**	**Proportion of CO_2 emitted by fossil fuel combustion**	**Proportion of CO_2 emitted by silviculture and land use changes**
Bolivia[a]	0,39	0,22	21,11	77,10
Colombia[b]	0,96	0,54	71,8	21,5
Ecuador[c]	0,50	0,28	28,8	69,5
Perú[d]	0,63	0,36	21	66
Venezuela [e]	1,14	0,65	76,8	14,9
sum	**3,62**	**2,05**		

Source: First National Climate Change Communication. [a] PNCC 2003; data to 2000. [b] Instituto de Hidrología, Meteorología y Estudios Ambientales 2001; data to 1994. [c] Ministerio del Ambiente de Ecuador 2000; data to 1990, [d] CNCC 2001; data to 2000. [e] Ministerio del Ambiente y de los Recursos Naturales 2005; data to 1999. Annex 1 countries refer to industrial countries as defined in the Kyoto protocol.

The production of biofuels has recently become a major driver of land use change in the Andean countries, and laws or programs that promote mixing bioethanol and biodiesel with commercial fuels are in place in Bolivia[1], Colombia[2], Ecuador[3], and Perú[4]. Main energy crops currently promoted in the region include sugar cane, oil palm, and soy. However these crops require special characteristics of precipitation, temperature, soils, topography, elevation, and

---

[1] Bolivia, Law 3207 (September 30, 2005).

[2] Colombia, Ministerio de Minas y Energía, Resolución No. 180687 de 2003; Ministerio de Ambiente, Vivienda y Desarrollo Territorial, Resolución No. 1289 de 2005.

[3] Ministerio de Agricultura, Ganadería, Acuacultura y Pesca, Ministerio del Ambiente, Ministerio de Electricidad y Energía Renovable y Ministerio de Minas y Petróleo de Ecuador (2007), "Biocombustibles". Available at: www.comunidadandina.org/desarrollo/biocombustibles_ecuador.pdf.

[4] Ministerio de Energía y Minas de Perú (2007), "Situación Actual y Perspectivas de los Biocombustibles en el Perú". Available at: www.comunidadandina.org/desarrollo/biocombustibles_peru.pdf.

hydrologic regime that the Andes can offer only in a few zones, especially in the inter-Andean valleys under 1500 m and on flat terrain adjacent to the lowlands. The use of corn, sugar beet, coffee waste, and wheat as energy crops has largely been neglected in Andean countries but may have potential in highland areas.

All of these land uses and drivers (cattle ranching, mining, agriculture, land tenure) have fragmented and isolated ecosystems in the Andean region, impacting biodiversity and its underlying processes. The positive relationship of species density and the size of forest patches has been demonstrated repeatedly (e.g., Kattan et al. 1994, Fernández and Sork 2007, Marsh and Pearman 2007). Andean forest fragmentation may hinder the natural or induced migration of species (Bustamante and Grez 1995) and may also affect microclimates (Didham and Lawton 1999).

The Future: Land Use, Climate Change and Biodiversity in the Tropical Andes

Given the multiple dimensions of the contemporary environmental crisis at multiple scales (MEA 2005) and the pressing need to adapt to climate change, it is pertinent to examine some of the possible relationships between land use change, habitat loss and fragmentation, and biodiversity vulnerability to climate change. Ecosystem modeling using time series of climate variables can be a powerful tool to reveal expected responses of biodiversity to climate changes at the landscape or ecosystem level (Cuesta-Camacho et al. 2008). Spatial modeling can also show how available habitat for a given species can increase or decrease as a consequence of climate change (see Graham et al., Chapter 21, this volume), provided that ecosystem fragmentation does not prevent its movement across landscapes.

A recent study carried out for the eastern Cordillera Real of Colombia, Ecuador, and Peru revealed that climatic changes could impact the distribution of life zones and vegetation types: whereas different types of dry shrub and forest could increase by up to 23-72% by 2050, wet montane forests could decrease by up to 11 - 83% during the same period (Hernández et al. 2010), which will surely increase fragmentation of those ecosystems occupying narrow elevational belts.

On a geologic time scale some species were capable of adjusting their distribution in response to natural climate change, literally running away from extinction (Jablonski 2001, 2008). However, this may no longer be possibile for many species in the near future (Myers and Knoll 2001, Travis 2003). Current ecosystem fragmentation obstructs movement, and fragmentation could disrupt population connectivity within species leading to extirpations and possibly extinctions, thereby altering community composition (Root et al. 2003),. Habitat specialists, especially those of relatively poor colonizing ability, are least able to keep pace with climate change (Travis 2003), and if favorable climate were constrained to areas that are heavily disturbed by land use, this would act as a bottleneck for their long-term survival (Higgins 2007).

The resilience of biodiversity to support agricultural systems must be considered under climate change. Hydrology, soil formation, pollination, seed dispersal, and predator-prey relationships become altered by land conversion processes (Primack and Ros 2002, Van Noordwijk et al. 2004), and these changes alter ecosystem processes and their resilience to environmental change. This has profound consequences for services that humans derive from ecosystems (Chapin et al. 2000). Since these functions depend on future deforestation and degradation, and on how much of the current remaining forests will be in place or even expand (Cramer et al. 2004), it is now more urgent than ever to control further transformation of the remaining natural ecosystems in the region and to prevent direct impacts on biodiversity and on the continued provision of ecosystem services.

Literature Cited

Achard, F., H. D. Eva, P. Mayaux, H.-J. Stibig, and A. Belward. 2004. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. Global Biogeochemical Cycle 18:GB2008.

Aramayo, C., F. Fonturbel, S. Palomeque, and R. Rocha. 2004. La region altoandina de Bolivia. In Ecología, medio ambiente y desarrollo sostenible: algunos ejemplos prácticos, edited by F. Fonturbel, C. Ibañez, and C. Aramayo. CD-ROM. La Paz: Editorial Publicaciones Integrales.

Arellano, P., S. Poats, M. Proaño, and C. Crissman. 2000. Pobreza rural y deterioro ambiental en la cuenca del rio El Angel, Carchi – Ecuador. Quito: Consorcio para el Desarrollo Sostenible de la Ecorregión Andina. Available at: http://www.condesan.org/memoria/Docspolitics.htm#Pobreza%20Rural.

Armenteras, D., G. Rudas, N. Rodriguez, S. Sua, and M. Romero. 2006. Patterns and causes of deforestation in the Colombian Amazon. Ecological Indicators 6:353-368.

Barié, C. G. 2003. Pueblos indígenas y derechos constitucionales en América Latina: un panorama. Mexico City: Instituto Indigenista Interamericano, Comisión Nacional para el Desarrollo de los Pueblos Indígenas, and Editorial Abya-Yala.

Bussink, C. B., and R. J. Hijmans. 2000. Land-use change in the Cajamarca catchment, Peru, 1975-1996. Pp. 421-428 in Enriching the portfolio: CIP's global and regional partnerships. CIP Program Report 1999-2000. Available at: http://www.cipotato.org/publications/program_reports/99_00/enriching.asp.

Bustamante, R., and A. Grez. 1995. Consecuencias ecológicas de la fragmentación de los bosques nativos. Ambiente y Desarrollo 11(2):58-63.

Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000. Consequences of changing biodiversity. Nature 405:234-242.

Corrales, E. 2001. Andes del norte: principales tendencias socioeconómicas y su relación con la biodiversidad. Appendix C in Visión de conservación de la biodiversidad en los Andes del Norte, edited by S. Palminteri and G. Powell. Cali, Colombia: WWF, FUDENA, and Fundación Natura.

Comisión Nacional de Cambio Climático. 2001. Comunicación nacional del Peru a la Convención de las Naciones Unidas sobre cambio climático: primera comunicación. Lima: Consejo Nacional del Ambiente. 155 pp. Available at: http://unfccc.int/resource/docs/natc/pernc1.pdf.

Cramer, W., A. Bondeau, S. Schaphoff, W. Lucht, B. Smith, and S. Sitch. 2004. Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. Philosophical Transactions of the Royal Society of London B, Biological Sciences 359:331-343.

Crespo Valdivia, F. 2000. Incidencia de las reformas estructurales sobre la agricultura boliviana. Serie Desarrollo Productivo 98. Santiago de Chile: Naciones Unidas. 55 pp. Available at: http://www.eclac.org/publicaciones/xml/3/5753/LCL1455P.pdf.

Crosby, A. W. 1986. Ecological imperialism: the biological expansion of Europe, 900-1900. New York: Cambridge University Press.

Cuesta-Camacho, F., M. Peralvo and A. Ganzenmüller. 2008. Posibles efectos del calentamiento global sobre el nicho climático de algunas especies en los Andes Tropicales. Chapter 4 in Páramo y Cambio Climático 23 – Serie Páramo, edited by P. Mena and G. Maldonado. Quito: Grupo de Trabajo en Páramos del Ecuador/EcoCiencia.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole, and J. Townshend. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 99:14256-14261.

Denevan, W. M. 1992. The native population of the Americas in 1492. Madison: University of Wisconsin Press.

Didham, R. K., and J. H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17-30.

Ellenberg, H. 1958. Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. Umschau 1958:645-681.

Eva, H. D., E. E. de Miranda, C. M. Di Bella, V. Gond, O. Huber, M. Sgrenzaroli, S. Jones, A. Coutinho, A. Dorado, M. Guimarães, C. Elvidge, F. Achard, A. S. Belward, E. Bartholomé, A. Baraldi, G. De Grandi, P. Vogt, S. Fritz, and A. Hartley. 2002. A vegetation map of South America. European Commission, Joint Research Centre. Available at: http://www.cobveget.cnpm.embrapa.br/resulta/relat/vegetation.pdf

FAO. 2005. Evaluación de los recursos forestales mundiales 2005: tablas mundiales 2005. Food and Agricultural Organization. Available at: http://www.fao.org/forestry/site/32006/sp

Fernández-Armesto, F. 2002. Civilizaciones, la lucha del hombre por controlar la naturaleza. Bogotá: Taurus.

Fernández-M., J. F., and V. L. Sork. 2007. Genetic variation in fragmented forest stands of the Andean Oak Quercus humboldtii Bonpl. (Fagaceae). Biotropica 39:72-78.

Fjeldså, J. 2002. Polylepis forests – vestiges of a vanishing ecosystem in the Andes. Ecotropica 8:111-123.

Frias, C. 1995. Pobreza campesina. Sólo un problema rural? Cajamarca: economía, espacio y tecnología. Lima: Intermediate Technology Development Group. 153 pp.

Guerrero, E. 2009. Implicaciones de la minería en los páramos de Colombia, Ecuador y Perú. CONDESAN – Proyecto Páramo Andino. Available at: http://www.infoandina.org/site.shtml?x=27822.

Hernández, O. L., C. F. Suárez, and L. G. Naranjo. 2010. Análisis de vulnerabilidad al cambio climático en la Cordillera Real Oriental (Colombia, Ecuador y Perú). Pp. 65-82 in Experiencias de adaptación al cambio climático en ecosistemas de montaña en los Andes del Norte, edited by C. L. Franco-Vidal, A. M. Muñoz, G. I. Andrade, and L. G. Naranjo. Santiago de Cali: Fundación Humedales and WWF Colombia. Available at: http://assets.panda.org/downloads/cambio_climatico_archivo_web_final.pdf.

Hervé, D., and S. Ayangma. 2000. Dynamique de l'occupation du sol dans une communauté agropastorale de l'altiplano bolivien. Revue de Géographie Alpine 88(2):69-84.

Higgins, P. A. T. 2007. Biodiversity loss under existing land use and climate change: an illustration using northern South America. Global Ecology and Biogeography 16:197-204.

Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000. Tellus, Series B, Chemical and Physical Meteorology 55:378-390.

Instituto de Hidrología, Meteorología y Estudios Ambientales. 2001. Colombia. Primera comunicación nacional ante la convención marco de las Naciones Unidas sobre cambio climático. Bogotá: Instituto de Hidrología, Meteorología y Estudios Ambientales. 267 pp. Available at: http://unfccc.int/resource/docs/natc/colnc1.pdf.

Instituto de Hidrología, Meteorología y Estudios Ambientales. 2008. Resumen técnico del módulo uso de la tierra, cambio en el uso de la tierra y silvicultura del inventario nacional de GEI años 2000 y 2004. Bogotá: Instituto de Hidrología, Meteorología y Estudios Ambientales. 11 pp. Available at: http://www.cambioclimatico.gov.co/documentos/lulucf.pdf.

IPCC. 2007. Couplings between changes in the climate system and biogeochemistry. In Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by S. Soloman, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

Jablonski, D. 2001. Lessons from the past: evolutionary impacts of mass extinctions. Proceedings of the National Academy of Sciences of the United States of America 98:5393-5398.

Jablonski, D. 2008. Extinction and the spatial dynamics of biodiversity. Proceedings of the National Academy of Sciences of the United States of America 105(Suppl. 1):11528-11535.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009a. Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

Kattan, G. H., H. Álvarez-López, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology 8:138-146.

Kessler, M. 2000. Observation on a human-induced fire event at a humid timberline in the Bolivian Andes. Ecotropica 6:89-93.

Kessler, M. 2002. The "Polylepis problem": where do we stand? Ecotropica 8:97-110.

Kessler, M. 2006. Bosques de Polylepis. Pp. 110-120 in in Botánica económica de los Andes centrales, edited by M. Moraes R., B. Øllgaard, L. P. Kvist, F. Borchsenius, and H. Balslev. La Paz: Universidad Mayor de San Andrés.

Killeen, T. J., T. Siles, L. Soria, and L. Correa. 2005. Estratificación de vegetación y cambio de uso de suelo en los Yungas y Alto Beni de La Paz. Ecología en Bolivia 40(3):32-69.

Lumbreras, L. G. (ed.). 1999. Historia de América Andina. Quito: Universidad Andina Simón Bolívar, Libresa. 605 pp.

Mann, C. C. 2005. 1491, new revelations of the Americas before Columbus. New York: Vintage Books.

Marsh, D. M., and P. B. Pearman. 2007. Effects of habitat fragmentation on the abundance of two species of leptodactylid frogs in an Andean montane forest. Conservation Biology 11:1323-1328.

Ministerio del Ambiente de Ecuador. 2000. Inventario Nacional de Gases de Efecto Invernadero Sector Forestal 1994. Quito: Ministerio del Ambiente. 47 pp. Available at: http://www.planetaverde.org/mudancasclimaticas/index.php?ling=por&cont=contribuicoes&codpais=6.

Ministerio del Ambiente y de los Recursos Naturales. 2005. Primera comunicación nacional en cambio climática de Venezuela. Caracas: Ministerio del Ambiente y de los Recursos Naturales, Programa de las Naciones Unidas para el Desarrollo, and Fondo Mundial para el Medio Ambiente.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Washington, DC: Island Press.

Morales, J. A. 1991. Reformas estructurales y crecimiento económico en Bolivia. Instituto de Investigaciones Socio Económicas, Universidad Católica Boliviana. 39 pp. Available at: http://www.iisec.ucb.edu.bo/.

Myers, N., and A. W. Knoll. 2001. The biotic crisis and the future of evolution. Proceedings of the National Academy of Sciences of the United States of America 98:5389-5392.

Palminteri, S., and G. Powell (eds). 2001. Visión de conservación de la biodiversidad en los Andes del Norte. Cali, Colombia: WWF, FUDENA, and Fundación Natura.

Primack, R., and J. Ros. 2002. Introducción a la biología de la conservación. Barcelona: Editorial Ariel.

Programa Nacional de Cambios Climáticos. 2003. Inventario nacional de emisiones de gases de efecto invernadero de Bolivia para la década 1990-2000 y su análisis tendencial. La Paz: Ministerio de Desarrollo Sostenible y Planificación, Viceministerio de Medio Ambiente y Recursos Naturales.

Rivera, C. C., L. G. Naranjo, and A. M. Duque. 2007. De “María” a un mar de caña. Imaginarios de naturaleza en el Valle del Cauca entre 1950 y 1970. Cali: Universidad Autónoma de Occidente.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweigk, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57-60.

Saavedra, C., and C. Freese. 1986. Prioridades biológicas de conservación en los Andes tropicales. Parks/Parques/Parcs 11:8-11.

Sarmiento, L., J. K. Smith, and M. Monasterio. 2002. Balancing conservation of biodiversity and economic profit in the high Venezuelan Andes: is fallow agriculture an alternative? Pp. 283-293 in Mountain biodiversity: a global assessment, edited by C. Körner and E. M. Spehn. London: Parthenon Publishing.

Torres Lozada, V. 2004. La agricultura peruana en los tiempos del TLC. Lima: Confederación Campesina del Perú. 16 pp. Available at: http://www.aprodeh.org.pe/tlc/documentos/victor_torres.pdf.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London B, Biological Sciences 270:467-473.

United Nations Office on Drugs and Crime. 2008a. World drug report 2008. United Nations Publication Nº E.08.XI.1. Vienna: United Nations Office on Drugs and Crime. 305 pp.

United Nations Office on Drugs and Crime. 2008b. Censo de cultivos de coca 2007. Bogotá: United Nations office on Drugs and Crime. 101 pp.

Van Noordwijk, M., J. G. Poulsen, and P. Ericksen. 2004. Quantifying off-site effects of land use change: filters, flows and fallacies. Agriculture, Ecosystems and Environment 104:19-34.

Weigend, M., N. Dostert, and E. Rodriguez-Rodriguez. 2006. Bosques relictos de los Andes peruanos: perspectivas económicas. Pp 130-145 in in Botánica económica de los Andes centrales, edited by M. Moraes R., B. Øllgaard, L. P. Kvist, F. Borchsenius, and H. Balslev. La Paz: Universidad Mayor de San Andrés.

Young, K. R. 2008. Stasis and flux in long-inhabited locales: change in rural Andean landscapes. Pp. 11-32 in Land-change science in the tropics: changing agricultural landscapes, edited by A. Millington and W. Jepson. New York: Springer.

10

Physical Geography and Ecosystems in the Tropical Andes

Carmen Josse, Francisco Cuesta, Gonzalo Navarro, Víctor Barrena, María Teresa Becerra, Edersson Cabrera, Eulogio Chacón-Moreno, Wanderley Ferreira, Manuel Peralvo, José Saito, Antonio Tovar, and Luis G. Naranjo

Due to their fairly recent uplifting, the Northern and Central Andes have played a key role in the diversification of tropical South American biota (e.g., Heindl and Schuchmann 1998; Kattan et al. 2004). Several studies focusing on Andean biogeography (e.g., Roy et al. 1997; García-Moreno et al. 1999) showed that montane biota are the product of a combination of two important factors: (a) geological events with local to regional impacts on community structure and ecological processes, and (b) recent continental to global ecological changes caused by Croll-Milankovitch climatic cycles that last about 20,000 years and are determined by variations in the earth's orbit around the sun.

The tropical Andes top the list of worldwide hotspots for endemism and the number of species/area ratio (Myers et al. 2000). The snow capped peaks, steep slopes, deep canyons, and isolated valleys of these mountains have led to a large diversity of microhabitats favoring speciation. Moreover, their location between the lowlands of the Amazon, the Chiquitanía, and the Gran Chaco to the east and the Chocó, Tumbes-Guayaquil, and the arid systems of the Sechura Desert to the west determines complex dynamics of species exchange and isolation.

This biodiversity hotspot is also identified as one of the most severely threatened areas in the tropics (Mittermeier et al. 1999; Jetz et al. 2007). The long history of human occupation in the Andean region has transformed and re-shaped a significant proportion of its landscapes. Human occupation has contributed to the domestication of numerous species, turning this region into one of the world's 12 major centers of origin of plants cultivated for food, medicine, and industry (Saavedra and Freese 1986). During the last century, concentration of the human population in the inter-Andean valleys and the valleys of the Andean ridge has transformed an important part of the natural vegetation cover, causing losses in its biological richness, especially in the Northern Andes (Wassenar et al. 2007; Bruinsma 2003).

The threats to the tropical Andes' biodiversity are myriad, and in recent years they have been compounded by the manifold impacts of climate change. Given the complexity of these dynamics, tackling the challenges imposed by global change in the region requires a basic understanding of its main geographic features and ecological systems. In this chapter we provide an overview.

Geographic Features

The tropical Andes are the longest and widest cool region in the tropics, as they extend over 1.5 million km2, from 11º N to 23º S, occupying an elevation range from around 600-800 m up to some 6,000 m above sea level. Besides the characteristic Andean features of steep slopes, deep gorges, and wide valleys, a vast mountain plain, the Altiplano, extends at elevations above 3,500 m across much of southern Peru and western Bolivia. A large number of snow-capped peaks are found throughout the tropical Andes; the treeline occurs between 3,800–4,500 m near the equator and above 4,500 m from 15º S to the southern limit of the region.

Compared to the Central Andes, the Northern Andes are relatively small, extending from Venezuela to northern Peru. In Venezuela, the Andes form two branches that originate in the 'Nudo de Pamplona', in the Colombian territory. The northerly branch forms the Sierra de Perijá. The other branch is the main cordilleran massif, commonly called the 'Cordillera de Mérida'. The Maracaibo Lake basin separates these two mountain ranges. In Colombia the Andes are divided into three main ridges, which stem from a massif located at 2ºN, and are separated by two valleys running from south to north: the Magdalena valley separates the Eastern from the Central Cordillera, and the Cauca valley separates the Central from the Western Cordillera. The latter mountain chain is relatively low and lacks snow-covered peaks. The Central Cordillera is the highest of the three branches and contains several active strato volcanoes, some of them partially covered by snow (Fjeldså and Krabbe 1990).

To the south of the Colombian massif (Nudo de Los Pastos), and across Ecuador until 3ºS, the Andes form two parallel mountain chains, the Eastern and Western cordilleras, which run from north to south forming a narrow (150–180 km wide) stretch of some 600 km (Clapperton 1993). These two branches of the Ecuadorian Andes are not completely defined as separate chains, but still give rise to a series of inter-Andean valleys above 2,000 m of elevation. South of the Paute–Cuenca–Girón Valley, the Northern Andes are lower. The tallest peaks are found southeast of Cuenca and reach 4,130 m, but all other areas are below 4,000 m.

In southern Ecuador and northern Peru the Andes form an intricate mosaic of mountain systems, some of them running from north to south and others from east to west. At this point, the Northern Andes not only get lower, but also loose humidity around the confluence of the Chinchipe River with the Marañón and Huancabamba rivers (Josse et al. 2009a). The Porculla Pass in the Huancabamba depression (6°S, 2,145 m) defines the limit between the northern and the central portions of the tropical Andes. South to the department of Cajamarca in Peru, the Marañón Valley separates the Central from the Western Cordillera. The Central Cordillera is continuous but lower than the Western Cordillera, crowned by snow peaks reaching more than 6,000 m, and separated into several discontinuous massifs (cordilleras Blanca, Huayhuash, and Raura).

In the Peruvian department of Junín the two cordilleras converge around Lake Junín. From this point to the south, the Andes are continuous and high, as there is not a single mountain pass lower than 4,000 m. From Cusco to central Bolivia the eastern Andes form a single mountain chain only interrupted by two deep canyons in La Paz (Josse et al. 2009a). West of the latter, the Peruvian-Bolivian altiplano is an area of wide, internally drained plains, containing large lake complexes. The whole region was historically covered by a giant lake that after several cycles of flooding and subsequent glacial periods is currently fragmented into several lakes (Servant and Fontes 1978, Ballivian and Risacher 1981, Argollo and Mourguiart 1995). In the north, Lake Titicaca occupies 8,300 km^2 and drains to the south into the brackish Lake Poopó. At the southern limit of the Altiplano, the also brackish Uyuni and Coipasa lakes are annually flooded during the rainy season. These two lakes cover 10,000 and 2,220 km^2, respectively. The Cordillera Real and the Central Andes reach their southern limit in the Tunari-Cochabamba complex (Fjeldså and Krabbe 1990).

Plant Geography

The Northern Andes occupy approximately 490,000 km^2, from 11ºN in the Sierra Nevada de Santa Marta Massif in northern Colombia to 6ºS at the Porculla Pass of Peru (Van der Hammen 1974, Simpson 1975). They form a large phyto-geographic region divided into two subregions: the so called Páramos and the North-Andean forest ecosystems (Josse et al. 2009a; Figure 10.1). The latter show a mixture of several floristic elements from the surrounding lowlands, and regional variations of species composition in the montane (upper and lower) and sub-Andean altitudinal belts towards the Caribbean, Chocó, Orinoco, and Amazon.

The vegetation of the Northern Andes can be grouped into moist montane forests, seasonal and xerophytic scrubs, and páramo grasslands proper, including shrubby boundaries with the forest downslope and superpáramo above. Montane forests cover most of the region, whereas páramos are insular formations around the highest peaks. Scrub is restricted to the lower portion of the inter-Andean valleys, following the course of main rivers such as the Magdalena and Guayllabamba and smaller deep gorges and valleys throughout the region (Josse et al. 2009a). Páramos occupy the lower section of the high-Andean belt and form distinct plant communities; these ecosystems harbor the most diverse mountain flora in the world (Smith and Cleef 1988) and have high levels of endemism both for species and genera (Sklenár and Ramsay 2001). Northern Andean forests occur mostly between 3,000–3,300 m and 1,500 m above sea level, with sub-Andean forests further down to around 700 m elevation.

Physiographic features have created a natural barrier between the Northern and the Central Andes, expressed in differences in species composition of flora and fauna among both regions (Duellman 1979, 1999, Duellman and Wild 1993, Weigend 2002). The area between the Porculla Pass and the beginning of the Cordillera Negra in the Peruvian departments of La Libertad and Ancash (8°30'S) is considered a transitional zone, called “Jalca” by some authors, between these two subdivisions of the tropical Andes (Simpson and Todzia 1990; Gentry 1982). This biogeographically distinct zone occurs throughout the high elevations of the Andes in northern Peru west of the Marañón River (Sánchez-Vega and Dillon 2006; Weigend 2002, 2004).

The area north of the Porculla pass up to the Giron-Paute valley at 3°S in southern Ecuador constitutes another transitional zone inside the Northern Andes; this region is sharply delineated by the Paute Cuenca-Giron valley in an area where the Andes decrease in size and form a complex pattern of ridges and junctions that run east-west rather than north-south (Ulloa and Jorgensen 1993; Jorgensen et al. 1995). The fundamental difference between the north and south portion of the Northern Andes is the active volcanism present in the north during the last 2.5 million years, which has had a profound impact on topography and soils.

The Central Andes encompass four phyto-regions: Yungas, Moist Puna, Xeric Puna and Bolivian-Tucuman (Josse et al. 2009a). The Yungas are found throughout the eastern side of the Central Andes following the eastern versant of the Marañon river in Peru to central Bolivia, between the Moist Puna to the west and the lowlands of the Amazon to the east (Cabrera and Willink 1973). From 6º to 13ºS, the Yungas are associated with a discontinuous sub-Andean mountain system which causes rivers descending the Eastern Cordillera to run in a northerly direction, forming wide valleys parallel to the cordillera, before continuing towards the Amazon lowlands (Josse et al. 2009a). The ecological conditions at the highest eastern peaks of this low sub-Andean belt are very peculiar; Andean and Amazonian species and ecosystems form spatial mosaics in the alluvial valleys above 1.000 m, surrounded by slopes covered by montane forests. The altitudinal range occupied by the Yungas is very wide (500–4,000 m). Because of the steep slopes of these mountains, it is possible to find altitudinal gradients of three to four thousand meters in a horizontal distance of only 50–100 km. These forests are distributed in two altitudinal belts that run along the eastern slopes of the Andes: the sub-Andean belt below 2,000 m of elevation and the cordilleran belt proper, which runs above 2,000 m and includes three ecological subdivisions: the montane, the upper-montane, and the lower portion of the high Andean zone.

The Moist Puna occurs from northern Peru to the central portion of the eastern cordillera in Bolivia, including the high-Andean basin of Lake Titicaca. This almost flat basin was filled up several times during the Holocene by sediments of fluviolacustrine and fluvioglacial origin. This biogeographic unit also covers a wide altitudinal range, from 2,000 m in the inter-Andean valleys to more than 6,000 m on the high peaks of the cordillera. Most of the original vegetation of the upper-montane and high Andean belts of the Moist Puna was probably formed by forests of *Polylepis* spp., dominated in each mountain massif by endemic species (Josse et al. 2009a). However, the ancestral land uses by the human settlers of this landscape have significantly reduced these forests, replacing them with grasslands and scrub which, too, harbor important diversity. In the topographic depressions, as well as surrounding lakes and other water courses, there are numerous wetlands and peat bogs, some of them of considerable size.

The Xeric Puna occurs mainly in the central-southern portion of western Bolivia and northwestern Argentina, and sparsely in adjacent areas of southwestern Peru and northeastern Chile. As the previous biogeographic units, this formation occupies a wide altitudinal belt, from approximately 2,000 m in the high eastern valleys (also called Pre-Puna) up to 6,000 m on the tall snow-capped peaks and volcanoes of the western cordillera. The Andean Altiplano, one of the largest mountain plains in the world, is part of the Xeric Puna. This vast plain has a mean altitude of 3,650 m and is located in the widest sector of the Andean chain. Vegetation of the Xeric Puna is highly diversified and forms several unique ecosystems, such as the salt flats, which comprise the largest saline mountain ecosystem on Earth.

The Bolivian-Tucuman biogeographic province extends beyond the Yungas to the south along the slopes of the eastern ridges of the Andean Cordillera, from central Bolivia to northwestern Argentina between 600 m and almost 4,000 m of elevation. To the west, it is bounded by the Xeric Puna and to the east by the Bolivian Chiquitanía and the Gran Chaco. Most of the Bolivian-Tucuman province occupies the sub-Andean belt below 2,000 m of elevation. Although the vegetation of this province shares some elements with these neighboring floristic provinces, it also contains a large number of endemics (Josse et al. 2009a).

Figure 10. 1. Map of floristic regions of the tropical Andes (Josse et al. 2009a).
This map does not represent official information of any of the five countries, but rather represents an exercise in information integration and analysis.

Ecosystems of the Tropical Andes

Classifying the wealth of ecosystems of the tropical Andes has proved to be a difficult task, especially because of the different approaches taken by researchers and institutions of the different countries and the lack of a coherent effort to unify criteria for classification. Josse et al. (2009a, b) made the most recent attempt to address this problem and produced an ecosystem map for the whole region (http://www.comunidadandina.org/public/libro_92.htm), integrating earlier maps for the different countries (Navarro and Ferreira 2007 for Bolivia; Rodríguez et al. 2004 for Colombia; Peralvo et al. 2006 for Ecuador; Josse et al. 2007 and INRENA 2000 for Peru; Ataroff and Sarmiento 2003 for Venezuela).

The thematic homologation of the cartographic information made by these authors was based on NatureServe's classification of ecological systems of the Western Hemisphere (Comer et al. 2003; Josse et al. 2003) (http://www.natureserve.org/infonatura). According to this classification, a terrestrial ecological system is defined as a group of local-scale plant communities that co-occur in a given landscape, thus sharing ecological processes (e.g., fire cycles, floods), substrates (e.g., superficial soils, parent rock), and/or environmental gradients (e.g., bioclimate, elevation, hydrologic patterns) (Josse et al. 2003).

Classification Framework

Historically, terrestrial ecosystems have been defined in a variety of ways. Some approaches focus on biotic components like vegetation, either as 'existing vegetation' – what one observes in the field (e.g., Rodwell et al. 2002) – or as 'potential vegetation' – what the presence of plant species indicate for successional sequences and potential biomass productivity of a site (Daubenmire 1966). Other approaches focus directly on abiotic components: the physical features of landscapes that define recurrent ecologically-relevant patterns (e.g., Rowe and Barnes 1994; Bailey 1995; Racey et al. 1996; USDA Forest Service 2006).

The NatureServe ecological systems classification borrows elements of each of these approaches to describe integrated units of recurring vegetative assemblages that depend on recurrent local-scaled physical features and dynamic processes. This approach is not unlike many previous efforts to characterize natural community types (e.g., Whittaker 1962; 1975). Whereas vegetation classifications provide a conceptual/taxonomic hierarchy to organize existing vegetation classification units, terrestrial ecological systems describe the common co-occurrence of local-scale vegetation units on the ground. Both forms of classification serve as practical tools for ecological mapping and assessment.

The ecological systems classification and derivative maps aim to provide comprehensive local-scale ecosystem information to natural resource managers. The approach of linking existing vegetation communities based on the similarity of their biophysical setting, environmental gradients and/or dynamic processes tends to produce more realistic interpretations of a given landscape, compared to many vegetation classification types. The modular structure of the NatureServe terrestrial ecological systems classification is a result of the core assumption that plant communities tend to co-occur in a given landscape and that the landscape can be characterized by particular combinations of environmental factors, with varying diagnostic classifiers depending upon the geography.

The complex topography, altitudinal and latitudinal gradients of the tropical Andes result in a significant climatic heterogeneity that must be taken into account in a classification of the numerous ecosystems in this region. To this end, Josse et al. (2009a) followed the system of bioclimatic classification developed by Rivas-Martínez et al. (1999), based on comparative analyses of primary data from meteorological stations and the types of vegetation present in a given area. This protocol allowed the homologation of existing classifications for the different countries, as well as grouping the ecosystems at a higher hierarchical level (macro-groups). Floristic composition is another key criterion in this classification approach, thus systems that otherwise share similar vegetation structure, environmental settings, and ecological processes, are distinguished based on their composition.

Classification Results and Discussion

Josse et al. (2009b) mapped 56 macro-groups and 133 ecosystems for the Tropical Andes (Table 10.1; descriptions for each type can be found at: http://www.natureserve.org/publications/pubs/EcosistemasAndesNorteYCentro.pdf. Most of the identified ecosystems have a limited/restricted distribution; for instance, 102 ecosystems have extensions of less than 1 million hectares, and only 31 (23%) present a broad distribution. This asymmetry in the spatial distribution of ecosystems reflects the high level of beta diversity (geographical species turnover) that characterize the Andean region.

Both the Northern Andes and the Bolivian - Tucuman floristic regions encompass the largest number of altitudinal belts in the region, as they span from the lower tropical thermal zone (~700 m) to the cryotropical zone (>4.500 m) in the Northern Andes, and from the tropical thermal zone to the supratropical in the Bolivian-Tucuman region. This explains why these two phytogeographic regions contain the largest number of ecosystems and macrogroups (Table 10.2). The highest number of forest ecosystems (beta diversity) is found in the Bolivian-Tucuman region, and the largest number of non forested ecosystems (grasslands, salt plains, high elevation wetlands) is found in the Xeric Puna and the Moist Puna. These latter two provinces also have several ecosystems with restricted distribution, which explains their high levels of endemism.

The distribution patterns of macro-groups among phytogeographic areas clearly show that both the Xeric Puna and the Moist Puna have the most widely distributed ecosystems in the tropical Andes. This is due, to a large extent, to the vastness of the Altiplano between Peru and Bolivia in the widest portion of the Andean range (450 km in southern Bolivia). The Northern Andes, on the other hand, contain the largest number of macro-groups with less than 2 million hectares, with the exception of the sub-Andean moist forest and the humid montane forest. The famed ecosystem diversity of this phytogeographic region is thus explained by the high turnover of environmental conditions across short distances.

According to Josse et al. (2009a), 78% of the area of the tropical Andes still maintains a natural vegetation cover. The distribution of the areas transformed by human intervention is asymmetrical and highly concentrated in the Northern Andes (Table 10.3), where anthropogenic areas (236,689 km^2) surpass natural vegetation (197,635 km^2) in extent. However, the identification of “natural” ecosystems in this complex region is still a matter of debate among specialists, remarkably so the classification of the high Andean grasslands in Peru and Bolivia, which in spite of mainly being composed of native species, are cultural landscapes that have been managed for centuries. The development of new methods using high resolution optical remote sensing data, together with ground-truthing should be seen as a main research priority to overcome this problem and reduce the omission error of classifying degraded puna areas as natural systems.

In spite of the unresolved discussion of which classification system should be used to represent the enormous biodiversity of the tropical Andes at the ecosystem level, this work presents a solid approach to produce an integrated regional ecosystem map for the five Andean countries. The map takes into account the single effort of each country and creates an integrated and coherent map that will be used for conservation planning at the regional level. Further, the presented ecosystem map represents a baseline to produce further climate change vulnerability analyses as well as a reference to develop deforestation analyses and other related research topics in the tropical Andes.

This exercise allowed the analysis of existing information on ecosystems and vegetation at national level. A need was identified to integrate methodological approaches to more accurately represent the current state of ecosystems at a regional scale since maps of the five countries were developed based on information of varying quality, particularly with respect to remnant natural vegetation

Table 10.1a. List of ecological systems by floristic region - **Northern Andes**

Sistema Ecologico	**Ecological System**
Arbustal montano xerico interandino de los Andes del Norte	Northern Andes inter-Andean montane xeric shrubland
Vegetacion saxicola montana interandina de los Andes del Norte	Northern Andes inter-Andean montane saxicolous vegetation
Arbustal saxicola montano de las cordilleras subandinas orientales	Eastern sub-Andean ridge montane saxicolous shrubland
Arbustal y herbazal sobre mesetas subandinas orientales	Eastern sub-Andean plateau shrubland and grassland
Arbustal montano de los Andes del Norte	Northern Andes montane shrubland
Arbustal montano bajo xerico interandino de los Andes del Norte	Northern Andes inter-Andean lower montane xeric shrubland
Bosque altimontano siempreverde de los Andes del Norte	Northern Andes upper montane evergreen forest
Bosque de *Polylepis* altimontano pluvial de los Andes del Norte	Northern Andes upper montane *Polylepis* pluvial forest
Bosques bajos y arbustales altoandinos paramunos	High Andean paramo dwarf shrubland
Bosque altimontano de las cordilleras subandinas orientales	Eastern sub-Andean ridge upper montane forest
Bosque montano bajo pluvial de la cordillera del Condor	Cordillera del Condor lower montane pluvial forest
Bosque montano pluvial de las cordilleras subandinas orientales	Eastern sub-Andean ridge montane pluvial forest
Bosque pluvial sobre mesetas de arenisca de la Cordillera del Condor	Cordillera del Condor sandstone plateau pluvial forest
Bosque montano pluviestacional de los Andes del Norte	Northern Andes montane seasonal evergreen forest
Bosque montano pluvial de los Andes del Norte	Northern Andes montane pluvial forest
Bosque montano bajo pluviestacional subhumedo de los Andes del Norte	Northern Andes lower montane semideciduous forest
Bosque piemontano pluviestacional subhumedo de los Andes del Norte	Northern Andes foothill semideciduous forest
Bosque montano bajo pluvial de los Andes del Norte	Northern Andes lower montane pluvial forest
Bosque montano bajo pluviestacional humedo de los Andes del Norte	Northern Andes lower montane seasonal evergreen forest
Bosque piemontano pluvial de los Andes del Norte	Northern Andes foothill pluvial forest
Bosque montano bajo xerico de los Andes del Norte	Northern Andes lower montane xeric forest
Bosque piemontano xerico de los Andes del Norte	Northern Andes foothill xeric forest
Bofedales altimontanos paramunos	Upper montane paramo bogs
Bofedales altoandinos paramunos (Turberas)	High-Andean paramo bogs
Arbustales bajos y matorrales altoandinos paramunos	High-Andean shrubby paramo
Arbustales y frailejonales altimontanos Paramunos	Upper montane paramo shrublands and frailejonales
Matorral edafoxerofilo en cojin altoandino paramuno	High-Andean paramo cushion vegetation
Pajonal altimontano y montano paramuno	Upper montane and montane paramo grassland
Pajonal arbustivo altimontano paramuno	Upper montane shrubby paramo
Pajonal edafoxerofilo altimontano paramuno	Upper montane subhumid paramo grassland
Sabana arbolada montano baja de los Andes del Norte	Northern Andes lower montane treed savanna
Vegetacion geliturbada y edafoxerofila subnival paramuna	High Andean fell fields

Table 10.1b. List of ecological systems by floristic region - **Bolivian - Tucuman**

Sistema Ecologico	**Ecological System**
Matorral xerico montano Boliviano-Tucumano	Bolivian-Tucuman montane xeric scrub
Bosque altimontano pluviestacional Boliviano-Tucumano	Bolivian-Tucuman upper montane seasonal evergreen forest
Bosque freatofilo del piso montano xerofitico	Bolivian-Tucuman dry montane riparian forest
Bosque freatofilo subandino interandino Boliviano-Tucumano	Bolivian-Tucuman inter-Andean foothill wash woodland
Bosque ribereño subandino interandino Boliviano-Tucumano	Bolivian-Tucuman inter-Andean foothill riparian forest
Vegetacion ribereña del piso montano xerofitico	Bolivian-Tucuman xeric montane riparian vegetation
Bosque montano Boliviano-Tucumano de Pino de Monte	Bolivian-Tucuman montane Podocarpus forest
Bosque montano subhumedo Boliviano-Tucumano	Bolivian-Tucuman montane semideciduous forest
Bosque subhumedo ribereño montano Boliviano-Tucumano	Bolivian-Tucuman dry montane riparian forest
Bosque humedo montano Boliviano-Tucumano de Aliso	Bolivian-Tucuman montane Alder forest
Bosque montano xerico interandino Boliviano-Tucumano	Bolivian-Tucuman inter-Andean montane xeric forest
Bosque subandino Boliviano-Tucumano de transicion con los Yungas	Transitional sub-Andean Bolivian-Tucuman Yungas forest
Bosque subhumedo Boliviano-Tucumano del subandino inferior	Lower sub-Andean Bolivian-Tucuman semideciduous forest
Bosque subhumedo Boliviano-Tucumano del subandino superior	Upper sub-Andean Bolivian-Tucuman semideciduous forest
Bosques bajos edafoxerofilos montanos y basimontanos Boliviano-Tucumanos	Bolivian-Tucuman montane and lower montane forests
Bosque subandino humedo Boliviano-Tucumano	Sub-Andean Bolivian-Tucuman moist forest
Bosque interandino subandino xerofitico Boliviano-Tucumano	Bolivian-Tucuman inter-Andean foothill xeric forest
Matorral altimontano secundario Boliviano-Tucumano	Bolivian-Tucuman upper montane shrubland
Pajonal altimontano Boliviano-Tucumano	Bolivian-Tucumane upper montane grassland
Matorral pluviestacional montano Boliviano-Tucumano	Bolivian-Tucuman montane dry mesic scrub
Pajonal pluviestacional montano Boliviano-Tucumano	Bolivian-Tucuman montane dry mesic grassland

Table 10.1c. List of ecological systems by floristic region - **Yungas**

Sistema Ecologico	**Ecological System**
Matorral xerico interandino de Yungas	Yungas inter-Andean xeric scrub
Vegetacion saxicola montana de Yungas	Yungas montane saxicolous vegetation
Bosque altimontano pluvial de Yungas	Yungas upper montane pluvial forest
Bosque altimontano pluviestacional de Yungas	Yungas upper montane seasonal evergreen forest
Bosque de *Polylepis* altimontano pluvial de Yungas	Yungas upper montane *Polylepis* pluvial forest
Bosque de *Polylepis* altimontano pluviestacional de Yungas	Yungas upper montane *Polylepis* seasonal evergreen forest
Bosque de *Polylepis* altoandino pluvial de Yungas	High Andean Yungas *Polylepis* pluvial forest
Bosque montano pluviestacional subhúmedo de Yungas	Yungas montane semideciduous forest
Bosque montano pluvial de Yungas	Yungas montane pluvial forest
Bosque montano pluviestacional humedo de Yungas	Yungas montane seasonal evergreen forest
Bosque y arbustal montano xerico interandino de Yungas	Yungas inter-Andean montane xeric forest and shrubland
Bosque basimontano pluviestacional subhúmedo de Yungas del Norte	Northern Yungas lower montane semideciduous forest
Bosque basimontano pluviestacional subhúmedo de Yungas del Sur	Southern Yungas lower montane semideciduous forest
Bosque bajo de crestas pluviestacional de Yungas	Yungas ridge seasonal evergreen dwarf forest
Bosque basimontano pluviestacional humedo de Yungas	Yungas lower montane seasonal evergreen forest
Bosque y palmar basimontano pluvial de Yungas	Yungas lower montane pluvial (palm dominated) forest
Vegetacion ribereña basimontana de Yungas	Yungas lower montane riparian vegetation
Bosque basimontano xerico de Yungas del sur	Southern Yungas lower montane xeric forest
Bosque y arbustal basimontano xerico de Yungas del Norte	Northern Yungas lower montane xeric forest and shrubland
Complejo submontano seco de Yungas del norte	Northern Yungas lower montane dry vegetation complex
Complejo submontano y montano seco de Yungas del norte	Northern Yungas montane and lower montane dry vegetation complex
Pajonal arbustivo altoandino y altimontano pluviestacional de Yungas	Yungas upper montane dry mesic shrubland and grassland
Pajonal arbustivo altoandino y altimontano pluvial de Yungas	Yungas upper montane pluvial shrubland and grassland
Sabana arbolada montana y basimontana de Yungas	Yungas montane and lower montane treed savanna

Table 10.1d. List of ecological systems by floristic region - **Moist Puna**

Sistema Ecologico	**Ecological System**
Arbustales montanos xericos interandinos de la Puna Humeda	Moist Puna inter-Aandean montane xeric shrubland
Bosques y arbustales montanos xericos interandinos de la Puna Humeda	Moist Puna inter-Andean montane xeric forest and shrubland
Matorrales y herbazales xericos internadinos de la Puna Humeda	Moist Puna inter-Andean xeric steppe
Bosques bajos y arbustales altimontanos de la Puna Humeda	Moist Puna upper montane dwarf forest and shrubland
Bosque bajo altoandino de la Puna Humeda	Moist Puna high Andean dwarf forest
Cardonales deserticos del piedemonte occidental de la Puna Humeda	Moist Puna western foothill succulent desert scrub
Cardonales y matorrales montanos deserticos occidentales de la Puna Humeda	Moist Puna western montane succulent desert scrub
Matorrales deserticos montanos noroccidentales	Puna northwestern montane desert scrub
Rosetales deserticos basimontanos	Pacific desert foothill rosetales
Bofedales altoandinos de la Puna Humeda	Moist Puna high-Andean bogs
Pajonal higrofitico altimontano de la Puna Humeda	Moist Puna upper montane wet meadow
Pajonal higrofitico altoandino de la Puna Humeda	Moist Puna high-Andean wet meadow
Vegetacion acuatica y palustre altoandina de la Puna Humeda	Moist Puna high-Andean marsh and aquatic vegetation
Pajonales y matorrales altimontanos de la Puna Humeda	Moist Puna upper montane grassland and shrubland
Matorral edafoxerofilo en cojin altoandino de la Puna Humeda	Moist Puna high-Andean cushion vegetation
Pajonal altoandino de la Puna Humeda	Moist Puna high-Andean grassland
Vegetacion saxicola altoandina de la Puna Humeda	Moist Puna high-Andean saxicolous vegetation
Vegetacion geliturbada subnival de la Puna Humeda	Moist Puna snow fields

Table 10.1e. List of ecological systems by floristic region - **Xeric Puna**

Sistema Ecologico	**Ecological System**
Bosque bajo altimontano de la Puna Xerofitica central	Central Xeric Puna upper montane forest
Bosque bajo xerofitico interandino de la Prepuna superior oriental	Eastern Prepuna upper inter-Andean xerophytic low forest
Bosque bajo altoandino de la Puna Xerofitica occidental	High-Andean western Xeric Puna low forest
Bosque bajo altoandino de la Puna Xerofitica oriental	High-Andean eastern Xeric Puna low forest
Cardonal altoandino de la Puna Xerofitica occidental	High-Andean western Xeric Puna succulent scrub
Matorral altimontano de la Puna Xerofitica desertica	Xeric Puna upper montane desert scrub
Cardonales deserticos montanos suroccidentales	Southwestern Xeric Puna montane succulent desert scrub
Matorrales deserticos montanos suroccidentales	Southwestern Xeric Puna montane desert scrub
Bofedales altoandinos de la Puna Xerofitica	High-Andean Xeric Puna bog
Pajonal higrofitico altoandino de la Puna Xerofitica	High-Andean Xeric Puna wet meadow
Vegetacion acuatica y palustre altoandina de la Puna Xerofitica	High-Andean Xeric Puna marsh and aquatic vegetation
Arbustal xerofitico interandino de la Prepuna inferior oriental	Eastern Prepuna lower inter-Andean xerophytic shrubland
Arbustal espinoso altimontano de la Puna Xerofitica	Xeric Puna upper montane thorn scrub
Matorral altimontano de la Puna Xerofitica noroccidental	Northwestern Xeric Puna upper montane scrub
Matorral altimontano y altoandino psamofilo de la Puna Xerofitica	Xeric Puna sand scrub
Matorral higrofilo altoandino de la Puna Xerofitica ("tholares")	High-Andean Xeric Puna hygrophilous scrub (tholares)
Matorrales y herbazales altimontanos y altoandinos de la Puna Xerofitica oriental	Eastern Xeric Puna shrublands and steppe
Pajonales y matorrales altoandinos de la Puna Xerofitica norte	High-Andean northern Xeric Puna grassland and scrub
Pajonales y matorrales altoandinos de la Puna Xerofitica suroccidental	High-Andean southwestern Xeric Puna grassland and scrub
Vegetacion de los salares altoandinos de la Puna Xerofitica	High-Andean Xeric Puna salt pan vegetation
Vegetacion abierta geliturbada altoandina de la Puna Xerofitica septentrional y oriental	High-Andean northeastern Xeric Puna open snow fields
Vegetacion abierta geliturbada altoandina de la Puna Xerofitica suroccidental	High-Andean southwestern Xeric Puna open snow fields
Glaciares	Glaciers

Table 10.1f. List of ecological systems by floristic region - **Transition or adjacent lowland**

Sistema Ecologico	**Ecological system**
Bosque del piedemonte del oeste de la Amazonia	Western Amazon foothill forest
Bosque del piedemonte del suroeste de la Amazonia	Southwestern Amazon foothill forest
Bosque inundable de la llanura aluvial de rios de aguas blancas del suroeste de Amazonia	Southwestern Amazon whitewater flooded forest
Bosque siempreverde estacional subandino del suroeste de Amazonia	Sub-Andean seasonal evergreen forest of southwestern Amazonia
Bosque siempreverde subandino del oeste de Amazonia	Sub-Andean evergreen forest of western Amazonia
Bosque siempreverde subandino del suroeste de Amazonia	Sub-Andean evergreen forests of southwestern Amazonia
Bosque humedo de tierras bajas y submontano del suroccidente Caribeño	Southwestern Caribbean foothill and lowland moist forest
Bosque transicional preandino del Chaco noroccidental	Sub-Andean transitional forest of the Northwest Chaco
Bosques freatofiticos del Chaco (Algarrobales)	Chaco hygrophilous forests (ground water Algarrobales)
Bosque subhumedo semideciduo de la Chiquitania sobre suelos bien drenados	Chiquitano semideciduous forest on well-drained soils
Bosque pluvial premontano del Choco-Darien	Sub-Andean Choco-Darien rain forest
Bosque transicional preandino de los Llanos del Orinoco	Sub-Andean transitional forest of the Llanos del Orinoco
Bosque Tumbesino deciduo de tierras bajas	Tumbesian lowland deciduous forest
Bosque Tumbesino deciduo espinoso	Tumbesian deciduous thorn forest
Bosque Tumbesino deciduo premontano	Tumbesian premontane deciduous forest

Table 10.2. Ecosystems, macro-groups and floristic regions included in the map of the Northern and Central Andes (Josse et al. 2009b).

Floristic region	Ecosystems	Macro-groups
Northern Andes	32	15
Yungas	22	11
Moist Puna	18	8
Xeric Puna	19	8
Bolivian-Tucumano	22	11
Total	113	53

Table 10.3. Extent of natural and anthropogenic areas in the Northern and Central Andes (Josse et al. 2009b).

Region	Anthropogenic Areas (km^2)	Natural Vegetation (km^2)
Northern Andes	236,689	197,635
Central Andes	96,733	983,492
Total	333,422	1,181,127

Acknowledgments

The Chapter presents the results of collaborative work undertaken by the Secretaría General de la Comunidad Andina, the Regional Programm ECOBONA from Intercooperation, Proyecto Páramo Andino from CONDESAN, BioAndes Programm, NatureServe, EcoCiencia, the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, the Instituto de Ciencias Ambientales y Ecológicas-Universidad de Los Andes (ICAE-ULA), the Laboratorio de Teledetección-Universidad Nacional Agraria La Molina (UNALM), the Centro de Datos para la Conservación-Universidad Nacional Agraria La Molina (CDC-UNALM), and RUMBOL SRL.

Literature Cited

Argollo, J., and P. H. Mourguiart (eds.). 1995. Climas cuaternarios en América del Sur. La Paz: ORSTOM-UMSA.

Ataroff, M., and L. Sarmiento. 2003. Diversidad en los Andes de Venezuela. I. Mapa de unidades ecológicas del estado Mérida. CD-ROM. Mérida: Ediciones Instituto de Ciencias Ambientales y Ecológicas (ICAE) and Universidad de Los Andes.

Bailey, R. G. 1995. Description of the ecoregions of the United States. Miscellaneous Publication No. 1391 (revised). Washington, DC: United States Department of Agriculture Forest Service.

Ballivian, O., and F. Risacher. 1981. Los salares del altiplano boliviano. Métodos de estudio y estimación económica. Paris: ORSTOM y Universidad Mayor de San Andrés. 246 pp.

Clapperton, C. M. 1993. Quaternary geology and geomorphology of South America. Amsterdam: Elsevier – Academic Press.

Bruinsma, J. (ed.). 2003. World agriculture: towards 2015/2030. An FAO perspective. London: Earthscan. 432 pp.

Cabrera, A., and A. Willink. 1973. Biogeografía de América Latina. Washington, DC: Organization of American States, Regional Program of Scientific and Technological Development. 120 pp.

Comer, P., D. Faber-Langendoen, R. Evans, S. Gawler, C. Josse, G. Kittel, S. Menard, M. Pyne,

M. Reid, K. Schulz, K. Snow, and J. Teague. 2003. Ecological systems of the United States: a working classification of U.S. terrestrial systems. Arlington VA: NatureServe.

Daubenmire, R. 1966. Vegetation: identification of typal communities. Science 151:291-298.

Duellman, W. E. 1979. The herpetofauna of the Andes: patterns of distribution, origin, differentiation, and present communities. Pp. 371-459 in The South American herpetofauna: its origin, evolution, and dispersal, edited by W. E. Duellman. Monograph of the Museum of Natural History, the University of Kansas No. 7.

Duellman, W. E. 1999. Distribution patterns of amphibians in South America. Pp. 255-328 in Patterns of distribution of amphibians: a global perspective, edited by W. E. Duellman. Baltimore MD: Johns Hopkins University Press.

Duellman, W., and E. Wild. 1993. Anuran amphibians from the Cordillera Huancabamba, northern Peru: systematics, ecology, and biogeography. Occasional Papers of the Museum of Natural History, the University of Kansas 57:1-53.

Fjeldså, J., and N. Krabbe. 1990. Birds of the high Andes. Svendborg, Denmark: Apollo Books.

García-Moreno, J., P. Arctander, and J. Fjeldså. 1999. Strong diversification at the treeline among Metallura hummingbirds. Auk 116:702-711.

Gentry, A. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or and accident of the Andean orogeny? Annals of the Missouri Botanical Garden 69:557-593.

Heindl, M., and K.-L. Schuchmann. 1998. Biogeography, geographical variation and taxonomy of the Andean genus Metallura, Gould, 1847. Journal für Ornithologie 139:425-473.

Instituto Nacional de Recursos Naturales del Perú. 2000. Mapa forestal del Perú. Lima: Instituto Nacional de Recursos Naturales del Perú.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology 5:1211-1219.

Jørgensen, P. M., C. Ulloa-Ulloa, J. Madsen, and R. Valencia. 1995. A floristic analysis of the high Andes of Ecuador. Pp. 221-237 in Biodiversity and conservation of Neotropical montane forests, edited by S. P. Churchill, H. Balslev, E. Forero, and L. Luteyn. New York: The New York Botanical Garden.

Josse, C., G. Navarro, P. Comer, R. Evans, D. Faber-Langendoen, M. Fellows, G. Kittel, S. Menard, M. Pyne, M. Reid, K Schulz, K. Snow, and J. Teague. 2003. Ecological systems of Latin America and the Caribbean: a working classification of terrestrial systems. Arlington VA: NatureServe.

Josse, C., G. Navarro, F. Encarnación, A. Tovar, P. Comer, W. Ferreira, F. Rodríguez, J. Saito, J. Sanjurjo, J. Dyson, E. Rubin de Celis, R. Zárate, J. Chang, M. Ahuite, C. Vargas, F. Paredes, W. Castro, J. Maco and F. Reátegui. 2007. Sistemas cológicos de la cuenca amazónica de Perú y Bolivia. Arlington VA: NatureServe.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009a. Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009b. Mapa de ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Lima: Secretaría General de la

Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. Journal of Biogeography 31:1829-1839.

Mittermeier, R. A., P. Robles Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, and G. A. B. da Fonseca. 2004. Hotspots revisited. Mexico City: CEMEX.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Navarro, G., and W. Ferreira. 2007. Mapa de vegetación de Bolivia a escala 1:250.000. Ed. digital. Santa Cruz de la Sierra: The Nature Conservancy.

Peralvo, M. F., F. Cuesta, F. Baquero, C. Josse, L. Grijalva, G. Riofrío, and K. Beltrán. 2006. Mapa de sistemas ecológicos del Ecuador continental. Anexo 1 (20 pp.) in Identificación de vacíos y prioridades de conservación para la biodiversidad terrestre en el Ecuador continental, edited by F. Cuesta-Camacho, M. F. Peralvo, A. Ganzenmüller, M. Sáenz, G. Riofrío, and K. Beltrán. Quito: EcoCiencia, The Nature Conservancy, Conservation International, and Ministerio del Ambiente del Ecuador.

Racey, G. D., A. G. Harris, J. K. Jeglum, R. F. Foster, and G. M. Wickware. 1996. Terrestrial and wetland ecosites of northwestern Ontario. Thunder Bay: Ontario Ministry of Natural Resources, Northwestern Science and Technology. 94 pp.

Rivas-Martínez, S., D. Sánchez-Mata, and M. Costa. 1999. North American boreal and western temperate forest vegetation. Itinera Geobotanica 12:5-316.

Rodríguez, N., D. Armenteras, M. Morales, and M. Romero. 2004. Ecosistemas de los Andes colombianos. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Rodwell, J. S., J. H. J. Schaminee, L. Mucina, S. Pignatti, J. Dring, and D. Moss. 2002. The diversity of European vegetation. An overview of phytosociological alliances and their relationships to EUNIS habitats. Report EC-LNV 2002/054. Wageningen, The Netherlands: EC-LNV. 168 pp.

Rowe, J. S., and B. V. Barnes. 1994. Geo-ecosystems and bio-ecosystems. Bulletin of the Ecological Society of America 75:40-41.

Roy, M. S., J. M. Cardoso da Silva, P. Arctander, J. García-Moreno, and J. Fjeldså. 1997. The speciation of South American and African birds in montane regions. Pp. 325-343 in Avian molecular evolution and systematics, edited by D. P. Mindell. San Diego: Academic Press.

Saavedra, C., and C. Freese. 1986. Prioridades biológicas de conservación en los Andes tropicales. Parks/Parques/Parcs 11:8-11.

Sánchez-Vega, I., and M. Dillon. 2006. Jalcas. Pp. 77-90 in Botánica económica de los Andes centrales, edited by M. Moraes R., B. Øllgaard, L. P. Kvist, F. Borchsenius, and H. Balslev. La Paz: Universidad Mayor de San Andrés.

Servant, M., and J. C. Fontes. 1978. Les lacs quaternaires des hauts plateaux des Andes boliviennes. Premiéres interprétations paléoclimatiques. Cahiers ORSTOM sér. Geologie 10:9-23.

Simpson, B. B. 1975. Pleistocene changes in the flora of the high tropical Andes. Paleobiology 1:273-294.

Simpson, B. B., and C. A. Todzia. 1990. Pattern and processes in the development of the high Andean flora. American Journal of Botany 77:1419-1432.

Smith, J. M. B., and A. M. Cleef. 1988. Composition and origins of the world's tropicalpine floras. Journal of Biogeography 15:631-645.

Sklenár, P., and P. M. Ramsay. 2001. Diversity of paramo plant communities in Ecuador. Diversity and Distributions 7:113-124.

Ulloa Ulloa, C., and P. M. Jørgensen. 1993. Arboles y arbustos de los Andes del Ecuador. AAU Reports 30:1-264.

USDA Forest Service. 2006. ECOMAP domains, divisions, provinces, and sections of the United States. Digital Map. Washington, DC: United States Department of Agriculture Forest Service.

Van der Hammen, T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. Journal of Biogeography 1:3-26.

Wassenaar, T., P. Gerber, P. H. Verburg, M. Rosales, M. Ibrahim, and H. Steinfeld. 2007. Projecting land use changes in the Neotropics: the geography of pasture expansion into forest. Global Environmental Change 17:86-104.

Weigend, M. 2002. Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. Botanical Review 68:38-54.

Weigend, M. 2004. Additional observations on the biogeography of the Amotape-Huancabamba zone in northern Peru: defining the south-eastern limits. Revista Peruana de Biología 11:127-134.

Whittaker, R. H. 1962. Classification of natural communities. Botanical Review 28:1-239.

Whittaker, R. H. 1975. Communities and ecosystems. New York: MacMillan.

11

Vulnerability of Tropical Andean Ecosystems to Climate Change

Bruce E. Young, Kenneth R. Young, and Carmen Josse

Temperature and the amount, seasonality, and form of precipitation are critical factors in determining plant architecture and community composition, in addition to constraining many ecosystem processes. Due to this close relationship between climate and ecosystems, current rapid climate change is expected to alter Andean ecosystems from the states in which we know them today (see Anderson et al., Chapter 1, this volume). The relative impact of global warming will likely be higher in the tropics than elsewhere because the magnitude of the change is greater relative to the interannual variability (Williams et al. 2007), with many implications for range shifts in species and possible species extinctions (Colwell et al. 2008; Larsen et al., Chapter 3, this volume).

Different Andean ecosystems are unlikely to be equally vulnerable to the stresses of climate change. These systems occur in heterogeneous landscapes, are made up of taxonomically, physiologically, and structurally different dominant species, and have different histories of confronting stressors, especially anthropogenic ones. How do ecosystems vary in their vulnerability? Although some studies point to specific systems that appear to be particularly vulnerable (e.g., Still et al. 1999), few have compared the relative vulnerability of the major ecosystems. Researchers have now characterized the key characteristics and climatic regimes of Andean ecosystems (Kappelle and Brown 2001; Young et al. 2007; Josse et al. 2009; see also Josse et al., Chapter 10, this volume). In this chapter, we use this information as a framework to assess relative vulnerability, i.e. the degree to which a system is susceptible to detrimental change (Smit et al. 2000). Our aim is to present defensible hypotheses that can be addressed in future research.

The ecological systems that comprise the landscapes described here consist of assemblages of species, each of which will respond individually to climate change (Overpeck et al. 1991). Entire ecosystems will not shift intact. Nevertheless, due to the large number of species involved and the lack of ecological information in many cases, discussing the probable effects of climate change on the suite of species that make up particular landscapes is a useful organizing framework. Although our focus here is the ecosystem level, consideration of both ecosystems and species allows a comprehensive approach in much the same way that conservationists have traditionally applied “coarse” and “fine” filters in their planning (Groves et al. 2002).

Tropical Andean Ecosystems

In order to begin to assess ecosystem vulnerabilities from among the varied landscapes and ecoregions that make up the tropical Andes, we need a consistent system of nomenclature to be able to speak unambiguously about particular systems. Spanning thirty degrees of latitude and covering over a million and a half square kilometers, the tropical Andes present a political and scientific challenge to formulating a coherent yet complete nomenclature of the ecosystem types. As a step in that direction, an ecosystem map with a single legend was recently developed. This effort was built on national forestry, ecological system, and ecological unit maps, and used a classification scheme applicable to all of Latin America and the Caribbean (Josse et al. 2003). The unified map of ecological systems for the region (Josse et al. 2009; see also Josse et al., Chapter 10, this volume) is now available and will be used in this analysis. An ecological system, referred to here as an ecosystem, is a group of vegetation communities that tend to co-occur in landscapes that share ecological processes (e.g., fire or flooding regimes), substrates (e.g., soils or parent material), and/or environmental gradients (e.g., microclimates, elevation, hydrological patterns) (Josse et al. 2003).

The resulting map delineates 113 ecosystems in the tropical Andes, defined as the mountainous area from Bolivia north and above about 800-1000 m, and 20 additional systems that are transitional to adjacent lowland systems (Josse et al. 2009). For the sake of brevity, we group the ecosystems into six Andean landscape types belonging to five phytogeographic regions, following the summary by Cuesta and Becerra (2009). The focus of this chapter is on natural systems, so we do not address the “cultural landscape” or “inter-Andean valley” divisions of Cuesta and Becerra (2009), although we recognize that a surprisingly large number of endemic plant species are restricted to inter-Andean valleys (Valencia et al. 2000, López 2003, León et al. 2006, López and Zambraba-Torrelio 2006), and we acknowledge the important historical and socioeconomic value of these environments for society (Denevan 2001, Dillehay et al. 2007). Because aquatic systems cut across multiple ecosystems, we consider aquatic habitats separately.

Determining Vulnerability

The study of climate change in the Andes is new enough that cordillera-wide analyses of vulnerability to climate change have not yet been completed. Indeed, few studies have been conducted on the vulnerability of individual ecosystems. What is more, the ability of ecosystems to resist or recover from disturbances is affected by many contingent factors, including human land use and the nature of particular species traits (Ives and Carpenter 2007). Based on this lack of available information, Josse et al. (2009) indicated to policy makers that studying the vulnerability of Andean ecosystems to climate change is a key priority.

For our survey of Andean landscapes, we use what is known about the key factors responsible for their formation, the history of human intervention, and projected changes in climate to estimate potential vulnerability to climate change. For each landscape, we provide a brief *description* (based on Cuesta and Becerra 2009 unless noted otherwise), identify *key processes* unique to the landscape, describe *human uses*, discuss *sensitivity* (to disruption of ecosystem processes) and *resilience* (ability to re-grow or re-establish after disturbance), and, based on these factors, hypothesize about *vulnerability to future climate change*.

Every Andean landscape will likely be subjected to some degree of ongoing climate change. Although climatological models differ in the details of change, all agree that temperatures will increase, especially at higher elevations, and that precipitation will likely increase in some areas, decrease in others, and occur in altered seasonal patterns and occasionally in greater intensity (Marengo et al., Chapter 7, this volume). Ecosystems are characterized by complex interactions among species (see Aguirre et al., Chapter 4, this volume) and between species and their environment. Due to the difficulty in predicting how these interactions will play out (Walther et al. 2002, Parmesan 2006), our hypotheses about vulnerability are preliminary.

Páramo

Description.—Páramos are among the highest ecosystems in the Andes, occurring above tree line and below snow fields and glaciers (if present) from Venezuela to northern Peru. They are typically open shrublands in a matrix of grasslands and other vegetation adapted to cold, wet conditions. Páramos occur as patches on mountain and ridge tops, isolated by surrounding forests. Plant endemism is very high, perhaps due to the fragmented distribution of this landscape.

Key processes.—Páramos are characterized by cold temperatures and a positive water balance caused by high rates of cloud cover, mist, and horizontal precipitation. Daily temperature variation is much greater than mean temperature is seasonally, with night frosts common. These conditions allow growth to occur only during brief periods each day. Seedling establishment is therefore difficult. Soils are often of volcanic origin and relatively fertile. Topography and slope aspects lead to a range of moisture conditions from dry to wet, and from full to limited exposure to prevailing winds and sunlight. Páramos are well known for their ability to store water and organic matter in soil and vegetation.

Human uses.—Permanent human occupation of the páramos has existed only since the end of the nineteenth century, although significant transformation has occurred throughout much of their extent during this time. Local residents typically burn the grasslands and shrublands when they want to improve conditions for livestock grazing, and they cultivate the soils when they want to grow crops such as potatoes. Humans are increasingly altering páramo habitat for agricultural and silvicultural (pine) uses, with ecosystem-level consequences (Farley 2007).

Sensitivity and resilience.—Páramos are likely sensitive to disturbance for a number of reasons. Their distribution in relatively small patches makes them especially vulnerable to edge effects. Given the high levels of endemism, species extinction is likely to be high as individual patches of páramo disappear and species migration between habitat patches becomes more difficult. Páramos may also be sensitive to repeated burning. Nevertheless, páramos can be resilient after disturbance. Given a seed source, a suitable climate, and time, the relatively fertile soils and humid conditions are conducive to regeneration. However, if the soil itself has been eroded, systems may take much longer to recuperate.

Vulnerability to future climate change.—Páramos appear to be highly vulnerable to climate change given what is known about their spatial arrangements on high mountain peaks. As the climate conditions required by páramos rise in elevation, areas of páramo vegetation will likely disappear due to invasion of woody plants from below and increased agricultural activity. On tall mountains with snow and ice above páramos, the steep rocky slopes may not have adequate soils for páramo vegetation to establish promptly after snow and ice melt. Páramos may be substantially altered or degraded with the increased fire regimes that may accompany warmer temperatures and increasing human land use pressures. It is unclear how carbon and water cycles will be altered under these conditions, but these ecosystem functions are critically important for many downslope northern Andean human communities. For a detailed account on páramo ecosystems and climate change see Ruiz et al., Chapter 12, this volume.

Humid Puna

Description.—The humid puna replaces páramos to the south as the highest ecosystem. The humid puna occurs at high elevations from northern Peru to Bolivia (and further south outside the tropics) and is dominated by grasses and shrubs. Some species are remarkably long lived, even the diminutive *Azorella* cushions and *Nototriche* as well as *Polylepis* trees (Halloy 1983, Halloy 1998, Halloy 2002, Argollo et al. 2004, Solíz et al. 2009).

Key processes.—The humid puna is characterized by cold temperatures and lower annual precipitation than the páramo. A 3-5 month dry and cold season also distinguishes this system from the páramo, where precipitation and temperature is less seasonal. Geomorphological conditions favor the formation of extensive wetlands in places with poor drainage, which buffer the effects of dry periods for nearby vegetation.

Human uses.—Human use of the humid puna has been extensive for hundreds to thousands of years. Inhabitants typically burn the habitat to improve conditions for livestock grazing and practice high-elevation cultivation of many crops, including potatoes and quinoa. Recently many new mining claims are appearing in puna areas, with increased effects on land cover and on water quality.

Sensitivity and resilience.— An unknown number of species have probably already disappeared as a result of millennia of human use, but the grassland species that persist are probably not particularly sensitive to disturbance. However, specific ecosystems nested within the Puna, such as the high-Andean *Polylepis* forests, are documented to be sensitive to human activities (Fjeldså and Kessler 1996, Fjeldså 2002). Habitats that depend on water runoff from melting glaciers are sensitive to the disappearance of these glaciers and to the diversion of water for human use. The humid puna is already adapted to a seasonal climate (regrowing after dry seasons) and to rebounding after fire and grazing, so it can be considered fairly resilient. Again, specific ecosystems occurring within humid puna landscapes may be less resilient.

Vulnerability to future climate change.— Puna habitats may be vulnerable to invasion by woody species from lower elevations, especially if increased precipitation accompanies warming. Intensive human use and burning may counteract this process in places. The available land on mountains upslope is considerably less than where puna occurs today, so the land area covered by these ecosystems may decrease in the future. Soils on recently deglaciated slopes may be too poor for rapid colonization by many puna species.

Dry Puna

Description.—The dry puna is more desert-like in appearance than the humid puna. It occupies high elevation sites with a relatively long dry season. It is characterized by extensive grasslands and small-leaved shrubs, some of which are deciduous in the dry season. One notable ecosystem in this landscape consists of extensive salt pans known as *salares* that have sparse vegetation with plant species adapted to saline soils. Just as in the humid puna, some species are long lived. The dry puna extends from southwestern Peru through western Bolivia and into Chile and northern Argentina.

Key processes.—The climate of the dry puna is cold and dry, with shorter wet seasons than the humid puna. Winds are often strong. Soils are heterogeneous with some plant communities adapted to specialized soil types.

Human uses.—The major human use is livestock grazing, although mineral extraction from *salares* is increasing (*salares* in Bolivia are a major source of lithium, increasingly used in battery manufacturing). In southern Peru, a shrublike vegetation called tolar (dominated by the aster *Parastrephia* spp.) is utilized as a fuel source (Intendencia Forestal y de Fauna Silvestre 2002). Burning is less frequent in the dry puna than in other landscapes due to the lack of fuel.

Sensitivity and resilience.—The dry puna resembles the humid puna in terms of its sensitivity. In addition to inset ecosystems such as *Polylepis* forests, the puna also contains a number of species that are adapted to a particular soil type and cannot grow elsewhere. The dry puna has the particular characteristic of being highly resistant to disturbance while at the same time having low resilience in the event of destruction. The low-stature, chemically defended shrubs are resistant to grazing and fire. Yet when removed, low growth rates and limited soil moisture cause many dry puna species to recover only very slowly.

Vulnerability to future climate change.—An increase in precipitation and CO_2 may make some dry puna habitats more susceptible to fire because increased growth leads to higher standing fuel availability. This switch in turn may potentially increase dominance by tussock grasses, making the vegetation more similar to that found in humid puna. Species adapted to specific, locally occurring soil types are vulnerable because they are unable to disperse to track a favorable climate. Other species are so resistant to disturbance and so well adapted to harsh conditions that they may tolerate moderate temperature increases (see also Anderson et al., Chapter 1, this volume).

Cloud Forest

Description.—Cloud forests occur along the east slope throughout the tropical Andes, and on the Pacific slope in Colombia and northern Ecuador. In Peru and Bolivia, cloud forests may also be referred to as Yungas. The forests have a closed canopy and trees are usually covered by dense mats of epiphytes, including orchids, ferns, lichens, and mosses. Cloud forest plants and animals exhibit high levels of endemism and often have narrow elevational distributions. The elevational range of cloud forests is more than 3,000 m in the tropical Andes, such that plant communities at the lower end of the range are substantially different from communities at the upper elevational limits.

Key processes.—The key process forming cloud forest is the high humidity maintained by both vertical rainfall and horizontal precipitation caused by cloud water intercepted by vegetation. Persistent cloud and mist simultaneously impede insolation and evaporation. Cloud forests often occur on steep slopes with highly acidic and leached soils. The steep slopes and high soil moisture content lead to frequent landslides. The dynamics of succession after landslide events help maintain relatively high levels of species turnover and habitat heterogeneity (Kessler 1999).

Human uses.—The steep slopes, poor soils, and high humidity have proven relatively inhospitable for human settlement except for the drier or more seasonal areas of cloud forest. Recent expansion of road construction in cloud forest landscapes provides improved access for timber extraction and cattle grazing, often leading to degraded forests and poor quality pastures.

Sensitivity and resilience.—Cloud forests are highly sensitive to changes in moisture. Even a single drying event can cause significant plant mortality (Benzing 1998, Foster 2001). In addition, many plant and animal species are adapted to very narrow elevational zones that are prone to being “squeezed out” by changing climates, isolating populations and leading to local extinctions. Because disturbance in the form of land slides is a regular event in cloud forests, this system may be fairly resistant to physical disturbance. Mobile cloud forest animals such as birds and bats may prove to be more flexible because they can move to new climate/forest zones in search of food by traveling relatively short distances.

Vulnerability to future climate change.—Warming temperatures cause the base levels of clouds, the key process forming cloud forests, to rise, making these habitats highly vulnerable to climate change (Still et al. 1999, Foster 2001). Forests on steep slopes are vulnerable to an increase in landslide frequency during extreme precipitation events, especially where landslides expose bare rock. Reduced humidity caused by increased temperature and less cloud-borne precipitation cause cloud forests to become more vulnerable to conversion and burning for agricultural uses and rangeland. The upper elevational limits of cloud forests are often bordered by puna or páramo vegetation and maintained by fire. In these situations, cloud forest species would be restricted in their ability to disperse upward in an attempt to track a favorable climate. Cloud forest trees may be slow to disperse upslope even in the absence of fire due to slow growth and the time needed for the formation of adequate soils.

Seasonal Andean Forest

Description.— Seasonal Andean forests occur on slopes and ridge tops throughout the tropical Andes, although they are more extensive in Peru and Bolivia. Trees are of medium stature with a portion being deciduous during the dry season. They are often found as relict fragments surrounded by anthropogenic shrubland and agricultural landscapes.

Key processes.—A 3–5 month dry season, moderate amounts of annual precipitation, and relatively fertile soils (derived from bedrock and not heavily leached) are typical for this Andean landscape.

Human uses.—Seasonal Andean forests are heavily used by humans due to the agreeable climate, which is well suited for agriculture such as coffee production and for small-scale farming of maize, wheat, citrus, and cocoa. Many areas were deforested hundreds to even thousands of years ago.

Sensitivity and resilience.—Remaining forests are highly sensitive because heavy human use has left them fragmented and susceptible to extirpation. Tree species are somewhat resilient because they are already adapted to a dry season. Soil fertility and moderate growth rates also contribute to possibilities for regrowth where protected and when seed sources are present.

Vulnerability to future climate change.—The inherent resilience make these forests less vulnerable to climate change, although if the dry season lengthens they would be more vulnerable to burning and cutting. An increase in rainfall may promote resistance to anthropogenic destruction. Alternatively, these would be attractive areas to implement reforestation programs to sequester carbon and to protect soils.

Dry Andean Forest

Description.—Dry Andean forests are adapted to extended and severe droughts. They are characterized by low stature trees with thick stems and small or thick, deciduous leaves. Many plants also have spines and heavy chemical defenses to protect against herbivory. These forests occur primarily in the inter-Andean valleys of Ecuador, Peru, and Bolivia, often as fragments surrounded by human-dominated landscapes. Some components of these dry-adapted systems, such as the Cactaceae, have high levels of endemism.

Key processes.—Dry forests receive small amounts of annual precipitation and have a 6-10 month dry season. Their location is highly dependent on rain shadows caused by local topography.

Human uses.—These landscapes have been heavily degraded and deforested since at least colonial times for extraction of high quality wood and for livestock grazing.

Sensitivity and resilience.—Vegetation in dry Andean forests is resistant to long dry seasons and therefore not very sensitive except to high frequency burning or intensive overgrazing, such as by goats. They may include plants with important dependencies on animals for their pollination and seed dispersal, making them susceptible to loss of mutualists. Dry forests can regrow after moderate levels of grazing and fire if protected from these stressors, but regeneration from denuded sites is difficult.

Vulnerability to future climate change.—Dry forests are somewhat vulnerable to drier conditions that may result from climate change because these would decrease tree survival and promote invasion by shrubs and cacti. However, they would be susceptible to potential increases in rainfall.

Aquatic Habitats

Description.—Aquatic habitats in the Andes include lakes, swamps, marshes, bogs (known as "bofedales" in Peru and Bolivia), rivers, and streams. They occur throughout the region at elevations up to the base of glaciers. These systems support a diverse array of fish, macroinvertebrate and algal species (see Maldonado et al., Chapter 20, this volume), as well as migratory and resident birds such as grebes, sandpipers, plovers, and flamingos.

Key processes.—The hydrological balance of aquatic habitats is governed by an interaction of water input via precipitation, snow and glacial melt, and ground water, and loss through runoff and evaporation, soils, vegetation, and human uses. Lakes, swamps, marshes and bogs were formed by glacial, tectonic, and volcanic processes (see Maldonado et al., Chapter 20, this volume). The dynamics of river systems vary significantly depending on the slope of the terrain over which they flow (see Anderson et al., Chapter 23, this volume).

Human uses.—Aquatic habitats sustain human life by providing water for consumption, agriculture, livestock, energy production, navigation, and fisheries (Luck et al. 2009).

Sensitivity and resilience.—Aquatic habitats are highly sensitive to water supply, both local and upstream, temperature (which affects oxygen levels), and precipitation. They are also sensitive to upstream sources of contamination and to biodiversity losses caused by introduced fish species. Their sensitivity is a function of their degree of connectivity to sources of degradation (Freeman et al. 2007). Aquatic systems are resilient in one sense because they can often be restored by supplying water in the appropriate quantity and seasonality. However, eliminating contamination and introduced fish can usually be accomplished only by expensive human intervention. Water demand often results in water being removed from natural systems (see Anderson et al., Chapter 23, this volume).

Vulnerability to future climate change.—Aquatic systems are vulnerable to rising temperatures that can disrupt the hydrologic balance (Vuille et al. 2008). After glacial meltoff has completed, many Andean wetlands will disappear causing local extirpation of associated biodiversity. Any decrease in water availability in natural ecosystems will be compounded by competing human needs.

Table 11.1. Characteristics of tropical Andean landscapes (from Cuesta and Becerra 2009). Does not include human-transformed areas (24.3 % of land area). Area of aquatic habitats is included within the landscape where they are found.

Landscape	Elevation (m)	Extent (km^2)	Percent of tropical Andes land area
Paramo	> 3,000	35,000	2.2
Humid Puna	2,000 – 6,000[1]	183,475	13.8
Dry Puna	2,000 – 6,000[1]	100,390	12.8
Cloud Forest	1000 – 3500 (as low as 600 in central and southeastern Bolivia)	211,068	11.3
Seasonal Andean Forest	800 – 3,100 (as low as 600 in Bolivia)	71,311	5.6
Dry Andean Forest	600 – 4,100	64,518	3.4

[1] The lower limit refers to “pre-puna” systems (Josse et al. 2009).

Conclusions

Although there are many local exceptions, the Andean landscapes most vulnerable to climate change are those that have had the shortest history of human intervention: the páramos and cloud forests. Páramos are subject to invasion by woody plants, localized elimination, and a lack of areas upslope available for associated species to colonize. Cloud forests are dependent on fragile atmospheric conditions that can change rapidly as climates warm. Climate change will likely improve the agricultural productivity of both páramos and cloud forests, compounding their vulnerability and the potential for extinction of the numerous endemic species that have evolved there (Valencia et al. 2000, Travis 2003, Leon et al. 2006).

Andean aquatic habitats may be equally vulnerable due to the direct effect of climate on hydrological processes. Climate change, especially patterns of precipitation, will be spatially heterogeneous in the Andes (Marengo et al., Chapter 7, this volume). This makes generalizations difficult, but the combination of rising temperatures and large reduction in glacial mass over the next few decades will likely lead to a significant reduction in the number and extent of Andean wetlands.

The species surviving today in dry and humid puna and seasonal and dry forests have all withstood long periods of human alteration. They are also adapted to stress in the form of dry seasons of varying length. These factors suggest that species in these landscapes may be on average less vulnerable to climate change than those in páramos and cloud forests. Changing precipitation regimes, especially increases, may cause shifts in species composition and promote invasions by plant forms that have previously been less dominant, but biodiversity losses may be less severe than in more vulnerable systems.

The high topographical relief of the Andes should play a role in buffering the extremes in climate change. Certainly species have more possibilities to move upslope in attempts to track favorable climates than species in low-lying regions such as the Amazon basin. Places with sharp climatic gradients over a small spatial scale and where the impacts of south polar winds are moderated orographically may provide an additional refuge against climate change. Concentrations of endemic species that coincide with these areas of climatic stability appear to support this hypothesis (Fjeldså et al. 1999).

Ecologists have just completed a first comprehensive map and descriptions of tropical Andean ecosystems. Considering the threat posed by climate change, we now need to shift focus to a closer study of the vulnerability of these ecosystems. Replacing ecosystem services of altered natural ecosystems may be difficult, but may be needed to provide products and water to local people. However, the survival of native species also depends on ecosystem integrity, so there is also a need to consider vulnerabilities in all their aspects. Deepening our understanding of the ideas presented here will enhance our ability to manage for adaptation to climate change and avert biodiversity loss where possible.

Literature Cited

Argollo, J., C. Soliz, and R. Villalba. 2004. Potencialidad dendrocronológica de *Polylepis tarapacana* en los Andes centrales de Bolivia. *Ecología en Bolivia* 39(1):5-24.

Benzing, D. H. 1998. Vulnerability of tropical forests to climate change: the significance of resident epiphytes. *Climate Change* 39:519-540.

Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261.

Cuesta, F., and M. T. Becerra. 2009. *Atlas de los Andes del norte y centro*. Lima: Secretaría General de la Comunidad Andina.

Denevan, W. M. 2001. *Cultivated landscapes of native Amazonia and the Andes*. Oxford: Oxford University Press.

Dillehay, T. D., J. Rossen, T. C. Andres, and D. E. Williams. 2007. Preceramic adoption of peanut, squash, and cotton in northern Peru. *Science* 316:1890-1893.

Farley, K. A. 2007. Grasslands to tree plantations: forest transition in the Andes of Ecuador. *Annals of the Association of American Geographers* 97:755-771.

Fjeldså, J. 2002. *Polylepis* forests – vestiges of a vanishing ecosystem in the Andes. *Ecotropica* 8:111-123.

Fjeldså, J., and M. Kessler. 1996. *Conserving the biological diversity of* Polylepis *woodlands of the highlands of Peru and Bolivia: a contribution to sustainable natural resource management*. Copenhagen: NORDECO.

Fjeldså, J., E. Lambin, and B. Mertens. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography* 22:63-87.

Foster, P. 2001. The potential negative impacts of global change on tropical montane cloud forests. *Earth-Science Reviews* 55:73-106.

Freeman, M. C., C. M. Pringle, and C. R. Jackson. 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *Journal of the American Water Resources Association* 43:5-14.

Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: putting conservation science into practice. *BioScience* 52:499-512.

Halloy, S. R. P. 1983. El límite superior de aridez, límite de vegetación y el problema de los lagos, nevés y glaciares activos en el "Núcleo Arido" de la Cordillera Andina. Actas 1era Reunión Grupo Periglacial Argentino, Mendoza. *Anales 83, IANIGLA* 5:91-108.

Halloy, S. R. P. 1998. A new and rare plate-shaped *Geranium* from the Cumbres Calchaquíes, Tucumán, Argentina. *Brittonia* 50:467-472.

Halloy, S. R. P. 2002. Variations in community structure and growth rates of high-Andean plants with climatic fluctuations. Pp. 227-239 in *Mountain biodiversity: a global assessment*, edited by C. Körner and E. M. Spehn. London: Parthenon Publishing.

Intendencia Forestal y de Fauna Silvestre. 2002. *Evaluación poblacional del suri en los departamentos de Tacna y Puno*. Lima: Dirección de Conservación de Biodiversidad, Instituto Nacional de Recursos Naturales. Available at: http://www.inrena.gob.pe/iffs/biodiv/est_poblacionales.pdf.

Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58-62.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009a. *Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela*. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

Josse, C., G. Navarro, P. Comer, R. Evans, D. Faber-Langendoen, M. Fellows, G. Kittel, S. Menard, M. Pyne, M. Reid, K Schulz, K. Snow, and J. Teague. 2003. *Ecological systems of Latin America and the Caribbean: a working classification of terrestrial systems*. Arlington, VA: NatureServe.

Kappelle, M., and A. D. Brown (eds.). 2001. *Bosques nublados del Neotrópico*. Santo Domingo de Heredia, Costa Rica: INBio.

Kessler, M. 1999. Plant species richness and endemism during natural landslide succession in a perhumid montane forest in the Bolivian Andes. *Ecotropica* 5:123-136.

León, B., J. Roque, C. Ulloa, N. Pitman, P. M. Jørgensen, and A. Cano. 2006. El libro rojo de las plantas endémicas del Perú. *Revista Peruana de Biología* 13(2):1-967.

López, R. P. 2003. Phytogeographical relations of the Andean dry valleys of Bolivia. *Journal of Biogeography* 30:1659-1668.

López, R. P., and C. Zambrana-Torrelio. 2006. Representation of Andean dry ecoregions in the protected areas of Bolivia: the situation in relation to the new phytogeographical findings. *Biodiversity and Conservation* 15:2163-2175.

Luck, G. W., K. M. A. Chan, and J. P. Fay. 2009. Protecting ecosystem services and biodiversity in the world's watersheds. *Conservation Letters* 2:179-188.

Overpeck, J. T., P. J. Bartlein, and T. Webb III. 1991. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* 254:692-695.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637-669.

Smit, B., I. Burton, R. J. T. Klein, and J. Wandel. 2000. An anatomy of adaptation to climate change and variability. *Climate Change* 45:223-251.

Solíz, C., R. Villalba, J. Argollo, M. S. Morales, D. A. Christie, J. Moya, and J. Pacajes. 2009. Spatio-temporal variations in *Polylepis tarapacana* radial growth across the Bolivian Altiplano during the 20th century. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281:296-308.

Still, C. J., P. N. Foster, and S. H. Schneider. 1999. Simulating the effects of climate change on tropical montante cloud forests. *Nature* 398:608-610.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B, Biological Sciences* 270:467-473.

Valencia Reyes, R., N. Pitman, S. León-Yánez, and P. M. Jørgensen. 2000. *Libro rojo de las plantas endémicas del Ecuador 2000*. Quito: Herbario QCA, Pontificia Universidad Católica del Ecuador. 493 pp.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. *Earth-Science Reviews* 89:79-96.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389-395.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475-482.

Young, K. R., B. León, P. M. Jørgensen, and C. Ulloa Ulloa. 2007. Tropical and subtropical landscapes of the Andes Mountains. Pp. 200-216 in *The physical geography of South America*, edited by T. T. Veblen, K. R. Young, and A. R. Orme. Oxford: Oxford University Press.

12

Increased Climatic Stress on High-Andean Ecosystems in the Cordillera Central of Colombia

Daniel Ruiz Carrascal, Maria del Pilar Arroyave Maya, Maria Elena Gutiérrez Lagoueyte, and Paula Andrea Zapata Jaramillo

The upper range of the northern Andes harbors unique neotropical alpine wetland ecosystems known as *páramos*. These occupy the narrow elevational belt above Andean cloud forests (ca. 2,000-3,500 m) and below areas of "permanent" snow (above ca. 4,500 m). Páramos provide valuable environmental goods and services such as a sustained water supply for domestic, agricultural, and industrial use (Buytaert et al. 2006). Historical climatic conditions of these high-elevation environments are characterized by average temperatures below 10°C, frequent cloud cover and fog, high UV radiation, low atmospheric pressure, strong winds, and precipitation in the form of drizzle (Castano 2002, Gutierrez et al. 2006, Ruiz et al. 2008). Some of these conditions have changed dramatically over recent decades. Human activity at local, regional, and global scales has begun to introduce anthropogenic stress on high elevation environments (Foster 2001, Diaz et al. 2003). In Colombia, for instance, rapid environmental changes and disruptions in the integrity of páramo ecosystems have been observed in recent years (Castano 2002, Gutierrez et al. 2006, Ruiz et al. 2008). Likely changes induced by human activities include, among others, water stress during dry seasons due to receding glaciers and the disappearance of high-elevation water bodies, abrupt loss of biodiversity, frequent occurrence and rapid spread of natural and human-induced fires, and increased erosion. We here review available information

The Páramos of Los Nevados Natural Park

One of the most representative Colombian páramos is located in Los Nevados Natural Park (04°25'to 05°15'N, 75°00' to 76°00'W) on the El Ruiz-Tolima Volcanic Massif in the Cordillera Central of the Colombian Andes. Los Nevados is a protected area located in the Alto Cauca hydroclimatic region. Numerous streams originating in the snowfields of the El Ruiz (5,321 m) and Santa Isabel (5,100 m) ice-capped mountains of the Cordillera Central feed the high-elevation watersheds of the Claro, Otún, and Chinchiná rivers, which provide a continuous water supply to communities in the adjacent lowlands. The orography of the El Ruiz-Tolima volcanic massif and the two inter-Andean Cauca and Magdalena river valleys extends from tropical to nival elevational belts. Historical climatic conditions provide for the presence of eleven Holdridge (1987) life zones in such a small spatial domain: from tropical moist forest (Tmf) to alpine rain tundra (Art). In terms of the Cuatrecasas (1934) system, historical climatic conditions in the area of the Claro River watershed support moist Andean forest, wet high Andean forest, rainy subpáramo, wet subpáramo, rainy páramo, and rainy superpáramo. Data from elevational experimental plots (Ruiz et al. 2009) show that many unique plant species inhabit the headwaters of the Claro River basin. Key species and potential bio-indicators of likely changes in the elevational location and distribution of life zones include: *Miconia salicifolia* (Melastomataceae) and *Berberis rigidifolia* (Berberidaceae) in the subpáramo; *Espeletia hartwegiana* (Asteraceae), *Plantago rigida* (Plantaginaceae), and *Valeriana plantaginae* (Valerianaceae) in the páramo; and *Senecio canescens* (Asteraceae), *Loricaria colombiana* (Asteraceae), and *Lycopodium crassum* (Lycopodiaceae) in the superpáramo.

Observed and Inferred Changes in Historical Climatic Conditions

Climatic patterns have changed in the central region of the Cordillera Central (Ruiz et al. 2008). Observed trends in minimum and maximum near-surface temperatures, rainfall amounts, relative humidity, cloud characteristics, sunshine, and diurnal temperature range suggest that climatic stress is increasing in high-Andean ecosystems of the Cordillera Central. Observed changes appear to be consistent with changes occurring worldwide (see Figure 12.1) and at national and regional spatial scales. Some key aspects of the observed changes in historical climatic conditions are discussed below.

Changes in Near-Surface Temperatures, Rainfall, and Relative Humidity

Studies on changing climatic conditions in páramo life zones are limited due to the lack of long-term historical records. However, there is considerable evidence suggesting that significant changes in near-surface ambient temperatures and annual rainfall have occurred in these tropical environments. Bradley et al. (2006), using temperature records gathered from several stations along the tropical Andes, concluded that the rate of increase in air temperatures was +0.11°C/decade over the period from 1939 to 1998. For Colombia, Pabón (2003, 2004) showed that mean annual ambient temperatures over the period 1961-1990 increased at a rate of about +0.1 to 0.2°C/decade. More recent analyses (Departamento de Geografía, Universidad Nacional de Colombia 2005) have suggested that increases in near-surface temperatures in the Alto Cauca hydroclimatic region reached +0.12°C/decade over the same period. Our recent studies support these findings. Analysis of weather station data (see nationwide scale in Ruiz et al. 2009) suggests increases of up to +0.3°C/decade in mean near-surface temperatures along the Andean mountain ranges. On a regional scale, most historical time series of mean annual near-surface temperatures observed at weather stations located along a 5° latitudinal transect, show increasing trends that could reach 0.4°C/decade on all mountain flanks.

With regard to rainfall (see nationwide scale in Ruiz et al. 2009), most stations along the mountain ranges show decreasing trends over the past 25 years. Stations located in the inter-Andean valleys exhibit increasing trends. Regional rainfall also shows important changes:

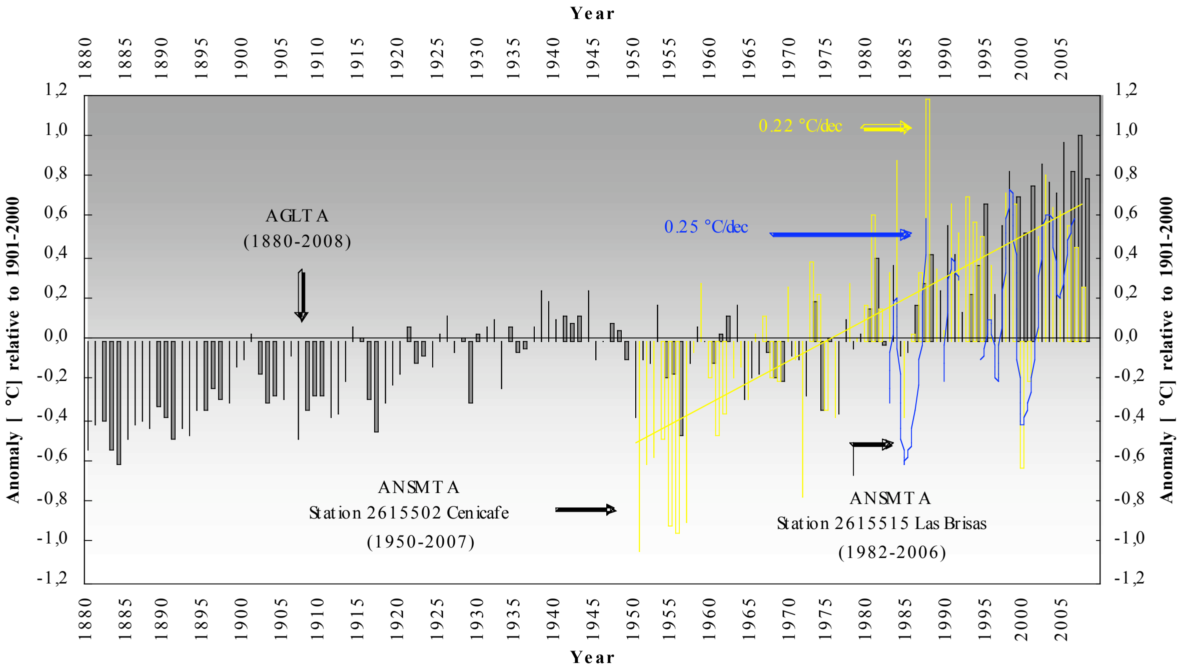

Figure 12.1. Annual global land temperature anomalies (AGLTA; source: NOAA Satellite and Information Service-National Environmental Satellite, Data and Information Service) and annual local near-surface mean temperature anomalies (ANSMTA, observed at stations XII-2615502 Cenicafé and I-2615515 Las Brisas). Anomalies are defined as departures from the 20th-century average (1901-2000). Linear trends in near-surface ambient temperatures observed in the area of the Claro River watershed exhibit rates of increase of about 0.22-0.25°C/decade.

increases have been observed over recent years on the western flank of the Cordillera Occidental, where total annual rainfall is strongly influenced by the orographic uplift of the westerly Chocó low-level jet (Poveda and Mesa 2000, Vernekar et al. 2003). By contrast, historical time series over the eastern flank of the Cordillera Central, where rainfall amounts are influenced by the behavior of the easterlies and the low-level jet to the east of the Cordillera Oriental (Vernekar et al. 2003), show general tendencies toward drier conditions. In the inter-Andean valleys some stations exhibit increasing trends in rainfall while others have seen decreases. Along these valleys rainfall amounts are affected by elevation and show influences of the northeasterly trade winds, which in the area become valley currents that blow southward.

In the areas surrounding Los Nevados Natural Park, most of the climatic variables that control the integrity of high-elevation ecosystems also show statistically significant changes (see local scale in Ruiz et al. 2009 for specific rates of change). These variables include total annual rainfall, maximum daily rainfall, minimum temperatures during the coldest days, maximum temperatures during the warmest days, and minimum relative humidity. Analyses suggest that in Los Nevados and at higher elevations on the western flank of the Cordillera Central, total annual rainfall at elevations above the pluviometric optimum (ca. 1,500 m) is decreasing. Below this elevation, some weather stations report slowly increasing trends. Daily precipitation records suggest, in general, an increased occurrence of unusually heavy rainfall events. Minimum temperatures on the coldest days show increasing trends at all elevations, suggesting that below-freezing temperatures and cold days are becoming less frequent. Increases in minimum temperatures at higher elevations are greater than those observed at lower elevations. Maximum temperatures on the warmest days are also rising and, much like minimum temperatures, exhibit faster increases at higher elevations. Finally, analyses suggest that minimum relative humidity values have significantly decreased at higher elevations.

Changes in Cloud Characteristics, Sunshine, and Diurnal Temperature Range

One of the key factors of increased climatic stress in Colombian páramos is the change in cloud cover (Ruiz et al. 2008). Cloud amounts are highly dependent on regional and local processes: coupled interactions between sea surface temperatures (SSTs), wind patterns, and the latitudinal displacement of the Inter-Tropical Convergence Zone drive regional cloudiness conditions on intra- to inter-annual timescales. Satellite data show important reductions in cloud cover over the high-elevation region over the last two decades of the 20th century. Observed changes in the region seem to reflect these changes in cloud cover. Most of the weather stations on the western flank of the Cordillera Central at elevations around the pluviometric optimum, exhibit statistically significant decreasing trends in the total annual sunshine and the maximum, minimum, and mean daily sunshine values. Such decreases in sunshine are consistent with statistically significant increases in the total number of foggy days and decreases in the total number of sunny days. By contrast, the total number of foggy days per month at higher elevations has decreased slightly over the past decades. Finally, homogeneity analyses conducted for Los Nevados Natural Park suggest that maximum, mean, and minimum diurnal temperature range (minDTR) at higher elevations have increased over the past decades. Maximum DTR, in particular, show statistically significant increasing trends at higher elevations, whereas lower elevations show decreasing trends. The upward trend at higher elevations is a consequence of the difference between the aforementioned rates of increase in minimum and maximum temperatures.

Water Balance, High-Elevation Water Bodies, and Ice Caps

Changes have also occurred in hydrological regimes. Besides rainfall, water inputs to the hydrological cycle in high-elevation watersheds include outflow from water bodies and aquatic micro-habitats, mist, glaciers, and snowmelt. Our analysis of intra-annual cycles of the mean streamflow of the Claro, Otún, and Chinchiná rivers suggest that water discharges follow the bi-modal annual cycles of rainfall observed in the surroundings of Los Nevados Natural Park, but with a one-month time lag. Periods of high mean water discharge are usually observed during April-May-June and October-November-December. Periods of low streamflow tend to occur during January-February and July-August. Although minimum streamflows show similar intra-annual distributions, observed records exhibit important differences during the dry periods January-February and July-August. During these months meltwater runoff from snow fields and glaciers, as well as water inputs from high-altitude water bodies and turberas (bogs) increase surface streamflow (i.e., streamflow is greater than would be expected from rainfall amounts alone due to meltwater runoff). This effect is particularly pronounced in the Claro and Otún river basins. By contrast, in the Chinchiná River, which does not receive meltwater runoff, and where aquatic microhabitats are limited to a few areas at its headwaters, reductions in streamflow during the critical dry months are considerable.

Decreases in annual rainfall observed at elevations above the pluviometric optimum and increases in near-surface temperatures, particularly at higher elevations, are likely to decrease streamflow. Exploratory analyses suggest decreasing trends in annual maximum and mean streamflow values in the Otún and the Chinchiná rivers over the past 40 and 20 years, respectively, although these trends are not statistically significant. Minimum discharges during the critical months January-February and July-August show changes in the available historical time series that are statistically significant. In the Otún River, minimum water discharges and minimum streamflows during the driest period January-February exhibit decreases of ca. 1.0% and >6.0% per decade, respectively, over the past 40 years.

Are these trends related to changes in the extent of high-elevation water bodies and ice-caps? Water bodies in the Los Nevados Natural Park have experienced reductions in surface area over recent years, and some have already experienced natural sediment-filling and drying processes, accompanied by a gradual colonization by local vegetation. However, water bodies also exhibit a marked seasonality driven by regional climatic conditions. Increases in their water levels are common during April-May and October-November, whereas decreases typically occur during December-January-February and July-August-September. On inter-annual timescales, high-elevation water bodies show dynamics related to the warm and cold events of the El Niño–Southern Oscillation. Specifically, significant drought-induced shrinkages with respect to “past” reference shorelines are observed after above-normal summers that commonly accompany the El Niño warm events.

On the other hand, the Molinos glacier on the western flank of El Ruiz Nevado and the Conejeras glacier tongue on the western flank of the Santa Isabel Nevado have retreated dramatically over recent years (Euscategui 2002, Ceballos et al. 2006, IDEAM 2008). These retreats have been forced by volcanic activity, changes in climatic conditions, and changes in local surface albedo. Although there is limited information to infer the potential impacts of the changes in the extent of high-elevation water bodies and ice-caps on the ecosystem as a whole, the disappearance of water bodies and turberas and the retreat of mountain glaciers are probably undermining the integrity of páramo ecosystems. It is likely that the change in water availability has and will continue to have a sizable effect.

High-Elevation Fires

Fire events are one of the most serious threats to the integrity of high-Andean ecosystems and one of the most critical challenges for the conservation of protected areas. At higher elevations, fires cause numerous and almost-irreversible damage to páramo soils, wetlands, fauna, and flora. Fire-induced changes in the structure and composition of páramo ecosystems affect their provision of several environmental goods and services. In the surroundings of Los Nevados, lower-elevation areas and buffer zones are inhabited by smallholder farmers whose main productive activities include grazing dairy cattle and the cultivation of potato crops. Fires are usually set to regenerate grass for livestock, prepare land after harvesting crops, and expand cultivated land areas. These burns are not controlled appropriately and often spread into “non-target” natural vegetation in páramo zones. Fires are particularly hazardous during the dry season given the high to very high vulnerability of páramo habitats to the occurrence and rapid spread of fires during this period.

Historical records of fires in Los Nevados extend back to 1994 (source: Unidad Administrativa Especial del Sistema de Parques Nacionales Naturales). These records include the worst ecological disaster that has occurred in protected Colombian high-elevation ecosystems, namely the fire of unprecedented severity that took place in the surroundings of the Laguna del Otún in July 2006 (Lotero et al. 2007). This event lasted for almost eight days and affected more than 4% of the of the park. Sadly, since 1994 the annual number of fire events, the total area affected per year, and the average fire duration show strong increasing trends. This is the result of several factors such as a weak institutional capacity to react to fires, more combustible material in the area, and climatic conditions more favorable to the spread of fires. Most events have been induced by or are related to human activities, but it is likely that changing climatic conditions have favored their rapid spread. Increases in the number of events and affected areas seem to correlate with the increasing and decreasing trends observed in temperature and relative humidity records (see above), respectively, gathered at nearby weather stations.

This link does not appear to be a coincidence. Testimonies of local experts and park guards support the links between the current rapid spread of fire events and the observed changes in climatic conditions in the area. Also, an association between the timing of fire events, the total area affected per month, and the intra-annual cycles of climatic conditions in the area of Los Nevados has been observed. Most fire events occur during the dry seasons June-July-August (JJA) and December-January-February (DJF). Higher values of maximum temperatures linked to lower relative humidity and rainfall set the stage for a potential increase in the spread of "small-scale" fire events during these trimesters. The maximum number of events and greatest area affected per month are observed during the trimester JJA. However, when excluding the unprecedented fire event of July 2006, the highest value of total area affected per month occurs during DJF. In summary, although changing conditions are not directly causing an increase in high-elevation fires, drier conditions may favor their rapid spread. Thus, larger affected areas and greater duration of fires are early warnings of the páramo ecosystems' increasing vulnerability.

Model Projections

Model projections consistently suggest future climatic conditions will be unfavorable for páramo life zones (Vuille et al. 2003, Diaz et al. 2003). Hulme and Sheard (1999) used the outputs of six Global Climate Models (GCMs) to propose future climate scenarios for the Northern Andes. According to their results, the total annual rainfall in the central region of the Cordillera Central is expected to be above the 1961-1990 normal annual value for all emission scenarios. They also suggest that increases in mean annual temperatures are expected throughout the region. Giorgi and Bi (2005) used atmosphere-ocean coupled GCM simulations for northern South America to predict increases in rainfall during future wet seasons and decreases during dry seasons. Also, near-surface temperatures are predicted to be above historical normal conditions. Bradley et al. (2006) used GCM results to suggest that, at 5°N and at elevations of 3,000-5,000 m, mean annual temperatures are expected to increase over this century under emission scenario A2 of Meehl et al. (2007). For Colombia recent statistical downscaling techniques of GCM outputs were used to estimate future climatic conditions under a 2xCO_2 emission scenario (Departamento de Geografía–Universidad Nacional de Colombia 2005). On a national scale and for the Alto

Cauca hydroclimatic region, total annual rainfall is expected to change up or down depending on the model, but mean annual ambient temperatures are consistently expected to be above the past mean.

GCM outputs indicate an increase in the elevation of clouds under a future warmer world (Meehl et al. 2007). They also suggest that most tropical areas will experience a decrease in net cloud cover over all layers. Based on our analyses of January SST anomalies (Ruiz et al. 2009), we suggest that a significant decrease in cloud cover in the high-elevation region is likely to occur over the next 50 years under normal conditions. Our predicted decrease of 6.8% in total cloud cover, relative to the period 1984-2001, is 1.4 times greater than (but consistent with) the -2.0% annual mean change suggested by Meehl et al. (2007) for the period 2080 to 2099, relative to 1980 to 1999. We also argue that if a strong El Niño event were to occur by 2050, the reduction in January monthly average cloud cover could be more critical.

Changes in the structure, composition, integrity, and extension of high-elevation ecosystems inhabiting the Claro River watershed and nearby areas are likely to occur over the first half of this century. Ongoing changes in climatic conditions could force upward shifts in the transitions between life zones, which would lead to the appearance of new environments, the expansion of some others, and reductions in the extent of the subalpine (páramo), alpine (superpáramo), and nival (glacial) elevational belts. The future distribution of these ecosystems will depend on their capacity to adapt to the expected climatic changes. Our analyses suggest that by 2050 climatic conditions in the watershed and the region will likely be suitable for the colonization of lower montane dry forest (LMdf) and montane moist forest (Mmf). A 56% increase in the montane wet forest (Mwf) surface area could also occur. On the other hand, subalpine rain páramo (SArp), alpine rain tundra (Art) and nival (N) life zones could experience reductions of about 31%, 53%, and 80%, respectively, by 2050. In terms of the Cuatrecasas classification, reductions in the areas of subpáramo, páramo, superpáramo, and nival zones could be 83%, 22%, 53%, and 80%, respectively. With respect to the entire páramo zone, such reductions correspond to a total decrease in area of about 54%.

Potential Impacts on Ecosystem Integrity

Although their impacts on the integrity of high-elevation habitats are very difficult to assess, changing climatic conditions could lead to the disruption of páramo and cloud forest ecosystems. Some of the expected impacts include:

- Upward migration of low-elevation plant species are expected to occur, reducing the extent of páramo habitats. As the climate warms and ice caps melt a shift in life zones to higher elevations could be expected as, over long time intervals, these zones would maintain their relationships to the snow line. However, the inferred rapid upward changes in the Lifting Condensation Level and field-observed retreats of snowline (both considered good approximations of upward shifts in the transitions between life zones) suggest that several high-elevation plant species will most likely be unable to migrate upward. Changes in temperature could favor the upslope migration of many montane species, but might also have a devastating impact on those species that have adapted to and become dependent on extreme conditions at high altitudes.

- Elevational changes in sunshine and rainfall could contribute to an increase in the rate of desertification of montane habitats, which today house an important fraction of global biodiversity.

- Areas where only snow or drizzle used to fall could be experiencing heavy rain due to the rapid upward shift of the freezing level. Glacier margins may be at increasing risk of retreat, contributing to a continued diminution of the self-regulation capacity of the hydrological system.

- Decreases in the amount of cloud and fog cover, driven by changes in atmospheric stability, will have significant impacts on the net radiation balance. As a consequence, glacier mass, high-elevation water bodies and mountain species could be further affected.

- Finally, higher solar energy is expected to accelerate the hydrological cycle and increase evapotranspiration, having strong effects on water bodies and aquatic microhabitats.

Combined, these impacts constitute a serious threat to unique páramo habitats and, consequently, to the water supply in the region. In the foreseeable future it will be more expensive to supply water for human consumption, power generation, and agriculture (Vergara et al. 2007, Vergara 2009). Ambitious sustainable management strategies are now urgently required to protect these unique, rich, fragile, and highly endangered environments.

Literature Cited

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 312:1755-1756.

Buytaert, W., R. Célleri, B. De Bièvre, F. Cisneros, G. Wyseure, J. Deckers, and R. Hofstede. 2006. Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews* 79:53-72.

Castaño, C. (ed.). 2002. *Páramos y ecosistemas alto andinos de Colombia en condición hotspot & global climatic tensor*. Bogotá: Ministerio del Medio Ambiente and Instituto de Hidrología, Meteorología y Estudios Ambientales. 387 pp.

Ceballos, J. L., C. Euscategui, J. Ramirez, M. Canon, C. Huggel, W. Haeberli, and H. Machguth. 2006. Fast shrinkage of tropical glaciers in Colombia. *Annals of Glaciology* 43:194-201.

Cuatrecasas, J. 1934. Observaciones geobotánicas en Colombia. *Trabajos del Museo Nacional de Ciencias Naturales*, *Serie Botanica* 27:1-144.

Departamento de Geografía–Universidad Nacional de Colombia. 2005. *Escenarios de cambio climático para el territorio colombiano. Fase PDF-B, Integrated National Adaptation Pilot (INAP) - Informe Ejecutivo*. Bogotá: Universidad Nacional de Colombia. 19 pp.

Diaz, H. F., M. Grosjean, and L. Graumlich. 2003. Climate variability and change in high elevation regions: past, present and future. *Climatic Change* 59:1-4.

Euscategui, C. 2002. Estado de los glaciares en Colombia y análisis de la dinámica glaciar en el Parque Los Nevados, asociada al cambio climático global. MSc thesis. Bogotá: Universidad Nacional de Colombia, Facultad de Ciencias, Departamento de Geociencias. Available at: http://www.ideam.gov.co/biblio/paginaabierta/galaciarparquenevados.pdf.

Foster, P. 2001. The potential negative impacts of global climate change on tropical *montane* cloud forests. *Earth-Science Reviews* 55:73-106.

Giorgi, F., and X. Bi. 2005. Updated regional precipitation and temperature changes for the 21st century from ensembles of recent AOGCM simulations. *Geophysical Research Letters* 32:L21715.

Gutierrez, M. E., P. A. Zapata, and D. Ruiz, 2006. *Entendimiento de las señales de cambio climático y variabilidad climática en la oferta hídrica superficial de cuencas hidrográficas en zonas de alta montaña*. Envigado, Antioquia: Environmental Engineering Program, Antioquia School of Engineering. 160 pp.

Hulme, M., and N. Sheard. 1999. Escenarios de cambio climático para países de los Andes del Norte. Norwich: Climatic Research Unit, University of East Anglia. 6 pp. Available at: http://www.climate.org/resources/climate-impacts/latinamerica.html.

Holdridge, L. R., 1987. *Ecología basada en zonas de vida*. San José, Costa Rica: Instituto Interamericano de Cooperación para la Agricultura.

Instituto de Hidrología, Meteorología y Estudios Ambientales. 2008. Los glaciares colombianos: expresión del cambio climático global. Available at: www.ideam.gov.co/publica/glaciares/glaciares.pdf.

Lotero, J. H., L. N. Trujillo, W. G. Vargas, and O. Castellanos. 2007. *Restauración ecológica en páramos del Parque Nacional Natural Los Nevados: experiencias de restauración ecológica en páramos luego de incendios forestales en la cuenca alta del río Otún*. Bogotá: Editorial Andina. 152 pp.

Meehl, G. A., T. F. Stocker, W. D. Collins, P. Friedlingstein, A. T. Gaye, J. M. Gregory, A. Kitoh, R. Knutti, J. M. Murphy, A. Noda, S. C. B. Raper, I. G. Watterson, A. J. Weaver, and Z.-C. Zhao. 2007. Global climate projections. In *Climate change 2007: the physical science basis*. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

Pabón, J. D. 2003. El cambio climático global y su manifestación en Colombia. *Cuadernos de Geografia* 12(1-2):111-119.

Pabón, J. D. 2004. El cambio climático y sus manifestaciones en Colombia. *Innovación y Ciencia* 11(3-4):68-73.

Poveda, G., and O. J. Mesa. 2000. On the existence of Lloró (the rainiest locality on Earth): enhanced ocean–land–atmosphere interaction by a low level jet. *Geophysical Research Letters* 27:1675-1678.

Ruiz, D., H. A. Moreno, M. E. Gutierrez, and P. A. Zapata. 2008. Changing climate and endangered high mountain ecosystems in Colombia. *Science of the Total Environment* 398:122-132.

Ruiz, D., M. P. Arroyave, A. M. Molina, J. F. Barros, M. E. Gutierrez, and P. A. Zapata. 2009. *Signals of climate variability/change in surface water supply of high-mountain watersheds – case study: Claro River high mountain basin, Los Nevados Natural Park, Andean Central Mountain Range, Colombia*. Medellin: World Bank Group and School of Engineering. 207 pp.

Vergara, W. (ed.). 2009. *Assessing the potential consequences of climate destabilization in Latin America. Latin America and Caribbean Region Sustainable Development Working Paper 32*. The World Bank. 115 pp. Available at: http://go.worldbank.org/RV4VNYC2U0.

Vergara, W., A. M. Deeb, A. M. Valencia, R. S. Bradley, B. Francou, A. Zarzar, A. Grünwaldt, and S. M. Haeussling. 2007. Economic impacts of rapid glacier retreat in the Andes. *EOS, Transactions American Geophysical Union* 88(25):261-264.

Vernekar, A. D., B. P. Kirtman, and M. J. Fennessy. 2003. Low-level jets and their effects on the South American summer climate as simulated by the NCEP Eta model. *Journal of Climate* 16:297-311.

Vuille, M., R. S. Bradley, M. Werner, and F. Keimig. 2003. 20th century climate change in the tropical Andes: observations and model results. *Climatic Change* 59:75-99.

13

Regional Patterns of Vascular Plant Diversity and Endemism

Peter M. Jørgensen, Carmen Ulloa Ulloa, Blanca León, Susana León-Yánez, Stephan G. Beck, Michael Nee, James L. Zarucchi, Marcela Celis, Rodrigo Bernal, and Robbert Gradstein

The total number of vascular plant species on Earth has been estimated to be between 223,000 and 420,000 (Govaerts 2003; Scotland and Wortley 2003). The South American flora alone may hold as many as 90,000 species (Henderson et al. 1991). The northern Andes are often considered the premier biodiversity hotspot on earth, although this is not based on plants alone (Rodríguez-Mahecha et al. 2004). The concept of hotspots is defined as areas of high biodiversity and high levels of endemism and is intended to focus conservation efforts towards these areas and thereby save the highest number of species for the least amount of effort and money (Myers 1998; Myers et al. 2000). Colombia, Ecuador, Peru, and Bolivia cover approximately 2.5% of Earth's terrestrial area or 21% of South America but harbor 12–22% of world's flora or 55% of the South American flora, and the percentage of endemics in each country is 25–30%.

Theory and empirical work indicate that the main determinants of species richness are available energy and water, topography and edaphic heterogeneity, historic factors, possibly geometric constraints (the mid-domain effect), and obviously the extent of the area under consideration (Simpson 1964; Rosenzweig 1995; O'Brien 1998; Colwell and Lees 2000; Field 2005; Jiménez et al. 2009; Distler et al. 2009). These determinants are covered in detail elsewhere in this volume (Kessler et al., Chapter 14), but several important geophysical features across the region help to explain the richness of plant species. Latitudinally, the Andes, with an orogeny that spans 18–20 million years, run through all four countries establishing wide ranges and variances in edaphic and topographical factors, which in turn often alter the humidity levels dramatically over very short distances. Many complex topographic features like the valleys of Huancabamba and the Girón–Paute, form barriers in the east-west direction, while the valleys of Magdalena and Cauca are examples of barriers in the north-south direction (Jørgensen and Ulloa Ulloa 1994, Weigend et al. 2005, Young et al. 2002; Josse et al., Chapter 10, this volume). The oldest parts of the Andes are found to the south while progressively younger mountains are found towards the north, creating gradual differences in the evolutionary history (Gregory-Wodzicki 2000; Josse et al., Chapter 10, this volume). Source areas for immigration to these rather young mountains are the older eroded mountainous areas of the Guyana and Brazilian shields, Central and North America through the Panamanian isthmus, and the temperate areas to the south (Graham 2009).

The mosaic nature and crisscrossing of many gradients sets the stage for an extremely plant-rich region. The mechanisms that create and maintain the richness are still poorly understood. This presents a serious impediment to evaluating what will happen in a changing climate. Since we do not fully understand the mechanisms behind the species richness patterns it is almost impossible to foresee what will happen to the biodiversity in the area when change is induced in one or more parameters.

Current Knowledge of the Tropical Andean Flora

The flora of the region has been the topic of research for more than 250 years, which has resulted in thousands of publications in the taxonomic literature. Synthesis of this information is found in four catalogues. In the case of Peru (Brako and Zarucchi 1993) and Ecuador (Jørgensen and León-Yánez 1999), they also have their respective supplements (Ulloa Ulloa et al. 2004; Ulloa Ulloa and Neill 2005). For Bolivia, there is an ongoing compilation of information towards a catalogue of the vascular plants. Similarly the Colombian catalogue is forthcoming; currently only preliminary information is available (Bernal et al. 2006; Bernal et al. 2007). Each of the four catalogues consulted and synthesized more than 3,000 references. The catalogues represent the most complete approximation of the species richness in these countries. Collection density and time passed since the last revision or floristic treatment poses a bias in our knowledge that can only be improved upon by generating new information, i.e. by generating more collections and floristic or monographic work.

Vascular Plant Richness at Different Taxonomic Levels

A total of 338 plant families are found in the four tropical Andes countries, 294 of which occur in Colombia, 238 in Ecuador, 242 in Peru, and 241 in Bolivia. Sørensen’s similarity index for pair-wise comparisons between countries of the families varies from 0.76 to 0.94. Fifty-two (52) families are only found in a single country, 74 in two countries, and 33 in three countries, whereas 179 families occur in all four countries. Table 13.1 lists the families with the highest species numbers. The floras at the family level are, as expected, very similar. Differences may be due to inclusion of exotic families and possibly due to differences in the taxonomic systems used. Not only is the number of families similar and most families are present in most countries, but the most species rich families are also largely the same (Table 13.1).

A total of 4,002 genera are found in the four countries, 2,944 of which occur in Colombia, 2,302 in Ecuador, 2,635 in Peru, and 2,507 in Bolivia. The number of genera is similar across countries. Sørensen’s similarity index for pair-wise comparisons between countries of the genera varies from 0.67 to 0.81. A total of 1,165 genera are only found in a single country, 697 in two countries, and 670 in three, whereas 1,428 are shared by all four countries. Table 13.2 lists the most species-rich genera for each country. The generic floras are similar, but display more difference than the families. Several genera appear to have a latitudinal tendency of becoming less species rich towards the south (Table 13.2), whereas others such as

Senecio and *Solanum* appear to show a different tendency. In the case of *Senecio*, however, true patterns are severely masked by how this genus is circumscribed in the different treatments.

Table 13.1. The 10 most species-rich families.

	Colombia	Ecuador	Peru	Bolivia
Orchidaceae	3,588	3,630	2,057	844
Asteraceae	1,420	966	1,655	1,361
Rubiaceae	1,214	658	822	444
Melastomataceae	948	572	663	354
Poaceae	813	560	755	840
Piperaceae	605	456	823	212*
Araceae	591	443	283*	139*
Fabaceae	568	601	1024	999
Bromeliaceae	493	514	465	327*
Solanaceae	441	368	614	400
Euphorbiaceae	394*	221*	285*	371
Cyperaceae	328*	222*	234*	312

* indicates ranking below the 10th position in the respective country

Table 13.2. The 10 most species-rich genera.

	Colombia	Ecuador	Peru	Bolivia
Epidendrum	465	443	251	115
Piper	373	225	438	92
Miconia	331	243	299	161
Anthurium	262	236	93*	39*
Lepanthes	262	313	46*	61*
Maxillaria	238	195	171	2*
Psychotria	234	136*	173	83*
Peperomia	230	229	384	120
Solanum	229	189*	299	230
Elaphoglossum	175	132*	143*	133
Pleurothallis	115*	429	148*	127
Stelis	115*	327	94*	55*
Masdevallia	101*	229	155	52*
Senecio	56*	11*	199	113
Lupinus	47*	22*	171	53*
Tillandsia	78*	104*	143*	107
Thelypteris	120*	110*	104*	98

* indicates ranking below the 10th position in the respective country

The number of vascular plant species found in Colombia is 24,405, whereas Ecuador holds 16,006, Peru 19,232, and Bolivia 14,387 species. The total number of species found in the three southernmost countries is 36,192. Between-country comparisons cannot include Colombia because a list of the species is not currently available for analysis. The total number of species found in the four countries is estimated at 45–50,000. The Sørensen similarity index between Ecuador and Peru is 0.40, between Ecuador and Bolivia 0.26, and between Peru and Bolivia

0.34. Only 3,365 species are found in all three countries, 6,687 are found in two countries, whereas 26,140 are only found in a single country each.

An assessment of threat due to climate change at the three taxonomic levels would indicate that threatened families should be sought among those with restricted distribution or endemic families and quite possibly families with very specific climatic adaptation. Examples of such families are: Alzateaceae, Columelliaceae, and Malesherbiaceae (Young et al. 2002). For entire genera to be under threat we would again look to the genera restricted both geographically and climatically. Endemic genera are numerous; examples are found in Ulloa Ulloa and Jørgensen (1995). About 50% of the species are restricted in distribution. This indicates that a high proportion of the species have small distribution ranges which places them at higher risk.

Elevation Richness Patterns

For Ecuador, Peru, and Bolivia, we were able to perform a comparison of the number of species in elevational bands of 500 m and to control for the area of each band with a logarithmic transformation. The results are presented in Figure 13.1a–d. Figure 13.1a shows the simple count of species per elevational band, and it is noteworthy that the shapes of the curves are very similar for all three countries. Ecuador has more species from 500 to 3500 m than the other two countries, but fewer species in the upper altitudinal bands where its area is smaller. In the lowlands Ecuador has more species than Bolivia, but fewer than Peru. Possible explanations center on the smaller area of Ecuador relative to Peru, Ecuador's humid Pacific coast, and the large dry area found in southeastern Bolivia. There may also be a latitudinal tendency, and other factors play a role as well. When the number of species is corrected by the logarithm of area of each altitudinal band (Figure 13.1b), linear regressions of the number of species per unit area against elevation are significant, and over 90% of the variability in the data is explained by available area for all countries. All area calculations were performed with ArcMap 9.3. The 90 m DEM was obtained from Jarvis et al. (2008). The slope of the regression lines varies. Ecuador has the highest corrected richness and the steepest decline in richness along the elevational gradient. A decrease in richness and a significant flattening occur progressively in Peru and Bolivia.

In Figure 13.1c–d we compare the number of species with the area of the elevational bands for each country (Figure 13.1c). After logarithmic transformation of areas (Figure 13.1d), a strong linear relationship emerges for Ecuador (black squares and black regression line, R^2=0.9), whereas no clear pattern is evident for Bolivia and Peru (R^2<0.15). The area of an elevational band is, in other words, a relatively good predictor for the number of species in Ecuador but not in Peru and Bolivia.

A way to assess whether or not a band is well collected is to examine the number of collections per unit area. Campbell (1989) proposed a threshold value of 1 collection/km^2 as indicating well collected areas. Using this threshold, data from Tropicos® indicate that Ecuador is well collected in all elevational bands except for the 0–500 m band (0.8 collections/km^2); all other bands have over 1.6 collections/km^2, with a maximum value of 3.2 at 2500–3000 m. In Peru, all bands have 0.6 collections/km^2 or less, i.e. less than the least explored band in Ecuador and well below the threshold. Minimum values are 0.02 and 0.03 collections/km^2 at >4500 m and 4000–4500 m, respectively. The maximum value 0.6 is found at 2000–2500 m. In Bolivia, the situation is only slightly better, with a maximum value of 0.7 at both 1500–2000 m and

2000–2500 m, and minimum values of 0.05–0.08 from 3500 m to >4500 m. The poor documentation of the flora in the uppermost areas is troublesome because the effects of climate change are expected to be most severe there.

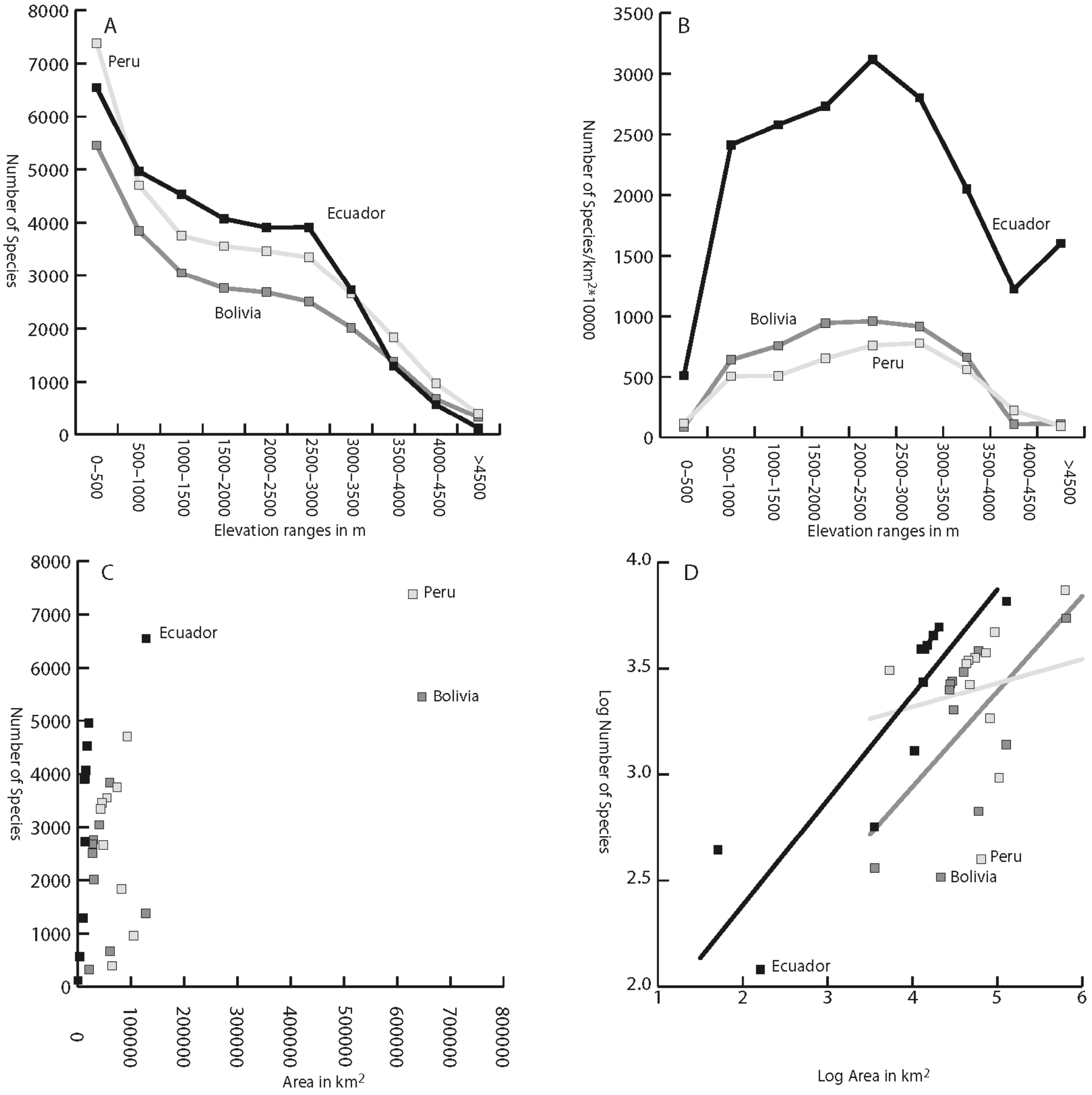

Figure 13.1. A. The number of species in altitudinal bands for the three countries Ecuador, Peru and Bolivia. B. The number of species per logarithm of the area of the bands in the altitudinal bands. Ecuador black squares and regression line (R^2=0.917), Peru light gray squares and regression line (R^2=0.9239), Bolivia dark gray squares and regression line (R^2=0.9587). C. The number of species in elevation zones versus the area of the elevation zones. D. The logarithm of the number of species in elevation zones versus the logarithm of area of the same. Ecuador black squares and regression line (R^2=0.7723), Peru light gray squares and regression line (R^2=0.024), Bolivia dark gray squares and regression line (R^2=0.3594).

Richness Patterns Based on Political Units (first political divisions)

We attempted to use the first political division (departments and provinces) in an analysis, to see if a latitudinal signal could be found in the data. The prediction would be that there would be more species in political units located closer to the Equator where more energy is available and seasonality is limited. A single logarithmic transformation i.e. number of species/Log area provided a linear regression with poor fit ($R^2 = 0.04$), while a logarithmic transformation of both the number of species and area gives a relatively good fit and a slope of 0.01 Log species/Log area decline per degree ($R^2 = 0.51$) (Figure 13.2).

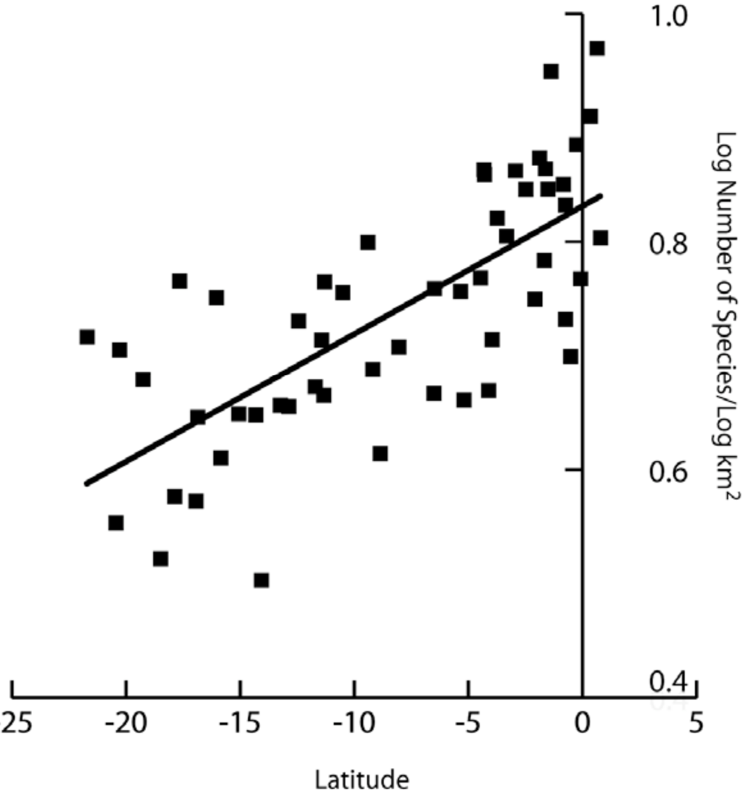

Figure 13.2. The first political division latitudinal midpoint versus logarithm of number of species per logarithm of area ($R^2 = 0.5154$).

National Endemic Species

In the following we are considering all species restricted to a country as endemic. The catalogues of Ecuador and Peru were used for the elaboration of red lists. The threat status was assessed using the International Union for Conservation of Nature (IUCN) criteria for national endemic species (IUCN 1994, 2001). This resulted in red lists for Ecuador (Valencia et al. 2000) and Peru (León et al. 2006) and an updated second edition for Ecuador. The number of endemic species found in Bolivia was extracted from the Bolivian catalogue. The species may therefore display a wide variety of distributional ranges depending on the size of the country in which they occur.

The two inventories for Ecuador from 2000 and 2008 (Valencia et al. 2000) include 4011 and 4433 endemic species respectively i.e., an increase of 422 species between the two time periods. Peru has 5581 endemic species of which 3483 taxa were assessed by León et al. (2006). In Ecuador, all IUCN categories (except Not Evaluated, Nearly Threatened, and Data Deficient) showed an increase over the eight year period between assessments, both in absolute numbers and in percentage of species. This negative development indicates that more and more species are in categories where conservation action or more careful monitoring is required.

We subdivided IUCN categories into a combined threatened category (TC) including Extinct, Critically Endangered, Endangered, and Vulnerable taxa, versus a non-threatened category (NTC) that includes Least Concern, Data Deficient, and Not Evaluated taxa. We expect that the difference between the TC and NTC in Ecuador will be larger than in Peru as an effect of its smaller size. In Figure 13.3a, the number of species per altitudinal band shows a clear midlevel maximum for the TC in both Ecuador and Peru. The NTC has a midlevel maximum in Peru, whereas the relationship could be close to negative linear in Ecuador. Ecuador has more species in the TC per altitudinal band than Peru. When looking at the proportion of TC and NTC of the total richness in the altitudinal band (Figure 13.3b) ascending the mountains makes the TC a more and more prominent part of the flora. In the 0–500 m bands 5–10% of the species are TC, the highest levels above 20% is found at elevations 1500–3000 m in Ecuador and 3000–3500 m in Peru. Using the logarithm of the area, the same general observation can be made except for the more dramatic drop in the upper elevation bands (Figure 13.3c). A combined control eliminates the reduction at upper elevations seen in figure 3c (Figure 13.3d), and shows that threatened species (TC) are particularly found in montane forest, puna and páramo vegetation, formations that will be reduced considerably by expected climate changes.

Threatened Plants in a Changing Climate

The Intergovernmental Panel on Climate Change (IPCC 2007) predicted that 20–30% of the plant species would be at risk of extinction with a moderate increase in temperature of 1.5–2.5ºC. At current levels at least 15–20% of the species in Ecuador and Peru are already at some risk of extinction (Valencia et al. 2000, Pitman and Jørgensen 2002, León et al. 2006). Plants have limited options in responding to climatic change. They are immobile through most of their life cycle and only in their distributional phase as seed or spore do they have a chance to move and establish themselves at different geographic locations within their preferred climatic niche. We know from studies of plant distribution in Europe that many tree species, even 10,000 years after the last glaciation, have yet to fill their current potential geographical range, i.e., they have not yet colonized areas as far north as they are capable of reaching and where they would be able to sustain viable populations (Svenning and Skov 2004; Svenning et al. 2008). In other instances migration speeds are at par with climatic changes or exceed what was thought possible (Cain et al. 1998; Clark 1998; Davis and Shaw 2001; Pakeman 2001). Vertical movements of vegetation zones in the Andes are well documented (Hammen 1974; Hooghiemstra 1989) and may cause some to think that the plants are moving fast enough so that climate change will not be as catastrophic as first thought. The changes we observe and are expecting in the future are, however, orders of magnitudes faster than what has been experienced by plants during the last 10,000 years, and each plant species will respond individually (Peters 1990). Plants may 1) be able to track the climate change and find new areas that correspond to their current niche, i.e., migrate synchronized with the change in climate, 2) be able to migrate irregularly through stochastic long distance dispersal, 3) be pre-adapted to the new situation, i.e., have sufficient genetic plasticity to survive and maybe even thrive and expand in the same area where they live today, 4) be able to genetically evolve into a form that is adapted to the new situation and will survive in place, or 5) go extinct (Jackson and Overpeck 2000; Pigliucci 2001; Ackerly 2003; Jump and Peñuelas 2005). Species that are unable to migrate synchronized with the climatic changes may need help in form of assisted migration (Hoegh-Guldberg et al. 2008; Hunter 2008).

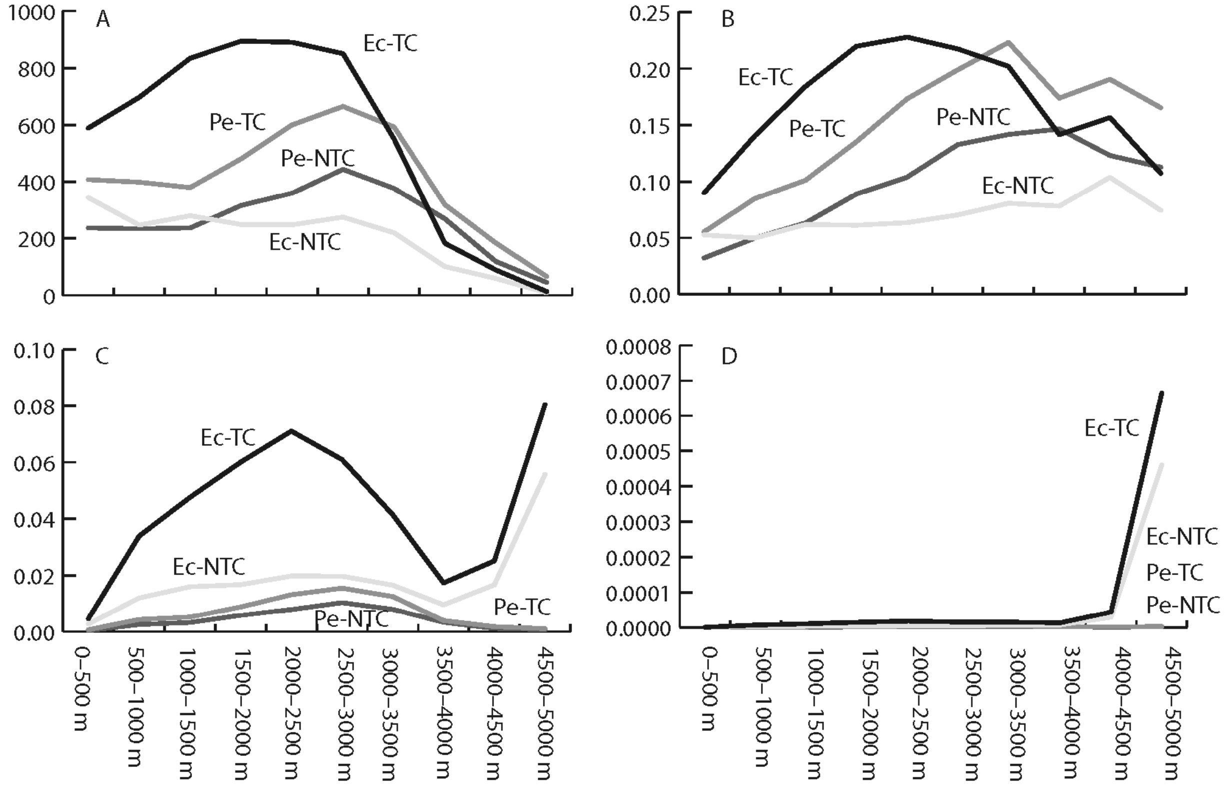

Figure 13.3. A. The number of endemic species in the threatened category (TC) and non-threatened category (NTC) in altitudinal bands for Ecuador and Peru. B. The number of TC and NTC endemic species per total number of species in altitudinals band for Ecuador and Peru. C. The number of TC and NTC endemic species per logarithm of area of the altitudinal bands in altitudinal bands for Ecuador and Peru. D. The number of species in TC and NTC endemic species per total number of species and per logarithm of area of the altitudinal bands for Ecuador and Peru.

Recommendations

We are reaching a better understanding of the pool of species in the region, their distributional ranges, as well as their threat status. However, the number of new species that continue to be discovered and described is, for Ecuador alone, in the order of a new species every two days. It will, consequently still be a long time before we have a comprehensive and complete overview.

Monitoring a single indicator species will not be enough in the future as species will be migrating individually (Peters 1990). We will need to monitor many species from each ecosystem to monitor threats and development, and we need to gain sufficient knowledge to intervene in time to assist a species or group of species to migrate to suitable new niches (Hoegh-Guldberg et al. 2008; Hunter 2008).

To achieve a complete understanding of all taxa within the available time will be very difficult considering the number of trained taxonomic specialists and the production time of floras and monographs, despite all good intentions by the Convention of Biological Diversity to complete a listing of the species in 2010. The Flora Neotropica Monographs series has a completion time that is about 200 years into the future at current rates of production. It will still be many decades before we have a monographic knowledge of the flora, and that does not even begin to answer the question of the full distribution range of the species included in such monographs. Having a solid taxonomic understanding is necessary and may occasionally be crucial for ecological or conservation work (Bortolus 2008).

Systematic conservation planning is based on biodiversity information already collected; an analysis of what is missing, and an attempt to fill the gaps (Margules and Pressey 2000). We are very close to having the first “complete” listing of plant species for the four countries in question. We do not always have enough information to either make expert maps of distribution or make reliable models of distribution; assessing all the narrow ranged-species is still in the initial stages for Colombia and Bolivia, and we know little about population densities and natural history except for trees in certain areas. However, the endemic red lists for Ecuador and Peru provide a good starting point for more research into which species are at risk as the climate continues to change. The efforts to produce a stable and reliable taxonomy, with information of distributional range, population densities, and threat level assessments should be further supported and we urgently need a growing and active taxonomic community that provides reliable baseline information. Taxonomic specialists working in solving the thousands of problems are themselves endangered “species” and particularly in the countries in question the lack of taxonomic expertise is not proportionate to the biodiversity or the need for information.

In summary, knowledge of taxonomy and distribution should be supported by a:

- continuously updated taxonomic framework;
- spatial distribution model or expert map for each species;
- spatial estimate of population density for each species; and
- continuously updated threat assessment of narrowly distributed species.

In addition, the following seed traits need to be known:

- generation time;
- distance dispersal potential; and
- quantity dispersal potential.

Acknowledgments

Trisha Distler and Isabel Loza are thanked for their help in using ArkMap. We thank John-Arvid Grytnes, Sebastian Herzog, and an anonymous reviewer for their help in improving this paper.

Literature Cited

Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164(3 Suppl.):S165-S184.

Bernal, R., M. Celis, and S. R. Gradstein. 2007. Plant diversity of Colombia catalogued. *Taxon* 56:273.

Bernal, R., S. R. Gradstein, and M. Celis. 2006. Catálogo de las plantas de Colombia, versión preliminar, vol. 1 (Líquenes–Laxmanniaceae):1-786; vol. 2 (Lecythidaceae–Zygophyllaceae):787-1619. Bogota: Universidad Nacional de Colombia.

Bortolus, A. 2008. Error cascades in the biological sciences: the unwanted consequences of using bad taxonomy in ecology. *Ambio* 37:114-118.

Brako, L., and J. L. Zarucchi. 1993. Catalogue of the flowering plants and gymnosperms of Peru. *Monographs in Systematic Botany from the Missouri Botanical Garden* 45:i-xi, 1-1286.

Cain, M. L., H. Damman, and A. Muir. 1998. Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs* 68:325-347.

Campbell, D. G. 1989. The importance of floristic inventories in the tropics. Pp. 5-30 in *Floristic inventories of tropical countries*, edited by D. G. Campbell and H. D. Hammond. New York: The New York Botanical Garden.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204-224.

Colwell, R. K. and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70-76.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673-679.

Distler, T., P. M. Jørgensen, A. Graham, G. Davidse, and I. Jiménez. 2009. Determinants and prediction of vascular plant richness across the western Neotropics. *Annals of Missouri Botanical Garden* 96:470-491.

Field, R. E. A. 2005. Global models for predicting woody plant richness from climate: development and evaluation. *Ecology Letters* 86:2263-2277.

Govaerts, R. 2003. How many species of seed plants are there? A response. *Taxon* 52:583-584.

Graham, A. 2009. The Andes: a geological overview from a biological perspective. *Annals of Missouri Botanical Garden* 96:371-385.

Gregory-Wodzicki, K. M. 2000. Uplift history of the central and northern Andes: a review. *Geological Society of America Bulletin* 112:1091-1105.

Hammen, T. v. d. 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* 1:3-26.

Henderson, A., S. P. Churchill, and J. L. Luteyn. 1991. Neotropical plant diversity. *Nature* 351:21-22.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* 321:345-346.

Hooghiemstra, H. 1989. Quaternary and upper-Pliocene glaciations and forest development in the tropical Andes: evidence from a long high-resolution pollen record from the sedimentary basin of Bogota. *Palaeogeography, Palaeoclimatology, Palaeoecology* 72:11-26.

Hunter, M. L. 2008. Climate change and moving species: furthering the debate on assisted colonization. *Conservation Biology* 21:1356-1358.

IPCC. 2007. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Soloman, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

IUCN. 1994. *IUCN Red List Categories.* Gland: IUCN.

IUCN. 2001. *IUCN Red List Categories and Criteria, Version 3.1.* Gland and Cambridge: IUCN.

Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late quarternary. *Paleobiology* 26:194-220.

Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. *Hole-filled seamless SRTM data V4.* International Centre for Tropical Agriculture (CIAT). Available at: http://srtm.csi.cgiar.org.

Jiménez, I., T. Consiglio and P. M. Jørgensen. 2009. Estimated plant richness pattern across northwest South America provides similar support for the species-energy and spatial heterogeneity hypotheses. *Ecography* 32:433-448.

Jørgensen, P. M., and C. Ulloa Ulloa. 1994. Seed plants of the high Andes of Ecuador – a checklist. *AAU Reports* 34:1-460.

Jørgensen, P. M., and S. León-Yánez. 1999. Catalogue of the vascular plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75:i-viii, 1-1182.

Jump, A. S., and J. Peñuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* 8:1010-1020.

León, B., J. Roque, C. Ulloa Ulloa, N. Pitman, P. M. Jørgensen, and A. Cano. 2006 [2007]. El libro rojo de las plantas endémicas del Perú. *Revista Peruana de Biología* 13:1-965.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.

Myers, N. 1998. Threatened biotas: "hot spots" in tropical forests. *Environmentalist* 8:187-208.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography* 25:379-398.

Pakeman, R. J. 2001. Plant migration rates and seed dispersal mechanisms. *Journal of Biogeography* 28:795-800.

Peters, R. L. 1990. Effects of global warming on forests. *Forest Ecology and Management* 35:13-33.

Pigliucci, M. 2001. *Phenotypic plasticity: beyond nature and nurture*. Baltimore, MD: Johns Hopkins University Press.

Pitman, N. C. A., and P. M. Jørgensen. 2002. Estimating the size of the world's Threatened Flora. *Science* 298:989.

Rodríguez-Mahecha, J. V., P. Salaman, P. Jørgensen, T. Consiglio, E. Forno, A. Telesca, L. Suárez, F. Arjona, F. Rojas, R. Bensted-Smith, and V. H. Inchausty. 2004. Tumbez–Chóco–Magdalena. Pp. 80-84 in *Hotspots revisited: Earth's biologically richest and most endangered ecoregions*, edited by R. A. Mittermeier, P. Robles-Gil, M. Hoffmann, J. D. Pilgrim, T. M. Brooks, C. G. Mittermeier, and G. Fonseca. Mexico City: CEMEX.

Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.

Scotland, R. W. and A. H. Wortley. 2003. How many species of seed plants are there? *Taxon* 52:101-104.

Simpson, G. G. 1964. Species density of North American recent mammals. *Systematic Zoology* 13:57-73.

Svenning, J.-C., F. Borchsenius, S. Bjorholm, and H. Balslev. 2008. High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. *Journal of Biogeography* 35:394-406.

Svenning, J.-C., and F. Skov. 2004. Limited filling of the potential range in European tree species. *Ecology Letters* 7:565-573.

Ulloa Ulloa, C., and P. M. Jørgensen. 1995. *Árboles y arbustos de los Andes del Ecuador*. 2nd ed. Quito: Abya-Yala. 329 pp.

Ulloa Ulloa, C., and D. A. Neill. 2005. *Cinco años de adiciones de la flora del Ecuador*. Loja: Editorial UTPL.

Ulloa Ulloa, C., J. L. Zarucchi, and B. León. 2004. Diez años de adiciones a la flora del Perú 1993-2003. *Arnaldoa Edicion Especial Noviembre 2004*:1-242.

Valencia Reyes, R., N. Pitman, S. León-Yánez and P. M. Jørgensen. 2000. *Libro rojo de las plantas endémicas del Ecuador 2000*. Quito: Herbario QCA, Pontificia Universidad Católica del Ecuador. 493 pp.

Weigend, M., A. Cano, and E. F. Rodríguez. 2005. New species and new records of the flora in Amotape-Huancabamba zone: endemics and biogeographic limits. *Revista Peruana de Biología* 12:249-274.

Young, K. R., C. Ulloa Ulloa, J. L. Luteyn, and S. Knapp. 2002. Plant evolution and endemism in the Andean South America: an introduction. *The Botanical Review* 68:4-21.

14

Gradients of Plant Diversity: Local Patterns and Processes

Michael Kessler, Jon-Arvid Grytnes, Stephan R.P. Halloy, Jürgen Kluge, Thorsten Krömer, Blanca León, Manuel J. Macía, and Kenneth R. Young

Patterns of plant diversity can be studied at different spatial scales, which, for convenience, can be divided into two overlapping categories (Srivastava 1999, Magurran 2004): Regional diversity (also known as gamma diversity) concerns the number of species in large geographical regions such as countries or biomes and is explored in Jørgensen et al., Chapter 13, this volume. Local richness (also known as alpha diversity) refers to the number of species co-occurring in areas of limited size, typically ≤1 ha. Studies of plant diversity at these two scales are subject to different methodological constraints and reveal different ecological aspects shaping plant diversity. Both methodologies have their special characteristics: regional species lists are typically incomplete, especially in tropical regions, whereas local surveys tend to be much more complete. On the other hand, local inventories only cover a minute portion of the land surface and are often conducted with different sampling methods, making it difficult to compare results across different studies. Also, whereas at the local scale all recorded plant species actually co-occur and thus potentially interact ecologically with each other through competition, facilitation, etc., at the regional scale many species occur in geographically or ecologically remote sites without direct interactions. However, because of the dispersal of individuals through populations, interactions can also play out over large, environmentally heterogeneous regions rather than only within local communities in relatively uniform habitats (Ricklefs 2004). Alpha and gamma diversity are connected through the degree of change in composition from one plot to another (beta diversity).

In the present chapter, we first briefly review patterns of local plant species richness along three important geographical and ecological gradients (latitude, elevation, amount and seasonality of precipitation). We do not specifically address other gradients such as energy availability or soil fertility because relevant data are very sparse for the tropical Andes. Then, we focus on the mechanisms and processes that determine and influence these patterns, because an understanding of the underlying causes is relevant for predicting possible responses of plant assemblages to climate change. Our focus is on natural habitats without human or natural disturbance, but diversity is also influenced by the disturbance regime of the sampled area.

Patterns

Latitude

Latitude itself is not an ecological factor directly affecting plant diversity (Hawkins and Diniz-Filho 2004). Rather, numerous ecological factors that vary with latitude may be responsible for creating latitudinal diversity patterns. Latitudinal patterns of plant diversity in the tropical Andes have mainly been studied at the regional scale (Jørgensen et al., Chapter 13, this volume). In contrast, there are very few specific studies using local plots to assess latitudinal trends in plant diversity. In Ecuador, Sklenár and Ramsay (2001) used a consistent sampling scheme to study plant diversity and community composition in páramos on volcanoes spanning some four degrees of latitude, but the focus of this study was on the effect of climate, geology, and topography, rather than latitude per se. Young and León (2007) showed that the diversity of trees and shrubs was an order of magnitude greater at a tropical timberline site compared to subtropical and mid-latitude sites in the Andes.

Compilations from different studies show that the diversity of woody plants (trees and lianas) increases with decreasing latitude in similar habitats and elevation, with marked declines around the Tropics of Cancer and Capricorn (e.g., Gentry 1982, 1988, 1995, Phillips and Miller 2002, Willig et al. 2003, Macía and Svenning 2005, Schnitzer 2005, Weiser et al. 2007). Whereas different Andean forests at a given elevation are similar in floristic composition at the generic and family levels, species composition varies strongly between sites. For epiphytes, local-scale inventories show that in the lowlands highest species numbers are found in Colombia and Ecuador (Ibisch 1996, Nieder et al. 1999, Acebey and Krömer 2001, Krömer and Gradstein 2003, Arévalo and Betancur 2004, Kreft et al. 2004, Benavides et al. 2005, Krömer et al. 2005, Krömer et al. 2008). These trends are primarily driven by decreasing numbers of Araceae and to a lesser degree of Orchidaceae away from the equator. In contrast, epiphyte inventories from montane sites (Ibisch 1996, Krömer and Gradstein 2003, Krömer et al. 2005) differ much less between countries, with, e.g., 196 species found on 10 canopy trees and its surroundings in Otonga, Ecuador (Nieder et al. 1999), versus 207 species found in 9 canopy tree plots in Mosetenes, Bolivia (Krömer et al. 2008). The diversity of ferns also remains roughly constant in humid montane forests at similar elevations within the tropical regions from Costa Rica to central Bolivia, and only drops noticeably further north and south as one reaches subtropical latitudes (Kessler 2001a, Kluge et al. 2006, Kessler and Kluge unpubl. data).

Elevation

As with latitude, elevation as such does not directly influence plants (Körner 2000, 2007). Rather, it is factors that are either directly related to elevation (e.g., air pressure, temperature) or that have a more complex relationship with elevation (available surface area, precipitation, etc.) that affect plants growing at different elevations.

Elevational patterns of local plant species richness have been studied much more intensively than latitudinal ones. For trees and lianas diversity is constantly high from the lowlands to about 1500 m, although a slight mid-elevation hump has also been found (La Torre-Cuadros et al. 2007). Below 1500 m, Leguminosae are the most important tree family, and Bignoniaceae and Leguminosae the most important for lianas (Gentry 1991, Macía et al. 2007, Macía 2008). Above this elevation, there is a linear decrease in species richness with elevation, and the floristic composition is dominated by montane genera and families such as Lauraceae, Melastomataceae, and Rubiaceae (Gentry 1995, Macía and Fuertes 2008). In the case of lianas, Asteraceae become predominant. Tree ferns are much more prevalent in mid-elevation forests, at 1200–1700 m (Gentry 1995). At the highest elevations, above 3000 m and near the timberline, floristic composition again changes dramatically and Asteraceae becomes one of the most important families together with Melastomataceae and Myrsinaceae, although this family composition may change locally. Here, lianas become scarce (Young 1993). The highest montane forests (3000 to >5000 m) are patchy in distribution and consist of monospecific stands of *Polylepis* spp. (Rosaceae) from Ecuador southwards, but they are more diverse in Colombia with about 4–6 other tree species and few lianas.

Focusing on individual woody and herbaceous plant families, mid-level maxima of elevational richness have been found in Bolivia for Acanthaceae, whereas Arecaceae and Melastomataceae have roughly constant richness to about 1000 m, followed by strong declines to high elevations (Kessler 2001b). Epiphytic plant species richness typically shows a mid-elevation bulge that peaks at 1500–1700 m (Cleef et al. 1984, Wolf 1994, Muñoz and Küper 2001, Krömer et al. 2005). Ferns also show such hump-shaped patterns, with maximum richness values at 1700–1800 m (Kessler 2001a,b, Kessler et al. 2001), while richness of Bromeliaceae peaks at 1000–1900 m (Kessler 2001a, Krömer et al. 2005, 2006). Araceae deviate from this general pattern in having highest local species counts in the lowlands (Ibisch et al. 1996, Kessler and Croat 1999). The recorded upper elevational limit of vascular plants increase from around 4800 m in Ecuador to 5400 m in southern Peru and 5800 m in Bolivia (Halloy 1989, Seimon et al. 2007).

Amount and Seasonality of Precipitation

Unlike the previous two factors, the availability of water, either through vertical (rain) or horizontal (fog) precipitation, or from ground water, directly affects plant growth and community composition. The tropical Andean region includes practically the entire range of humidity conditions experienced by plants on the globe, ranging from the Atacama desert, which has been practically rain-free for over 10 million years (Placzek et al. in press), to the perhumid Chocó region in Colombia, one of the world's wettest areas with up to 15 m mean annual precipitation (Galeano et al. 1998). Patterns of water availability often co-vary with other ecological or geographical gradients, making it difficult to separate the influences of different factors. Thus, the western Amazon basin experiences highest precipitation levels in Ecuador and declining values both to the north and the south, although with local pockets of high rainfall along the east Andean base (Killeen et al. 2007). Cloud condensation often peaks at mid-elevation on tropical mountains, although cloud forests can also be found at low elevations (Gradstein 2006). Although humidity shows some broad gradients, it is highly heterogeneous at a much smaller scale; within kilometers or even hundreds of meters conditions may vary from perhumid to semi-arid, and this is repeated throughout mountainous terrains.

There have been few studies specifically designed to study the influence of water availability on plant community diversity and composition in the tropical Andes. However, all available information shows that overall plant diversity typically declines with decreasing water availability, with the exception of a few drought-adapted families. In central Bolivia, e.g., in three almost adjacent plots of 1 ha differing in water availability, overall plant diversity declined from the wet to the dry site, although some specific plant families such as Bromeliaceae and Cactaceae showed opposite patterns (Linares-Palomino et al. 2008, 2009). Trees and lianas have a strong relationship with water availability, reflecting annual rainfall and rainfall seasonality at all geographical scales (Gentry 1988, Clinebell et al. 1995, Schnitzer 2005). The same pattern was also documented for palms throughout the Americas by Bjørholm et al. (2005), an example of a large-scale study that documents local scale patterns. One of the most striking distributional patterns shown by epiphytes is a tremendous decrease in both numbers of species and individuals in drier habitats. Already Schimper (1888) considered air humidity to be the most important factor determining epiphytic plant diversity, a suggestion followed by Gentry and Dodson (1987), Kessler (2001a), Kreft et al. (2004), Küper et al. (2004), and Krömer et al. (2005), among many others. Ecophysiologically, this relationship appears to be well founded, as water availability is of critical importance to epiphytes (Benzing 1990, Zotz and Hietz 2001). One main difference between lowland and montane forests is that regular dry periods, but also periodically occurring events such as El Niño, reduce the abundance and diversity of epiphytes in Amazonian lowland forests. In contrast, in montane rain forests, the impact of dry periods is mitigated by 'horizontal precipitation', which in cloud forests frequently contributes 20% or more to total water input (Hölscher et al. 2004, Thies et al. 2008). Local species richness of ferns is also closely linked to water availability (León and Valencia 1989, Kessler 2001a).

Processes

Understanding the ecological processes determining these patterns will help us make predictions with respect to the potential impacts of future environmental changes and for predicting plant diversity in undersampled regions, which is important for identifying areas of high conservation value. In addition, to give a better understanding of the most important factors in the region, studies of diversity patterns in the tropical Andes with their steep environmental gradients, have the potential to play an important role in understanding the processes behind global diversity patterns.

Recently considered, partly interlinked explanations for richness patterns involve five groups of processes and mechanisms (Grytnes and McCain 2007)(Table 14.1). As with the surveys of patterns, an analysis of the processes and mechanisms influencing the patterns must distinguish between regional and local scales. Direct ecological interactions such as competition and facilitation take place at the local scale while regional patterns are more likely to reflect historical, evolutionary, and biogeographical processes, although dispersal may link these scales and their processes (Ricklefs 2004). Several of the explanations, both at the local and regional scales, involve climatic factors, which therefore allow direct inferences to be made regarding possible effects of climate change. There is general agreement that more than one of these factors plays a role and that their relative impact depends on the spatial and temporal scale, as well as on the taxon under consideration, but it is still unclear when and how any of these factors predominate (e.g., Cornell and Lawton 1992, Gaston and Blackburn 2000, Ricklefs 2004, Shurin and Srivastava 2005). Contrasting patterns in the tropical Andes may give valuable clues to a better understanding of this.

The influence of area on species richness is well-documented at all scales (Rosenzweig 1995) and has been implicated in determining patterns of species richness through a variety of mechanisms (e.g., Losos & Schluter 2000, Stropp et al. 2009; see Table 14.1). However, area alone can probably not fully explain patterns of species richness along latitudinal and elevational gradients and typically only modifies the more basic patterns determined by climatic and other factors (Rahbek 1995, McCain 2007, Romdal and Grytnes 2007). For example, the Altiplano region of the central Andes has a larger surface area than the adjacent slopes but much lower plant diversity because of its low temperatures and aridity. Thus, although area always has to be considered (or controlled for) when interpreting patterns of species richness, it can rarely be considered to be the main cause. Population processes such as dispersal limitation or source-sink effects have a potential to modify

Table 14.1. Summary of some important potential processes and mechanisms that may determine or influence regional (reg) and local (loc) patterns of species richness. "+" indicates the scale at which these may become relevant, a "–" indicates that this factor is unlikely to be of major importance at a given scale.

	Processes and Mechanisms	**Predicted scale of impact**	
		reg	loc
	1. Area		
	key sources: Lomolino 2001		
a	Larger area – higher number of individuals – decreased extinction risks – larger number of species ("*Island Biogeography*": MacArthur and Wilson 1967).	+	–
b	Smaller area – lower number of individuals – faster genetic changes at population level – faster evolution of new species (Losos and Schluter 2000).	+	–
c	Larger area – higher number of habitats – larger number of species (Kallimanis et al. 2008).	+	+
d	Larger species pool due to larger area (see above) – higher local richness ("*Echo effect*": Rosenzweig and Ziv 1999).	–	+
e	Larger sampling areas – larger number of species recorded (Gleason 1922, Rosenzweig 1995).	+	+
	2. Climatic variables – energy – productivity		
	Key sources: Rohde 1992, Mittelbach et al. 2001, Rahbek and Graves 2001, Hawkins et al. 2003, Willig et al. 2003, Currie et al. 2004, Evans et al. 2005, Mönkkönen et al. 2006, Laanisto et al. 2008		
a	More energy – higher productivity – larger number of individuals – larger number of species ("*Sampling Hypothesis*": Srivastava and Lawton 1998, Kaspari et al. 2000).	–	+
b	More energy – higher productivity – larger number of individuals – decreased extinction risks – larger number of species ("*Population Size Hypothesis*": Kaspari et al. 2000, Hurlbert 2004, Pautasso and Gaston 2005, 2006).	+	+
c	More energy – higher productivity – larger number of rare resources – larger number of niche position specialists ("*Niche Position Hypothesis*": Abrams 1995).	–	+
d	More energy – higher productivity – reduced niche breadth by focusing on preferred resource types – increased co-existence ("*Niche Breadth Hypothesis*": Evans et al. 2005).	–	+
	3. Historical and evolutionary processes		
	Key sources: Wiens and Donoghue 2004, Ricklefs 2005, Roy and Goldberg 2007, Jablonski et al. 2006		
a	Under specific conditions, speciation rates may be higher, increasing species richness ("*Tropics as a Cradle Hypothesis*": Cardillo 1999).	+	–
b	Under specific conditions, extinction rates may be higher, reducing species richness ("*Tropics as a Museum Hypothesis*": Stebbins 1974).	+	+
c	Phylogenetic lineages may be older in some areas than in others, thus providing more time for diversification ("*Out of the Tropics Hypothesis*": Jablonski et al. 2006; "*Niche Conservatism Hypothesis*": Wiens and Donoghue 2004).	+	–
	4. Null models and neutral theories		
	Key sources: Gotelli and Graves 1996		
a	Variations in the dispersal ability of species, their population size, and the immigration (resp. speciation) rate determine the composition and abundance distribution of species ("*Neutral Theory of Biodiversity and Biogeography*": Hubbell 2001).	+	+
b	Random placement of species with different species-specific geographical or ecological amplitudes within a constrained geographical or ecological domain leads to maximum richness in the middle of the domain ("*Mid-Domain Effect*": Colwell and Hurtt 1994, Colwell et al. 2004).	+	–
	5. Population dynamics		
a	Dispersal from suitable habitats to less suitable habitats can create non-self-supporting sink populations, especially at locations surrounded by numerous habitats such as mid-elevations on mountains ("*Source-sink effects*": Shmida and Wilson 1985, Pulliam 1998, Kessler 2000, Grytnes et al. 2008a).	–	+
b	Limitations in dispersal may limit the number of species that occur in an area or site, despite potentially suitable conditions ("*Dispersal Limitation*": Tilman 1997, Turnbull et al. 2000).	+	+

patterns of species richness at the local scale (Grytnes et al. 2008a), but it is unclear how strong their impact is (Kessler 2009). There are essentially no studies that allow a quantitative evaluation of the importance of population processes on patterns of species richness. These require population-level studies of reproduction and dispersal, and although such studies require long-term efforts, they are indispensable and urgently needed.

In the study of the remaining factor complexes, null models are probably the most debated (Clark 2008). Mid-domain effect (MDE) models have been shown to correlate closely to diversity patterns especially along some elevational gradients (Kessler 2001b, Colwell et al. 2004, McCain 2004), but the meaning and implications of these models is hotly debated on theoretical grounds (Bokma and Mönkkönen 2000, Colwell and Lees 2000, Jetz and Rahbek 2001, Hawkins and Diniz-Filho 2002, Grytnes 2003, Colwell et al. 2004, Herzog et al. 2005). In its most extreme form, the MDE model predicts that the diversity patterns should primarily be dependent on the upper and lower boundary of the domain. This would imply that all groups of organisms should show very similar patterns and that similar patterns should be found when comparing different regions (e.g. the western and eastern slopes of the Andes), which is clearly not the case, as exemplified by the wide range of elevational richness patterns discussed above. However, the mid-domain effect may still be a modifying factor (Grytnes et al. 2008b). Hubbel's (2001) null model, which assumes that species are ecologically equivalent, has commonly been found not to apply at regional scales and across strong ecological gradients, where niche assembly models appear to be more adequate (e.g., Harms et al. 2001, Phillips et al. 2003, Tuomisto et al. 2003, Jones et al. 2006, 2007, Ruokolainen et al. 2007). However, it may still be important for the maintenance of high local diversity when the environment is homogenous (Hubbel 2001).

The remaining two factor complexes (climate/productivity and history/evolution) are most likely to include the most important processes and mechanisms, and should probably receive most research attention. One of the long-standing debates in biodiversity research is to which degree local diversity is either limited by local resources (niche or energy availability) in concert with species interactions (competition, herbivory, etc.) or by a limited regional species pool (Terborgh and Faaborg 1980, Ricklefs 1987, 2004, Cornell and Karlson 1996, Herzog and Kessler 2006, Jiménez et al. 2009). In the latter case, more species could co-occur at a given site but are simply not available within the historical and evolutionary framework of that particular region.

Ecosystems with a high level of productivity are believed to exhibit high levels of species richness, and there are several mechanisms suggested to be the link between these two ecosystem properties. These mechanisms involve the number of individuals and levels of niches and resources (see Table 14.1) and all predict a positive correlation between energy input and species richness at a local scale. However, the most challenging aspect in addressing the species-energy hypothesis is getting the appropriate measure for productivity at the ecosystem level (Waide et al. 1999) and of the amount of energy that is used by a given focal group (Gaston 2000, Chase and Leibold 2002). Important theoretical and empirical advances have recently been made, at least with regard to trees, and important insights are to be expected in the near future (Mittelbach et al. 2001, Hawkins et al. 2007).

The past few years have seen considerable effort directed at generating time-referenced phylogenetic hypotheses that may allow an assessment of historical evolutionary hypotheses (Antonelli 2008). However, only a tiny proportion of tropical Andean plants has been included in these efforts, and for those groups for which data are available, their interpretation is frequently limited by geographically or taxonomically incomplete sampling, or by difficulties in obtaining reliable age estimates. For example, Linder (2008) proposed that plant radiations may saturate (i.e., reach stable limits of species richness) after roughly 10 million years, and that young radiations are typical of young (Pliocene) environments whereas mature radiations are characteristic of regions that have been geologically and climatically stable throughout the Neogene. He concluded that “the hyperdiverse Neotropical flora is the result of both mature as well as recent and rapid radiations”. As intriguing as it is, Linder’s (2008) study only included seven Neotropical examples. Clearly, additional efforts have to be directed at generating a larger number of geographically and temporally explicit phylogenetic hypotheses of tropical Andean plants. Further, analytical approaches have to be refined to be able to distinguish between alternative hypotheses. For example, in a case study of Neotropical frogs, Algar et al. (2009) conclude that the phylogenetic processes can only determine which species occur in a given area, but not how many species, and that species numbers may actually be determined by local ecological processes. Yet, for higher taxonomic levels (families, genera), well-resolved phylogenetic hypotheses are available for many taxa (http://www.tolweb.org/tree/ ; http://www.mobot.org/mobot/research/apweb/welcome.html) and recent work has resulted in free open software that allows ecologists to make use of the available phylogenetic information (http://www.phylodiversity.net/phylocom/). Clearly, the time is ripe to link ecological and phylogenetic information.

Conclusions and Research Recommendations

The knowledge of local patterns of plant diversity in the tropical Andean region remains fragmentary. Elevational patterns are documented best, while latitudinal and moisture gradients have been neglected. To complicate matters, many studies have employed different methods (plot size and shape, plant groups included), which makes it difficult to compare data from different surveys and regions.

Despite these shortcomings, it appears to be possible to arrive at some rough, preliminary generalizations on patterns of plant diversity. In the western Amazonian lowlands, overall plant diversity appears to be highest around equatorial latitudes, declining towards higher latitudes. In contrast, on the eastern Andean slope richness remains roughly constant in the tropical regions south to about 18°S, and only then declines markedly. The western Andean slope has high local diversity in Colombia and northern Ecuador which declines strongly further south. Probably, floristic turnover from site to site remains high throughout the tropical Andes, but specific studies of beta diversity along environmental gradients are needed. Above the treeline, species richness exhibits complex latitudinal patterns related to topography and its influence on moisture regimes. High species richness in the equatorial páramos declines towards the north and south as humidity decreases. South of around 10°S an east-west gradient also becomes dominant, with diverse cloud-grasslands to the east and poorer semi-arid to arid altiplano in the center and west.

Along elevational gradients, overall plant diversity appears to show a hump-shaped pattern with maximum richness at around 1000–1500 m in humid regions (Rahbek 1995, 2005) and higher in arid ones (Lauer 1976). This pattern appears to be mostly driven by terrestrial and epiphytic herbaceous taxa, whereas woody plants show a more gradual decline of richness with elevation. Above treeline, release from arboreal competition may produce a pronounced increase in species richness of herbaceous and shrub species, particularly in tussock and shrub paramo. Finally, with the exception of a few specialized taxa, plant diversity generally decreases with increasing aridity. Overall, these patterns thus closely reflect the regional patterns outlined in Jørgensen et al., Chapter 13, this volume. However, detailed comparisons of local and regional patterns have only been conducted for ferns along elevational gradients, where they reveal minor but potentially important differences of biological significance (Kessler et al. 2009).

Despite the wide range of discussion about the processes that determine richness patterns, the most promising approaches are certainly held by evolution/history at the regional and climate/productivity at the local scale. Recent literature provides hypotheses to test underlying mechanisms, but specific field studies are few, because fully resolved phylogenetic trees of study groups are rarely available and because the development of a consistent measure of productivity is a difficult task. However, comparing prevalent richness patterns with surrogates of productivity may lead to rough conclusions about the processes driving these patterns. For example, comparisons of the arid western and humid eastern Andean slopes in Peru may help to unravel the impact of water availability on local plant species richness. Because climatic factors directly influence levels of ecosystem productivity, understanding the causal relationships between productivity and species richness will be critical for predicting responses of plant assemblages to climate change (Colwell et al. 2008).

To meet the needs for documenting and monitoring levels of species richness, and to predict responses to climate change, three main lines of activity are needed. First, additional well-designed surveys aimed at testing hypotheses are necessary, ideally tackling those ecological gradients that have been neglected to date. Second, networks of permanent plots are needed to monitor future changes in plant community richness and composition to determine the effects of climate change on plant communities. The GLORIA project (www.gloria.ac.at), which focuses on high-elevation sites above treeline (Halloy et al. 2008), and the extensive network of 1-ha tree plots in Amazonia are important steps in this direction, (www.geog.leeds.ac.uk/projects/rainfor/) and a similar, badly needed initiative (Rainfor-Andes) is about to start in highly diverse Andean forests. Third, well-designed experimental and observational studies on the relationship between ecosystem productivity and local species richness are needed, with the aim of distinguishing between different potential mechanisms that in turn predict different responses to climate change (Evans et al. 2005). Those data should also be linked to the increasingly available phylogenetic information.

Literature cited

Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients, what does competition theory predict? *Ecology* 76:2019-2027.

Acebey, A., and T. Krömer. 2001. Diversidad y distribución vertical de epífitas en los alrededores del campamento río Eslabón y de la laguna Chalalán, Parque Nacional Madidi, Dpto. La Paz, Bolivia. *Revista de la Sociedad Boliviana de Botánica* 3:104-123.

Algar, A. C., J. T. Kerr, and D. J. Currie. 2009. Evolutionary constraints on regional faunas: whom, but not how many. *Ecology Letters* 12:57-65.

Antonelli, A. 2008. *Spatiotemporal evolution of Neotropical organisms*. PhD thesis. Gothenburg: Department of Plant and Environmental Sciences, University of Gothenburg.

Arévalo, R., and J. Betancur. 2004. Diversidad de epífitas vasculares en cuatro bosques del sector suroriental de la serranía de Chiribiquete, Guayana colombiana. *Caldasia* 26:359-380.

Benavides, A. M., A. Duque, J. Duivenvorden, A. Vasco, and R. Callejas. 2005. A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. *Biodiversity and Conservation* 14:739-758.

Benzing, D. H. 1990. *Vascular epiphytes: general biology and related biota*. Cambridge: Cambridge University Press.

Bjørholm, S., J.-C. Svenning, F. Skov, F., and H. Balslev. 2005. Environmental and spatial controls of palm (Arecaceae) species richness across the Americas. *Global Ecology and Biogeography* 14:423-429.

Bokma, F., and M. Mönkkönen 2000. The mid-domain effect and the longitudinal dimension of continents. *Trends in Ecology and Evolution* 15:288-289

Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society of London B, Biological Sciences* 266:1221-1225.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416:427-430.

Clark, J. S. 2008. Beyond neutral science. *Trends in Ecology and Evolution* 24:8-15.

Cleef, A. M., O. Rangel, T. van der Hammen, and R. Jaramillo. 1984. La Vegetación de las selvas del transecto Buritaca. Pp. 267-407 in *Studies on tropical Andean ecosystems 2*, edited by T. van der Hammen and P. M. Ruiz. Berlin: J. Cramer.

Clinebell, R., O. L. Phillips, A. H. Gentry, N. Stark, and H. Zuuring. 1995. Prediction of Neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* 4:56-90.

Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrotion in the wet tropics. *Science* 322:258-261.

Colwell, R. K., and G. C. Hurtt. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist* 144:570-595

Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70-76.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163:E1-E23.

Cornell, H. V., and R. D. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* 65:233-241.

Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61:1-12.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guégan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121-1134.

Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* 80:1-25.

Galeano, G., S. Suárez, and H. Balslev. 1998. Vascular plant species count in a wet forest in the Chocó area on the Pacific coast of Colombia. *Biodiversity and Conservation* 7:1563-1575.

Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and process in macroecology*. London: Blackwell.

Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405:220-227.

Gentry, A. H. 1982. Patterns of Neotropical plant species diversity. *Evolutionary Biology* 15:1-84.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1-34.

Gentry, A. H. 1991. The distribution and evolution of climbing plants. Pp. 3-42 in *The biology of vines*, edited by F. E. Putz and H. A. Mooney. Cambridge: Cambridge University Press.

Gentry, A. H. 1995. Patterns of diversity and floristic composition in Neotropical montane forests. Pp. 103-126 in *Biodiversity and conservation of Neotropical montane forests*, edited by S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn. New York: The New York Botanical Garden.

Gentry, A. H. and C. H. Dodson. 1987. Diversity and biogeography of Neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* 74:205-233.

Gleason, H. A. 1922. On the relation between species and area. *Ecology* 3:158-162.

Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Washington, DC: Smithsonian Institution Press.

Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. *Cryptogamie, Bryologie* 27:141-152.

Grytnes, J. A., and C. M. McCain. 2007. Elevational patterns in species richness. Pp. 1-8 in *Encyclopedia of biodiversity*, edited by S. Levin. The Hague: Elsevier.

Grytnes, J. A. 2003. Ecological interpretations of the mid-domain effect. *Ecology Letters* 6:883-888

Grytnes, J. A., J. H. Beaman, T. S. Romdal, and C. Rahbek. 2008b. The mid-domain effect matters: simulation analyses of range-size distribution data from Mount Kinabalu, Borneo. *Journal of Biogeography* 35:2138-2147.

Grytnes, J. A., E. Heegaard, and T. S. Romdal. 2008a. Can the mass effect explain the mid-altitudinal peak in vascular species richness? *Basic and Applied Ecology* 9:371-382.

Halloy, S. R. P. 1989. Altitudinal limits of life in subtropical mountains: what do we know? *Pacific Science* 43:170-184.

Halloy, S. R. P., K. Yager, C. García, S. G. Beck, J. Carilla, A. Tupayachi, J. Jácome, R. I. Meneses, J. Farfán, A. Seimon, T. A. Seimon, P. Rodriguez, S. Cuello, and A. Grau. 2008. South America: climate monitoring and adaptation integrated across regions and disciplines. Pp. 86-91 in *Atlas of biodiversity risks – from Europe to the globe, from stories to maps*, edited by J. Settele, L. Penev, T. Georgiev, R. Grabaum, V. Grobelnik, V. Hammen, S. Klotz, M. Kotarac, and I. Kühn. Sofia and Moscow: Pensoft.

Harms, K. E., R. Condit, S. P. Hubbell, and R. B. Foster. 2001. Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology* 89:947-959.

Hawkins, B. A., and J. A. F. Diniz-Filho. 2002. The mid-domain effect cannot explain the diversity gradient of Nearctic birds. *Global Ecology and Biogeography* 11:419-426.

Hawkins, B. A., and J. A. F. Diniz-Filho. 2004. 'Latitude' and geographic patterns in species richness. *Ecography* 27:268-272.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guègan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner.

2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105-3117.

Hawkins, B. A., F. S. Albuquerque, M. B. Araújo, J. Beck, L. M. Bini, F. J. Cabrero-Sañudo, I. Castro-Parga, J. A. F. Diniz-Filho, D. Ferrer-Castán, R. Field, J. F. Gómez, J. Hortal, J. T. Kerr, I. J. Kitching, J. L. León-Cortés, J. M. Lobo, D. Montoya, J. C. Moreno, M. Á. Olalla-Tárraga, J. G. Pausas, H. Qian, C. Rahbek, M. Á. Rodríguez, N. J. Sanders, and P. Williams. 2007. A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology* 88:1877-1888.

Herzog, S. K., and M. Kessler. 2006. Local vs. regional control of species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography* 15:163-172.

Herzog, S. K., M. Kessler, and K. Bach. 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography* 28:209-222

Hölscher, D., L. Köhler, A. I. J. M. Van Dijk, and L. A. Bruijnzeel. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology* 292:308-322.

Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press.

Hurlbert, A. H. 2004. Species-energy relationships and habitat complexity in bird communities. *Ecology Letters* 7:714-720.

Ibisch, P. L. 1996. *Neotropische Epiphytendiversität – das Beispiel Bolivien*. Archiv naturwissenschaftlicher Dissertationen, Band 1. 357 pp.

Ibisch, P. L., A. Boegner, J. Nieder, and W. Barthlott. 1996. How diverse are Neotropical epiphytes? An analysis based on the "Catalogue of flowering plants and gymnosperms of Peru". *Ecotropica* 2:13-28.

Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102-106.

Jetz, W., and C. Rahbek. 2001. Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Science of the United States of America* 98:5661-5666.

Jiménez, I., T. Distler, and P. M. Jørgensen. 2009. Estimated plant richness patterns across northwest South America provides similar support for the species-energy and spatial heterogeneity hypotheses. *Ecography* 32:433-448.

Jones, M. M., P. Olivas-Rojas, H. Tuomisto, and D. B. Clark. 2007. Environmental and neighbourhood effects on tree fern distributions in a Neotropical lowland rain forest. *Journal of Vegetation Science* 18:13-24.

Jones, M. M., H. Tuomisto, D. B. Clark, and P. Olivas. 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *Journal of Ecology* 94:181-195.

Kallimanis, A. S., A. D. Mazaris, J. Tzanopoulos, J. M. Halley, J. D. Pantis, and S. P. Sgardelis. 2008. How does habitat diversity affect the species-area relationship? *Global Ecology and Biogeography* 17:532-538.

Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *American Naturalist* 155:280-293.

Kessler, M. 2000. Upslope-directed mass effect in palms along an Andean elevational gradient: a cause for high diversity at mid-elevations? *Biotropica* 32:756-759.

Kessler, M. 2001a. Pteridophyte species richness in Andean forests in Bolivia. *Biodiversity and Conservation* 10:1473-1495.

Kessler, M. 2001b. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation* 10:1897-1920.

Kessler, M. 2009. The impact of population processes on patterns of species richness: lessons from elevational gradients. *Basic and Applied Ecology* 10:295-299.

Kessler, M., and T. Croat. 1999. State of knowledge of Bolivian Araceae. *Selbyana* 20:224-234.

Kessler, M., S. K. Herzog, J. Fjeldså, and K. Bach. 2001. Species richness and endemism of plant and bird communities along two gradients of elevation, humidity, and land use in the Bolivian Andes. *Diversity and Distributions* 7:61-77.

Kessler, M., T. Krömer, J. Kluge, D. N. Karger, A. Acebey, A. Hemp, S. K. Herzog, and M. Lehnert. 2009. Elevational gradients of species richness derived from local field surveys versus 'mining' of archive data. Pp. 57-63 in *Data mining for global trends in mountain biodiversity*, edited by E. M. Spehn and C. Körner. Boca Raton, FL: CRC Press/Taylor and Francis.

Killeen, T. J., M. Douglas, T. Consiglio, P. M. Jørgensen, J. Mejia. 2007. Wet spots and dry spots in the Andean hotspot. *Journal of Biogeography* 34:1357-1373.

Kluge, J., M. Kessler, and R. R. Dunn. 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography* 15:358-371.

Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology and Evolution* 15:513-514.

Körner, C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* 22:569-574.

Kreft, H., N. Köster, W. Küper, J. Nieder, and W. Barthlott. 2004. Diversity and biogeography of vascular epiphytes in western Amazonia, Yasuní, Ecuador. *Journal of Biogeography* 31:1463-1476.

Krömer, T., and S. R. Gradstein. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana* 24:190-195.

Krömer, T., I. Jimenez, and M. Kessler. 2008. Diversity and vertical distribution patterns of vascular epiphytes in the Cordillera Mosetenes, Cochabamba, Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 23:27-38.

Krömer, T., M. Kessler, and S. K. Herzog. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica* 38:183-195.

Krömer, T., M. Kessler, S. R. Gradstein, and A. Acebey. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* 32:1799-1810.

Küper, W., H. Kreft, J. Nieder, N. Köster, and W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. *Journal of Biogeography* 31:1477-1487.

Laanisto, L., P. Urbas, and M. Pärtel. 2008. Why does the unimodal species richness-productivity relationship not apply to woody sopecies: a lack of clonality or a legacy of tropical evolutionary history. *Global Ecology and Biogeography* 17:320-326.

La Torre-Cuadros, M. de los A., S. Herrando-Pérez, and K. R. Young. 2007. Diversity and structural patterns for tropical montane and premontane forests of central Peru, with an assessment of the use of higher-taxon surrogacy. *Biodiversity and Conservation* 16:2965-2988.

Lauer, W. 1976. Zur hygrischen Höhenstufung tropischer Gebirge. Pp. 169-181 in *Neotropische Ökosysteme. Biogeographica VII*, edited by O. Schmidthüsen. The Hague: Junk.

León, B. and N. Valencia. 1989. Pteridophytes of Zarate, a forest on the western side of the Peruvian Andes. *Fern Gazette* 13:217-224.

Linares-Palomino, R., V. Cardona, E. I. Hennig, I. Hensen, D. Hoffmann, J. Lendzion, D. Soto, S. K. Herzog, and M. Kessler. 2009. Non-woody life form contribution to vascular plant species richness in a tropical American forest. *Plant Ecology* 201:87-99.

Linares-Palomino, R., V. Cardona, D. Soto, S. K. Herzog, and M. Kessler. 2008. Tree community patterns along a deciduous to evergreen forest gradient in central Bolivia. *Ecología en Bolivia* 43:1-20.

Linder, P. 2008. Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 363:3097-3105.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10:3-13.

Losos, J. B., and D. Schluter. 2000. Analysis of an evolutionary species-area relationship. *Nature* 408:847-850

MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography. Monographs in Population Biology no. 1*. Princeton: Princeton University Press.

Macía, M. J. 2008. Woody plants diversity, floristic composition and land use history in the Amazonian rain forests of Madidi National Park, Bolivia. *Biodiversity and Conservation* 17:2671-2690.

Macía, M. J., and J. Fuertes. 2008. Composición florística y estructura de los árboles en un bosque tropical montano de la Cordillera Mosetenes, Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 23:1-14.

Macía, M. J., K. Ruokolainen, H. Tuomisto, J. Quisbert, and V. Cala. 2007. Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest. *Ecography* 30:561-577.

Macía, M. J., and J.-C. Svenning. 2005. Oligarchic dominance in western Amazonian plant communities. *Journal of Tropical Ecology* 21:613-626.

Magurran, A. E. 2004. *Measuring biological diversity*. Oxford: Blackwell.

McCain, C. M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography* 31:19-31

McCain, C. M. 2007. Area and mammalian elevational diversity. *Ecology* 88:76-86.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381-2396.

Mönkkönen, M., J. T. Forsman, and F. Bokma. 2006. Energy availability, abundance, energy-use and species richness in forest bird communities: a test of the species-energy theory. *Global Ecology and Biogeography* 15:290-302.

Muñoz, A., and W. Küper. 2001. Diversity and distribution of vascular epiphytes along an altitudinal gradient in an Andean cloud forest (Reserva Otonga, Ecuador). Epiphytes and canopy fauna of the Otonga rain forest (Ecuador). Pp. 189–216 in *Results of the Bonn-Quito epiphyte project, funded by the Volkswagen Foundation, Vol. 2*, edited by J. Nieder and W. Barthlott. Norderstedt: Books on Demand.

Nieder, J., S. Engwald, and W. Barthlott. 1999. Patterns of Neotropical epiphyte diversity. *Selbyana* 20:66-75.

Pautasso, M., and K. J. Gaston. 2005. Resources and global avian assemblage structure in forests. *Ecology Letters* 8:282-289.

Pautasso, M., and K. J. Gaston. 2006. A test of the mechanisms behind avian generalized individuals-area relationships. *Global Ecology and Biogeography* 15:303-317.

Phillips, O. L., P. Núñez Vargas, A. Lorenzo Monteagudo, A. Peña Cruz, M.-E. Chuspe Zans, W. Galiano Sánchez, M. Yli-Halla, and S. Rose. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* 91:757-775.

Phillips, O. L., and J. S. Miller. 2002. *Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set*. St. Louis: Missouri Botanical Garden Press.

Placzek, C., J. Quade, J. L. Betancourt, P. J. Patchett, J. A. Rech, C. Latorre, A. Matmon, C. Holmgren, and N. B. English. 2009. Climate in the dry, central Andes over geologic, millennial, and interannual timescales. *Annals of the Missouri Botanical Garden* 96:386-397.

Pulliam, H. R. 1998. Sources, sinks and population regulation. *American Naturalist* 132:652-661

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200-205.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* 8:224-239.

Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Science of the United States of America* 98:4534-4539.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167-171.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1-15.

Ricklefs, R. E. 2005. Phylogenetic perspectives on patterns of regional and local richness. Pp. 16-40 in *Tropical rainforest: past, present, and future*, edited by E. Bermingham, C. W. Dick and C. Moritz. Chicago: University of Chicago Press.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514-527.

Romdal, T. S., and J. A. Grytnes. 2007. An indirect area effect on elevational species richness patterns. *Ecography* 30:440-448.

Rosenzweig, M. L. 1995. *Species diversity in space and time.* Cambridge: Cambridge University Press.

Rosenzweig, M. L., and Y. Ziv. 1999. The echo pattern of species diversity: pattern and process. *Ecography* 22:614-628.

Roy, K., and E. E. Goldberg. 2007. Origination, extinction, and dispersal: integrative models for understanding present-day diversity gradients. *American Naturalist* 170:S71-S85.

Ruokolainen, K., H. Tuomisto, M. J. Macía, M. A. Higgins, and M. Yli-Halla. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? *Journal of Tropical Ecology* 23:13-25.

Schimper, A. F. W. 1888. *Die epiphytische Vegetation Amerikas*. Jena: G. Fischer.

Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166:262-276.

Seimon, A., S. R. P. Halloy, and T. A. Seimon. 2007. Global high-altitude limits for aquatic vascular plants. *Arctic, Antarctic, and Alpine Research* 39:340-341.

Shmida, A., and M. W. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.

Shurin, J., and D. S. Srivastava. 2005. New perspectives on local and regional diversity: beyond saturation. Pp. 399-417 in *Metacommunities*, edited by M. Holyoak, M. Leibold, and R. Holt. Chicago: University of Chicago Press.

Sklenár, P., and P. M. Ramsay. 2001. Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions* 7:113-124.

Srivastava, D. S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* 68:1-17.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* 152:510-529.

Stebbins, G. L. 1974. *Flowering plants: evolution above the species level.* Cambridge, MA: Harvard University Press.

Stropp, J., H. ter Steege, and Y. Malhi. 2009. Disentangling regional and local tree diversity in the Amazon. *Ecography* 32:46-54.

Terborgh, J. W., and J. Faaborg. 1980. Saturation of bird communities in the West Indies. *American Naturalist* 116:178-195.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81-92.

Thies, B., T. Nauss, and J. Bendix. 2008. Discriminating raining from non-raining clouds at mid-latitudes using Meteosat Second Generation daytime data. *Atmospheric and Chemical Physics* 8:2341-2349.

Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299:241-244.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225-238.

Waide, R. B., M. R. Willig, C. F. Steiner, G. G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257-300.

Weiser, M. D., B. J. Enquist, B. Boyle, T. J. Killeen, P. M. Jørgensen, G. Fonseca, M. D. Jennings, A. J. Kerkhoff, T. E. Lacher Jr., A. Monteagudo, M. P. Núñez V., O. L. Phillips, N. G. Swenson, and R. Vásquez M. 2007. Latitudinal patterns of range size and species richness of New World woody plants. *Global Ecology and Biogeography* 16:679-688.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* 19:639-644.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Reviews of Ecology Evolution and Systematics* 34:273-309.

Wolf, J. H. D. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112:15-28.

Young, K. R. 1993. Tropical timberlines: changes in forest structure and regeneration between two Peruvian timberline margins. *Arctic and Alpine Research* 25:167-174.

Young, K. R., and B. Leon. 2007. Tree-line changes along the Andes: implications of spatial patterns and dynamics. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 362:263-272.

Zotz, G., and P. Hietz. 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. *Journal of Experimental Botany* 52:2067-2078

15

Diversity of Lichenized Fungi in the Tropical Andes

Harrie J. M. Sipman

Lichens (lichenized fungi) are a diverse component of the natural vegetation in the tropical Andes. Not only at higher elevations where on fog-exposed sites branches and twigs may be densely covered with bushy or leafy lichens, but also in the rainforests of the foothills, where over 100, mostly crustose species may be found on a single tree.

The exploration of this biodiversity is still very incomplete. A good start in the nineteenth century, mainly by Nylander (1859, 1861, 1863, 1867) and Müller Argoviensis (1879), revealed close to 1000 species in the region. After ca. 1960 this number increased much due to field exploration by trained lichenologists and taxonomic revisions (e.g., Hale 1965, 1975, 1976a, 1976b, 1976c, Hafellner 1981, Kurokawa 1962, Lamb 1977, 1978, Esslinger 1989, Nash et al. 1995, Ahti 2000). However, the collecting effort was concentrated on Ecuador, Colombia and Venezuela, whereas large parts of Peru and Bolivia are poorly represented in the herbaria. Taxonomically, the available collections are also biased towards genera with large thalli, in particular foliose and fruticose growth forms, which may be effectively sampled by persons with limited experience. The vast majority of crustose lichens, often distinguishable only with a lens, is much less documented and needs experienced persons with a good knowledge of the local diversity for representative sampling.

A recent checklist for Colombia alone (Sipman et al. 2008) contains 1444 species. This figure seems not exceptional, because it compares well with a web-published checklist for Costa Rica with 1527 species (http://www.biologie.uni-hamburg.de/checklists/lichens/middle-america/costa-rica_l.htm, 2008). Because ongoing revisions keep finding many new species (e.g., Lücking et al. 2008, Sipman et al. 2009), even recent checklists appear still far from complete, and the actual species number for Colombia is estimated to be 3000–4000 (Sipman et al. 2008). Thus, the whole tropical Andes might harbor close to 5000 species. These are arranged in about 300 genera, but the number of genera is currently rapidly increasing as new insights in classification are resulting in much splitting of genera. About 25% of these are large species with foliose or fruticose growth forms, the remainder are crustose.

In other tropical areas worldwide knowledge of lichen diversity is also very limited. Therefore a comparison of the tropical Andes with the surrounding areas can only be based on estimates using the high turnover in species composition along elevational gradients. Thus, Andean countries with their high mountains are likely to have the highest diversity. Only Costa Rica may have a similar number of species. Brazil is an exception and may also come close to the tropical Andes in diversity, because of its large size and the important centre of endemism for lichens in its southeast. Its current checklist has 2851 species (http://www.biologie.uni-hamburg.de/checklists/lichens/south-america/brazil_l.htm, 2008).

For similar tropical areas outside the New World, only a web checklist for Papua New Guinea presents comparable information: 1250 species (http://www.biologie.uni-hamburg.de/checklists/lichens/asia/papua-new-guinea_l.htm, 2003) . This may indicate a lower diversity, reflecting the isolated position of the area. A comparison with extra-tropical mountain areas suggests that these areas have a higher diversity, but this may simply reflect the much better knowledge rather than exceptional levels of diversity. For instance the European Alps, a somewhat comparable area in relief, but smaller and lower, hold an estimated 4000 species. Here, an individual country alone like Austria has 2227 known species (http://www.biologie.uni-hamburg.de/checklists/lichens/europe/austria_l.htm).

Lücking (2008) used the phytogeographical division of Takhtajan to investigate the distribution of leaf-inhabiting lichens, a rather well-studied group, and found that the Neotropics are the richest area worldwide. Within the Neotropics the tropical Andes are surpassed by the Amazon Basin, the Guayana Highlands, and Central America. Since the group is mainly distributed in the lowlands, it should be well represented in the foothill forests of the Andes, and the result probably reflects the poor exploration of these forests.

Particularly well represented lichen groups in the tropical Andes include the genera *Heterodermia* (Kurokawa 1962), *Hypotrachyna* (Hale 1975), *Oropogon* (Esslinger 1989), *Parmotrema* (Hale 1965), and *Stereocaulon* (Lamb 1977), to name just a few. The genera *Leptogium*, *Sticta*, and *Usnea* are also well represented but taxonomic treatments to appreciate their species richness are still lacking. These groups belong to the more conspicuous and better known macrolichens. The vast majority of crustose lichens is unsuitable for comparisons because their taxonomy is usually poorly known and their diversity can only be guessed.

For more detailed information about the distribution of lichen diversity only a few better-collected, recently revised macrolichen groups appear suitable, for which the current knowledge may approach the actual diversity: the family Cladoniaceae and the genera *Hypotrachyna* and *Xanthoparmelia* (Table 15.1). This table shows the wide range of many lichens. Only about half of the species are restricted to the Neotropics, and few species are restricted to the tropical Andes, even though this area is one of the two main centers of endemism, next to southeast Brazil (Ahti 2000, Sipman et al. 2009).

Table 15.1. Species numbers of selected lichen groups (after Ahti 2000, Sipman et al. 2009, Nash et al. 1995) illustrating the significance of the tropical Andes for lichen diversity.

Cladoniaceae	*Hypotrachyna*	*Xanthoparmelia*	
occurring in the Neotropics	184	140	77
restricted to the Neotropics	90	85	46
occurring in the tropical Andes	56	78	60
restricted to the tropical Andes	6	11	7

The tropical Andes do not form a sharply delimited area for lichen distribution, and many species with main distribution centre here extend to the mountains of Venezuela and Costa Rica, sometimes even the Caribbean and the Appalachians in North America. A few species are shared with southeast Brazil; these tend to be more common in Peru and Bolivia. Within the tropical Andes four endemism centers are indicated by information from the genera *Everniastrum*, *Oropogon and Stereocaulon* (Sipman 1992), *Cladonia* (Ahti 2000), *Umbilicaria* (Sipman and Topham 1992), *Xanthoparmelia* (Nash et al. 1995), and *Hypotrachyna* (Sipman et al. 2009): 1. extended northernmost Andes, from Costa Rica to Ecuador; 2. Venezuelan Andes + Eastern Cordillera of Colombia, i.e. a limited area inside 1; 3. southern Ecuador + northern Peru; 4. Peru (+ Bolivia). The scarcity of data from Peru and Bolivia obscures the distribution patterns there.

In summary, recent studies revealed that the tropical Andes are among the World's top diversity centers for lichens. A considerable part of this diversity seems endemic, but current knowledge is too fragmentary for the preparation of comprehensive lists of endemic species or for an accurate delimitation of the areas where they grow. The large distributional ranges of many species suggests that the effect of global climatic change may be easily compensated by shifts in the ranges in most species. Probably this is not the case for the endemics. The main threat seems to come from habitat destruction. Experience in temperate areas indicates that many lichen species are bound to forest with a natural structure and long history (e.g., Rose and Coppins 2002, Rivas Plata et al. 2008), so that deforestation will lead to their disappearance.

Literature Cited

Ahti, T. 2000. Cladoniaceae. *Flora Neotropica Monograph* 78:1-362.

Esslinger, T. L. 1989. Systematics of *Oropogon* (Alectoriaceae) in the New World. *Systematic Botany Monographs* 28:1-111.

Hafellner, J. 1981. Monographie der Flechtengattung *Letrouitia* (Lecanorales, Teloschistineae). *Nova Hedwigia* 35:645-729.

Hale, M. E. 1965. A monograph of *Parmelia* subgenus *Amphigymnia*. *Contributions from the United States National Herbarium* 36:193-358.

Hale, M. E. 1975. A revision of the lichen genus *Hypotrachyna* (Parmeliaceae) in tropical America. *Smithsonian Contributions to Botany* 25:1-73.

Hale, M. E. 1976a. A monograph of the lichen genus *Bulbothrix* Hale (Parmeliaceae). *Smithsonian Contributions to Botany* 32:1-29.

Hale, M. E. 1976b. A monograph of the lichen genus *Parmelina* Hale (Parmeliaceae). *Smithsonian Contributions to Botany* 33:1-60.

Hale, M. E. 1976c. A monograph of the lichen genus *Pseudoparmelia* Lynge (Parmeliaceae). *Smithsonian Contributions to Botany* 31:1-62.

Kurokawa, S. 1962. A monograph of the genus *Anaptychia*. *Beihefte zur Nova Hedwigia* 6:1-115.

Lamb, I. M. 1977. A conspectus of the lichen genus *Stereocaulon* (Schreb.) Hoffm. *Journal of the Hattori Botanical Laboratory* 43:191-355.

Lamb, I. M. 1978. Keys to the species of the lichen genus *Stereocaulon* (Schreb.) Hoffm. *Journal of the Hattori Botanical Laboratory* 44:209-250.

Lücking, R. 2008. Foliicolous lichenized fungi. *Flora Neotropica Monograph* 103:1-866.

Lücking, R., J. L. Chaves, H. J. M. Sipman, L. Umaña, and A. Aptroot. 2008. A first assessment of the ticolichen biodiversity inventory in Costa Rica: the genus *Graphis*, with notes on the genus *Hemithecium* (Ascomycota: Ostropales: Graphidaceae). *Fieldiana, Botany, New Series* 46:1-131.

Müller, J. 1879. Lichenes aequinoctiali-americanici a Cl. Ed. André, annis 1875-1876, praesertim in editioribus Ecuador (E.) et in Nova Granata (N. Gr.) lecti (Les lichens neo-grenadins et ecuadoriens, récoltés par M. Ed. André). *Revue Mycologique* 1:163-171.

Nash III, T. H., C. Gries, and J. A. Elix. 1995. A revision of the lichen genus *Xanthoparmelia* in South America. *Bibliotheca Lichenologica* 56:1-157.

Nylander, W. 1859. Lichenes exotici, lichenes in regionibus exoticis quibusdam vigentes exponit synopticis enumerationibus. *Annales des Sciences Naturelles* 11:205-264.

Nylander, W. 1861. Additamentum ad lichenographiam andium boliviensium. *Annales des Sciences Naturelles* 15:365-382.

Nylander, W. 1863. Lichenes. In: Prodromus Florae Novo-Granatensis ou Énumération des plantes de la Nouvelle-Grénade avec description des espèces nouvelles, edited by J. Triana, and J. E. Planchon. *Annales des Sciences Naturelles* 19, 20:286-382, 228-279.

Nylander, W. 1867. Lichenes, additamentum. In: Prodromus Florae Novo-Granatensis, edited by J. Triana, and J. E. Planchon. *Annales des Sciences Naturelles* 7:301-354 (in repr. 533-586).

Rivas Plata, E., R. Lücking, and H. T. Lumbsch. 2008. When family matters: an analysis of Thelotremataceae (lichenized Ascomycota: Ostropales) as bioindicators of ecological continuity in tropical forests. *Biodiversity and Conservation* 17:1319-1351.

Rose, F., and S. Coppins. 2002. Site assessment of epiphytic habitats using lichen indices. Pp. 343-348 in *Monitoring with lichens - monitoring lichens. NATO Science Series: IV: Earth and Environmental Sciences,* edited by P. L. Nimis, C. Scheidegger, P. A. Wolseley. Dordrecht: Kluwer Academic Publishers.

Sipman, H. J. M. 1992. The origin of the lichen flora of the Colombian páramos. Pp. 95-109 in *Páramo. An Andean ecosystem under human influence*, edited by H. Balslev and J. L. Luteyn. London: Academic Press.

Sipman, H. J. M., J. A. Elix, and T. H. Nash III. 2009. *Hypotrachyna* (Parmeliaceae, Lichenized Fungi). *Flora Neotropica Monograph* 104:1-176.

Sipman, H. J. M., W. Hekking, and J. Aguirre-C. 2008. Checklist of lichenized and lichenicolous fungi from Colombia. *Bibliotheca José Jerónimo Triana* 20:1-242.

Sipman, H. J. M., and P. Topham. 1992. The genus *Umbilicaria* (lichenized ascomycetes) in Colombia. *Nova Hedwigia* 54:63-75.

16

Diversity of Mosses in the Tropical Andes

Steven P. Churchill

The Andean region contains the highest diversity for mosses in the tropics, and it is one of the two or three richest regions of the world (Tan and Pócs 2000). Mosses and liverworts are an important group of plants responsible for the conservation of soil and water in the Andes. Degradation of humid páramo-puna and montane forest disrupting the bryophytic functionality will result in accelerated loss of soil and water. Pertinent references for the tropical Andean countries include a general overview of diversity (Churchill et al. 1995, Churchill 2009), a checklist (Churchill et al. 2000), and a catalogue of the Amazon basin (Churchill 1998) including the four countries covered by this volume. Floristic treatments available for the area covered include a guide to the Neotropical bryophyte families and genera (Gradstein et al. 2001), and specifically for mosses, a guide for the Ecuadorian Amazon (Churchill 1994) and for Colombia (Churchill and Linares C. 1995). Additional information is available on the website for tropical Andean mosses (Churchill and collaborators 2009) and linked to nearly 50,000 databased collections (Tropicos 2009).

Taxonomic Diversity

Moss diversity for the four countries is estimated at 1298 species, 334 genera, and 71 families. This represents 14% of the estimated 9000 moss species for the world. The ten most diverse families (Table 16.1) account for 66% of the total. The Pottiaceae, the most speciose family, is also the most diverse in genera (42) and endemics (53). The ten most speciose genera (Table 16.1) account for 28% of the total recorded.

Endemism and Diversity

Species endemism for the four countries combined is estimated at 405 (31%). The number of endemics unique to a single country represents 58% of the total number of tropical Andean endemics (Table 16.2); the remaining 42% are shared between two or more countries (including Venezuela). Nineteen genera are endemic and restricted to the Andes (Churchill 2009); six genera are from páramo or puna ecosystems and 13 from montane forest ecosystems. There are no endemic families.

Among the four countries Colombia is the most diverse, followed closely by Bolivia, then Ecuador and Peru (Table 16.2). The number of species recorded for any one country ranges from 777 to 915, while the regional total is 1298. This demonstrates that many species are widespread. The number of species restricted to one country is 31% (or 403 species) of the 1298. The number of country endemics account for 48% of the 405 regional endemics recorded.

Table 16.1. The 10 most diverse moss families and genera for the four individual Andean countries.

Family	No. Species	Genus	No. Species
Pottiaceae	171	*Sphagnum*	60
Bryaceae	126	*Fissidens*	52
Dicranaceae	125	*Campylopus*	48
Pilotrichaceae	107	*Bryum*	41
Bartramiaceae	63	*Zygodon*	30
Sphagnaceae	60	*Macromitrium*	29
Sematophyllaceae	57	*Didymodon*	26
Fissidentaceae	52	*Lepidopilum*	26
Macromitriaceae	46	*Sematophyllum*	25
Orthotrichaceae	46	*Syntrichia*	25
Total	853		362

Table 16.2. Summary of moss diversity for the four individual Andean countries.

Country	Species total	Occurring in one country only	Endemic
Colombia	915	147	60
Ecuador	816	67	43
Peru	777	52	30
Bolivia	909	137	60
Total		403	193

Ecoregions and Diversity

One simple but important geographical division is between the highlands (páramo, puna, montane forest, dry inter-Andean valleys) and lowlands (Amazon, Chiquitano and Chaco forest, and coastal wet to dry forest and sub-desert) for the four countries. The area occupied by lowlands is half of or more than that of the highlands. The number of mosses present in the lowlands is 309 (18%), however only 55 species (4%) are restricted to the lowlands; the remaining 254 extend into the Andes, most extending above 1000 m. Most mosses, that is 96% of the 1298 species in the four countries, occur in the highlands. Within the highlands the montane forest ecosystems are the most diverse. In Bolivia, for example, montane forest (Yungas and Tucuman-Bolivian) occupy only 8% of the countries land surface, but contains 88% of the liverworts and 74% of the mosses recorded from the country (Churchill et al. 2009).

Future Needs

The estimate of the moss diversity and endemism presented above is still very preliminary. The following assessments are made for the tropical Andean mosses: 1) Greater inventory efforts are needed in all four countries; knowledge of Colombia, Ecuador, and Bolivia can be rated as low median, Peru however is sub-minimal, with extensive collecting needed for the montane forest. 2) Basic monographs are still needed for about 40% of the taxa. The general reduction of systematic revisions over the last two decades stands as the greatest impediment to our understanding of moss diversity in the tropical Andes. Descriptive and illustrated floras are required, and may meet the need for keys to unrevised groups in a preliminary way. 3) Ecological studies are needed to better understand the major role bryophytes play in the ecosystem, with particular emphasis on the aquatic systems of the páramo and humid puna, and on montane forest. 4) All of the above is important for the quality of knowledge for conservation. "Sustainable development" is not a viable option with regard to montane forest or to the páramo and puna. Rather it is the conservation and regeneration of those Andean ecosystems that is required to assure continued water availability, and to prevent extreme erosion (cf. Bradley et al. 2006, Vergara et al. 2007). There is an immediate need to declare some ecoregions or ecosystems, e.g., montane forest, as endangered and to give them full protection.

Acknowledgments

This work was supported by grants from the National Science Foundation (DEB–0542422) and by the Taylor Fund for Ecological Research through the Missouri Botanical Garden. The author is grateful to M.J. Cano, M.T. Gallego, and J.A. Jiménez for providing data on the Pottiaceae. Finally to R.E. Magill for assistance with development of the Andean web page and Tropicos data base.

Literature Cited

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 312:1755-1756.

Churchill, S. P. 1994. The mosses of Amazonian Ecuador. *AAU Reports* 35:1-211.

Churchill, S. P. 1998. Catalog of Amazonian mosses. *Journal of the Hattori Botanical Laboratory* 85:191-238.

Churchill, S. P. 2009. Moss diversity and endemism of the tropical Andes. *Annals of the Missouri Botanical Garden* 96:434-449.

Churchill, S. P., and E. L. Linares C. 1995. Prodromus bryologiae novo granatensis. *Biblioteca José Jerónimo Triana* 12:1-924.

Churchill, S. P. and collaborators. 2009. Mosses of the tropical Andes. Available at: http://www.tropicos.org/Project/ANBRY.

Churchill, S. P., D. Griffin III, and M. Lewis. 1995. Moss diversity of the tropical Andes. Pp. 335-346 in *Biodiversity and conservation of Neotropical montane forests*, edited by S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn. Bronx: New York Botanical Garden Press.

Churchill, S. P., D. Griffin III, and J. Muñoz. 2000. A checklist of the mosses of the tropical Andean countries. *Ruizia* 17:1-203.

Churchill, S. P., N. Sanjines A., and C. Aldana M. 2009. Catálogo de los briofítas de Bolivia: diversidad, distribución y ecología. Santa Cruz de la Sierra: Museo de Historia Natural Noel Kempff Mercardo and Missouri Botanical Garden.

Gradstein, S. R., S. P. Churchill, and N. Salazar Allen. 2001. Guide to the bryophytes of tropical America. *Memoirs of the New York Botanical Garden* 86:1-577.

Tan, B. C., and T. Pócs. 2000. Bryogeography and conservation of bryophytes. Pp. 403-448 in *Bryophyte biology*, edited by A. J. Shaw and B. Goffinet. Cambridge, MA: Cambridge University Press.

Tropicos.org. Missouri Botanical Garden. 2009 <http://www.tropicos.org>.

Vergara, W., A. M. Deeb, A. M. Valencia, R. S. Bradley, B. Francou, A. Zarzar, A. Grünwaldt, and S. M. Haeussling. 2007. Economic impacts of rapid glacier retreat in the Andes. *Eos* 88:261-268.

17

Insects of the Tropical Andes: Diversity Patterns, Processes and Global Change

Trond H. Larsen, Federico Escobar, and Inge Armbrecht

Insects represent a dominant component of terrestrial and freshwater biodiversity in terms of species richness (they comprise about 80% of known animal species), animal biomass, and critical ecological functions (Samways 2005). Their evolutionary success and relatively high diversity in virtually all terrestrial habitats makes them valuable for understanding the origin, distribution, and maintenance of biodiversity, and for developing biodiversity conservation strategies (Brown 1991). Insects are important to people: a few are detrimental such as agricultural pests and disease vectors, others are beneficial such as pollinators, decomposers, seed dispersers or pest controllers (Dourojeanni 1990).

The enormous diversity of tropical insects is a challenge to entomological research, and we still know relatively little about tropical insects (Samways 2005). Because of their immense species richness, exhaustive inventories are not usually feasible, and most studies focus on selected taxonomic groups (Spector 2006). Comparisons among studies are hampered by incomplete taxonomic work and difficulties with identification. Probably less than 10% of insect species are known to science; most estimates suggest that globally 5-10 million insect species exist (Odegaard 2000), but some estimates are over 30 million species (Erwin 1982).

The tropical Andes are a global biodiversity hotspot for plants and vertebrates (Myers et al. 2000), a pattern almost certainly reflected in the insects but for which few data exist (Hernández-Camacho et al. 1992; Fandiño-Lozano and van Wyngaarden 2005). Because so many insects are associated with plants, the extreme plant endemism of the tropical Andes (approximately half of all species; Myers et al. 2000) suggests a similarly high level of insect diversity and endemism. Extreme heterogeneity over relatively short distances in montane regions influences insect distribution, morphology, physiology, and behavior (Wolda 1987; Hodkinson 2005). Because of their sensitivity to anthropogenic disturbances, habitat loss, pollution and climate change, many insect taxa are used as indicators of global change (Brown 1991; Menendez 2007). Here, we synthesize the scarce data that exist for insects in the tropical Andes.

Alpha Diversity and Endemism

Insects show exceptional diversity and endemism in the tropical Andes, an area which includes global records of species richness and endemism rates for many taxa. The region is recognized as an important center of speciation because of its complex geological history and climate (Hooghiemstra et al. 2006). The Andes are a center of speciation for members of insect groups ranging from Phanaeine dung beetles (Price 2009) to Riodinid butterflies (Hall 2005). Although many insect groups originated in the lowlands, recent evidence suggests that young species are more frequent in montane regions and that species originating in the Andes are colonizing lowland Amazonia (Hall 2005).

Peru is the most diverse country in the world for butterflies, with 3,700 species described (for perspective, this represents over 20% of the global total and more than five times the number of species found in all of North America), followed by about 3,200 species in Colombia and Ecuador (Lamas 1999). More species are concentrated in mid-elevation Andean cloud forests on the eastern slopes than in any comparably sized area in Peru, including an unusually high proportion of endemic species (Rodríguez 1996; Lamas 1999). The eastern slopes of the eastern cordillera in Colombia also support by far the richest butterfly communities of all the subregions of the Colombian Andes (Kattán et al. 2004). Of 658 species, 12% are endemic (Kattán et al. 2004), including rare genera that are only found in virgin cloud forest (Balint et al. 2006). Of 112 species of pronophilini butterflies (Satyrini) collected in the highlands of northern Peru, the highest rate of endemism occurs above the timberline (Pyrcz 2004). Within the hairstreak genus *Timaeta*, which is endemic to Andean montane forests, the highest diversity occurs between 1500-2000 m in eastern Ecuador (Robbins and Busby 2008).

Moths have not been collected nearly as frequently as butterflies. However, studies in southern Ecuador identify the region as a global hotspot for moth diversity (Brehm et al. 2005); 1266 species of geometrid moths, the highest known richness in the world for this group, were found along a gradient from 1040 – 3100 m. Thirty-seven percent of these species could not be reliably named, a large proportion of which are likely to be undescribed, and most of them were rare (Brehm et al. 2005; Hilt et al. 2006). This represents an astounding 6% of the entire known global fauna of geometrid moths.

Apart from butterflies, dung beetles and ants are two of the most studied insect taxa in the tropics (Figure 17.1; Jiménez et al. 2007; Nichols et al. 2007). Within Colombia, montane ecosystems have been identified as the highest priority for conservation of hunting ants (Ponerinae) (Jiménez et al. 2007). Of 60 species in montane forests of the eastern Cordillera, 8 are endemic and 24 are considered a conservation priority based on their restricted distribution and vulnerability to habitat loss.

Like many taxa, dung beetle communities in the Andes are dominated by rare species (Celi et al. 2004; Larsen 2004; Hamel-Leigue et al. 2008). Of 71 species collected between 730 and 2210 m along a transect in Peru, it is estimated that between 14-50% are new to science (Larsen 2004). Of 30 species collected in the Yungas of Cochabamba, Bolivia (1250-1600 m), at least two species were previously undescribed and 14 species were endemic (Hamel-Leigue et al. 2008). Twenty-three out of all 35 species of *Cryptocanthon* are endemic to areas above 1000 m, and most of these species have lost the ability to fly, which likely contributes to their restricted range (Cook 2002).

Beetles are the most abundant group of insects, accounting for about 20% of all species, and several other beetle families have been studied in the Andes (Amat-García 1999; Chalumeau and Brochier 2007). The highest tiger beetle species richness in South America occurs along the eastern slope of the Andes, and these species tend to have very restricted ranges (Pearson and Carroll 2001). The Ecuadorian paramo supports an exceptionally high diversity of carabid ground beetles, about 94% of which are endemic, especially to the high paramo (4100-4400m) (Moret 2005). Out of 204 species known from the Ecuadorian paramo, 57 were only recently described, indicating how little is still known about montane insect communities. Like *Cryptocanthon* dung beetles, many of these high elevation species are flightless.

Aquatic macroinvertebrate diversity appears to be high in the Andes from Colombia to Bolivia (Guevara Cardona et al. 2007), with 85 species in a single study above 2000 m (Sites et al. 2003). Species show highly varied dispersal abilities, contributing to a range of distributions from widespread to endemic (Sites et al. 2003). In the high oak forests of Colombia, Amat-García et al. (2004) found the richest community (48 species) of mycophagous insects known in the country. Bees are also highly diverse, especially in cloud forests. At high elevations, above 2500 m, 65 species are found in Colombia, and 90 species in Venezuela, Ecuador, and Peru (González and Engel 2004).

In addition to the insects, a few other studies have contributed to our understanding of invertebrate diversity in the Andes. 19 of 24 scorpion species found in the Andean corridor of southern Peru are endemic (Ochoa 2005). Seventy-six genera and an estimated 3000 species (9% of global total) of spiders are found in Peru, with about 50-80% endemic to the country (Rodríguez 1996). Most endemic spider species are restricted to montane areas above 1500 m. Terrestrial mollusks show similarly high endemism on the eastern slopes of the Andes relative to the lowlands (Rodríguez 1996).

Species Richness Gradients

Latitudinal and altitudinal gradients of species richness are important for understanding the processes that generate and maintain biodiversity (Willig et al. 2003; Hodkinson 2005). Temperature is one of several factors that drive commonly observed patterns of higher species richness at lower latitudes and lower elevations; however, many other factors are important determinants of species richness patterns (e.g. total area, biogeographic history, energy availability, seasonality, precipitation), and these are reviewed in detail elsewhere (e.g. McCoy 1990; Willig et al. 2003; Hodkinson 2005; Körner 2007). Many communities along elevational gradients show a low or mid-elevation peak in species richness, especially after sampling effort is adjusted to account for sampling area (Rahbek 1995).

Dung beetle communities on the eastern slopes of the Andes show a strong overall decrease in species richness at higher altitudes, described by an exponential regression (Figure 17.1a). In all studies reviewed here, the lowest species richness was recorded at the highest elevations. Within this overall trend, six of twelve studies found a peak in species richness at the lowest elevation sites, whereas six found a peak at low to mid-elevation. However, the six studies that did not find a peak in richness at the lowest site did not sample in the adjacent lowlands where the most diverse dung beetle communities are known (Larsen et al. 2006).

Dung beetle species richness appears to show a general increase at lower latitudes across a gradient from Colombia to Bolivia, with a peak at about seven degrees south of the equator (Figure 17.1b). However, to confirm this trend, more data are needed for central and northern Peru. A similar trend is observed in plants and other taxa.

Jacobsen (2004) found an approximately linear decrease in aquatic invertebrate species richness from sea level to 4000 m, with 50% reduction in species richness from bottom to top. Ant diversity in Colombia may peak between 900-1700 m, with more species occurring at the wettest sites (van der Hammen and Ward 2005). As an exception to these patterns, moth diversity along an altitudinal transect in Ecuador was not correlated with altitude or temperature (Brehm et al. 2003).

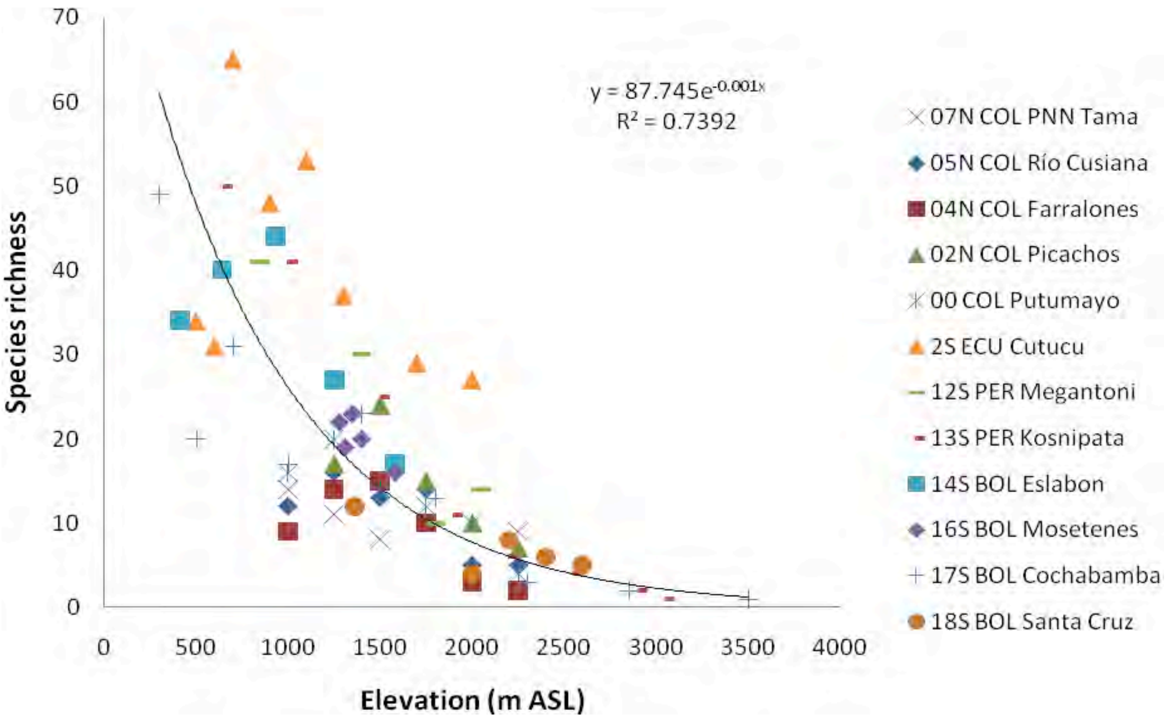

Figure 17.1a. Dung beetle species richness gradients from 12 altitudinal transects along the eastern slopes of the tropical Andes. Exponential regression fitted to pooled data. Each legend entry indicates latitudinal degrees north/south, country abbreviation and site name. All Colombia data (COL) from Escobar et al. (2005); Ecuador (ECU) from Celi et al. (2004); Peru (PER): Megantoni from Larsen (2004), Kosnipata from Larsen (unpub. data); Bolivia (BOL): Eslabon from Spector (unpub. data), Mosetenes from Hamel-Leigue et al. (2008), Cochabamba and Santa Cruz from Genier (unpub. data).

Range Size and Species Turnover

The restricted ranges of many species in the tropical Andes (Molau 2004) make them a global center of endemism and priority for conservation (Myers et al. 2000). While few data exist to describe the entire distribution of most insect species, altitudinal range is relatively simple to measure. Altitudinal range sizes are generally smaller in the tropics than they are in temperate regions, primarily because tropical species have a more narrow physiological tolerance (Janzen 1967; McCain 2009). This also appears to be true for insects. For example, all satyrine butterfly species assessed in northern Peru showed elevational ranges of less than 550m (Pyrcz 2004). Larsen (2004 and unpubl. data) found that 80% of individual dung beetle species along a transect from 290-3500 m occupied an elevational range of less than 300 m. Dung beetles also show high altitudinal turnover in Colombia (Escobar et al. 2005), Bolivia (Hamel-Leigue et al. 2008), and Ecuador (Celi et al. 2004). Narrow altitudinal range does not necessarily contribute to endemism and vulnerability if the species is broadly distributed latitudinally across the Andes. However, latitudinal turnover is also high for dung beetles, ranging from 69% of species shared with comparable habitat less than 100 km away (Larsen 2004) to 33% of species shared with comparable habitat 360 km away (Hamel-Leigue et al. 2008).

The altitudinal extension of Rapoport's rule, which predicts that species at higher elevations show wider elevational distributions, does not appear to be consistently supported in the few studies that have examined this for Andean insects. Jacobsen (2003) found higher species turnover of aquatic macroinvertebrates at higher elevations. Butterflies and ground beetles at high elevations tend to show especially high endemism (Pyrcz 2004; Moret 2005). On the other hand, Escobar et al. (2005) found more restricted-range dung beetle species at low elevations, although this study considered a relatively narrow altitudinal range (1000-2250m). Another pattern, called Bergmann's rule, which predicts larger body size of species in colder climates (including high elevations), also does not appear to be supported by Andean insects, at least not in geometrid moths (Brehm and Fiedler 2004).

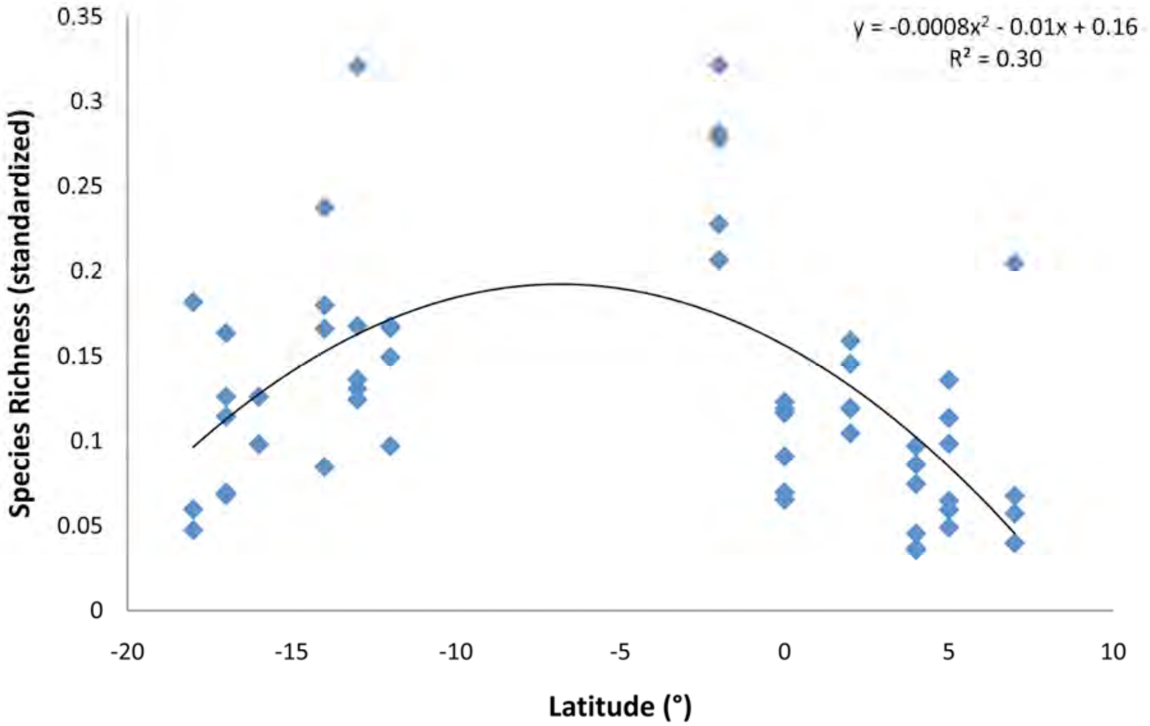

Figure 17.1b. Latitudinal gradient of dung beetle species richness (same 12 transects as in Fig. 1a), showing polynomial regression. To control for the influence of elevation, we standardized species richness by categorizing datapoints (sites) into seven altitudinal bands from 410 – 2300m. For each altitudinal band, we calculated standardized species richness at each sampled latitude as the proportion of total species richness observed in the entire altitudinal band.

Parapatric Species Replacement

A diverse array of taxa show distinct, non-overlapping (or barely overlapping) species ranges among congeners and other closely related species (e.g., Figure 17.2). This pattern, known as parapatry, is commonly observed along altitudinal gradients where a relatively wide range of environmental conditions are compacted over a small geographic space. Altitudinal replacement or segregation among species is important for understanding processes structuring ecological communities, and in most cases is believed to be driven primarily by competition (e.g., Terborgh and Weske 1975; Terborgh 1977; Herzog et al. 2009; but see Cadena 2007). Species replacement along elevational gradients appears to be widespread among insects in the tropical Andes, and has been observed in dung beetles (Figure17. 2; Medina et al. 2002; Larsen 2004), riodinid butterflies (Hall 2005), satyrine butterflies (Pyrcz 2004), sandflies (Le Pont et al. 1990), caddisflies (Guevara Cardona et al. 2007), and other aquatic macroinvertebrates (Jacobsen 2003). This high level of parapatry further supports the Andes as a center of speciation in South America.

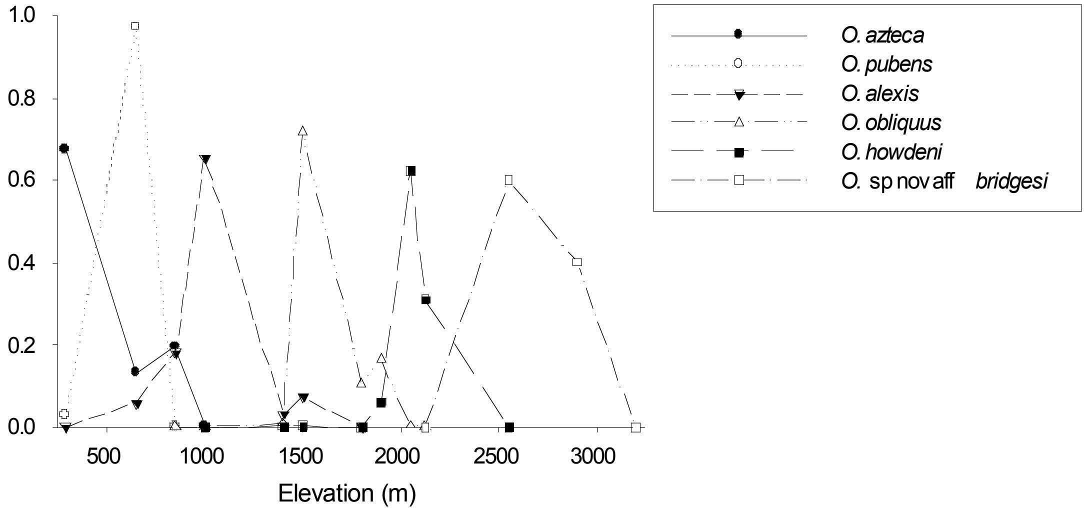

Figure 17.2. Parapatric congener segregation by elevation in the dung beetle genus *Ontherus* in Peru. Data shown from Larsen (2004).

Seasonality

Many tropical insects show strong changes in abundance related to seasonal changes in rainfall and humidity (Wolda 1988). Understanding seasonal patterns is important for determining ecological dynamics as well as interpreting the conservation significance of inventory and monitoring studies which can inadvertently be biased by time of sampling (DeVries et al. 1999). Very few studies have examined seasonality of Andean insects. In Ecuador, arctiid moths showed little seasonality, whereas geometrid moths doubled in abundance from the wet to the dry season (Hilt et al. 2007). However, only a few individual species changed strongly in abundance, and most species were present as adults year round. Dung beetle species richness and abundance at one site were unaffected by rainfall throughout the year (Escobar and de Ulloa 2000). Stream macroinvertebrates appear to be more species rich and abundant during the dry season, probably related to instability associated with flooding during the wet season (Jacobsen and Encalada 1998).

Land-use and Habitat Disturbance

Although insect species are rarely endangered by overexploitation as are many vertebrates, they are often threatened by habitat loss or agrochemicals. In general, tropical insects tend to be ecologically more specialized than temperate ones (Dyer et al. 2007). Because tropical species often occur in only one habitat type, they can be especially sensitive to land use and habitat loss (Nichols et al. 2007). Andean ecosystems are highly threatened by rapidly changing land use patterns, as well as a long history of occupation (Suárez et al., Chapter 9, this volume). For example, in Colombia, 69% of Andean forests have been cleared (Etter et al. 2006).

The response of dung beetles to land use in the tropical Andes has been relatively well studied. In general, dung beetle species richness, diversity, abundance, and biomass decline strongly in response to disturbances that include pasture, maize, coffee, tree plantations, secondary forests, etc. (e.g. Escobar 2004; Horgan 2005). The most mature and structurally complex habitats generally support the most species and individuals, following a gradient of vegetational succession (Escobar and de Ulloa 2000; Larsen 2004). Pastures and open habitats support very few species and individuals and block dispersal of forest species (Escobar and de Ulloa 2000); 8 of 22 species in one study never entered pasture (Medina et al. 2002).

Other taxa, such as geometrid moths and ants, also show greater diversity with increasing maturity of successional vegetation, structural complexity and proximity to intact forest (Bustos and Ulloa-Chacon 1996; Hilt et al. 2006). The presence of trees in pasture systems supports twice as many ant species as empty pastures and many more species of staphylinid beetles (Rivera et al. 2008; Sanabria et al. 2008). Mature forest in Ecuador supported the rarest species of arctiid moths, while common species tended to be widespread (Hilt and Fiedler 2005). Butterflies in *Polylepis* forests of Bolivia showed higher richness at intermediate levels of habitat disturbance, a trend often observed in butterflies (Quinteros et al. 2006).

Because plant biomass and vegetation structure contribute to insect biodiversity, agroforestry systems have potential to harbor a significant number of Andean species and may be used to partially restore biodiversity in degraded areas (Schroth et al. 2004). For example, organic shaded polyculture coffee supports ant communities much more similar to natural forest than unshaded coffee plantations, and both kinds of coffee plantations have more ants than pastures (Perfecto and Vandermeer 1996; Armbrecht et al. 2005). Coffee and agroforestry systems also may permit dispersal of forest species across the landscape (Perfecto 2003). Unfortunately, coffee systems are increasingly being intensified or cleared for cattle, leading to considerable biodiversity loss (Philpott et al. 2008).

Aquatic macroinvertebrates are frequently used in studies to assess and monitor biodiversity because of their sensitivity to disturbance and ease of sampling. Invertebrate species richness of high Bolivian streams was reduced by acid mine drainage and sewage (Jacobsen and Marin 2008; Van Damme et al. 2008). Sedimentation caused by road construction in Bolivia caused a 6-fold decrease in richness and a 200-fold decrease in abundance of aquatic invertebrates (Fossati et al. 2001).

Despite some general patterns, species response to land use change is highly context dependent and also depends on geographic region and elevation. For example, a contrasting response to the loss of dung beetles in Andean pastures was observed in Mexico where dung beetle species presumably of holarctic and afrotropical origin predominated and were able to thrive in deforested pasture habitats (Escobar et al. 2007). Despite an apparent lack of support for Rapoport's rule, species that occur at high elevations may be more resilient to land-use and habitat alteration because some are able to use a wider variety of habitats. Larsen (2004) found that 32% of all dung beetle species from 730-2210 m were found in only one habitat type, but that species at higher elevations were less habitat specific, possibly due to lower competition and reduced resource partitioning in communities with fewer species.

High elevation dung beetle species adapted to grasslands appeared largely unaffected by habitat disturbance and expanded their range downwards into newly created pasture habitats (Larsen, unpubl. data). Lowland species adapted to open, disturbed areas have also expanded upwards into pastures (Escobar and de Ulloa 2000). However, dung beetle species from low to mid-elevation forests appear the most sensitive to habitat loss (Medina et al. 2002; Larsen unpubl. data). For example, high elevation tree plantations supported many species from adjacent forest whereas low elevation tree plantations along the same transect did not, showing a 60% decline (Medina et al. 2002). Although high elevation species may be less intrinsically sensitive than lowland species to habitat loss, high elevation species are predicted to be the most vulnerable to climate change (Chen et al. 2009), a topic discussed in the next section.

Climate Change

Despite many reviews of the impacts of climate change on the Earth's ecosystems and biodiversity, virtually none have addressed consequences for the tropical Andes and none have considered Andean insects. This is especially alarming given that tropical ectotherms, such as insects, are predicted to be even more sensitive to climate change than their temperate counterparts (Deutsch et al. 2008). To make matters worse, climatic shifts are predicted to be greater in the Andes than in the lowlands (Bradley et al. 2006). Upslope shifts are more likely than poleward shifts in the tropics due to the shallow latitudinal temperature gradient (Colwell et al. 2008).

Available evidence, almost all of which comes from the best studied insect taxon, butterflies, suggests that climate change has already strongly altered insect species distributions, causing range retractions and extinctions (Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2006). In Britain, rising temperatures are causing butterflies and other taxa to move poleward and upward (Hickling et al. 2006). Species extinctions in the mountains are primarily expected to occur due to the loss of high elevation species that have nowhere to move upwards (mountaintop extinctions) and due to the local loss of species from the lower portion of their elevational range (Wilson et al. 2007), although several other climate driven threats also exist (see Larsen et al., Chapter 3, and Aguirre et al., Chapter 4, this volume).

Butterfly communities in Spain have shifted uphill by an average of 293 m between 1967-1973 and 2004-2005 (Wilson et al. 2007). Moth species on a Bornean mountain have shifted upwards by an average of 67 m from 1965 to 2007, providing some of the first evidence of a range shift for tropical montane insects (Chen et al. 2009). Tropical ectotherms are responding to changes in climate because they exhibit a narrow range of physiological tolerance and live at or near their thermal optimum (Deutsch et al. 2008). Anecdotal evidence suggests that two scarab species in the Ecuadorian Andes may have shifted upwards with changing temperature (Onore and Bartolozzi 2008), but this is largely conjecture, and we are not aware of any data regarding Andean insects and climate change.

Climate change and habitat loss act simultaneously and sometimes synergistically to impact insect biodiversity (Franco et al. 2006). Butterflies are shifting their habitat associations (Davies et al. 2006) and generalist species appear to adapt more quickly than specialists to climate change by moving into newly suitable areas (Warren et al. 2001; Menendez et al. 2006). This suggests that the high percentage of habitat specialists that occur in the tropics will be especially susceptible to climate change. For example, rising temperatures are making tropical forest ectotherms (in this case, lizards) susceptible to invasion by open area species (Huey et al. 2009).

Habitat loss exacerbates the effects of climate change in several ways. It blocks the dispersal and redistribution of species that might otherwise adapt to climate change (Root et al. 2003; Travis 2003). This is especially important along the Andes-Amazon interface where numerous species are expected to be forced upwards to adjust to a changing climate but may depend on intact habitat corridors (Larsen et al., Chapter 3, this volume). However, only a few intact corridors of habitat exist from the lowlands to the treeline or above in the Andes and these lie mostly within a handful of protected areas (Hole et al., Chapter 2, this volume). Establishing new protected areas along altitudinal and precipitation gradients can help maintain escape routes for species responding to climate change. Implementing risk management strategies and promoting adaptive agricultural systems can also help cushion the negative impacts of climate change on Andean ecosystems (IAASTD 2009; see also Hole et al., Chapter 2, this volume).

At a local scale, deforestation makes conditions hotter and drier. Because insects such as dung beetles are physiologically constrained to a narrow range of temperature and humidity and are known to seek wetter and more heavily forested habitats during unusually warm, dry weather (Davis et al. 2000; Duncan and Byrne 2000), increasing temperature and decreasing humidity associated with habitat loss may be augmented by climate change and affect all but the most tolerant species.

Ecological Consequences of Disturbance

Climate change, habitat loss, and other anthropogenic disturbances are causing cascading extinctions by altering species interactions and trophic dynamics (Tylianakis et al. 2008; Brook 2009; Aguirre et al., Chapter 4, this volume). Climate change can disrupt species interactions both spatially and temporally. For example, shifts in the timing of plant phenology may make host plants unavailable to some seasonally active insects (Tylianakis et al. 2008). Naturally co-occurring species such as butterflies and plants may also become spatially mismatched due to unequal shifts in their distribution (Schweiger et al. 2008), especially if ectotherms are impacted more rapidly by climate change than the species they depend on.

A review of the impacts of global change, including climate change, shows that a vast suite of insect species interactions are being affected, including pollination, seed dispersal, decomposition, predation, herbivory and pathogen infection (Tylianakis et al. 2008). The disruption of these processes can have cascading effects throughout the ecosystem, leading to further extinctions and the loss of vital ecosystem services to people (Kremen 2005; Botes et al. 2006). Insect mediated services in the Andes, such as pollination, seed dispersal, and dung burial, may be easily disrupted by habitat loss and changes in temperature and humidity (Kessler and Krömer 2000; Horgan 2005). Because the distribution of insects, including invasive and pest species, is largely regulated by temperature, climate change could have severe economic consequences for agriculture in the Andes and may alter disease dynamics and human health (Etter and van Wyngaarden 2000; Jacobsen 2007; Dangles et al. 2008).

Research and Conservation Priorities

The paucity of research on insects of the tropical Andes and the context of vulnerability outlined above provide a number of priorities that include:

- Inventories of poorly studied insect taxa, especially studies using standardized methods that compare patterns across multiple taxa;
- Long-term monitoring of insect communities, especially along altitudinal gradients and at high elevations where species may be especially vulnerable;
- Identifying priority areas and habitats for conservation within the tropical Andes based on insect diversity, endemism, and threat level;
- Understanding biodiversity patterns from local to regional scales;
- Determining elevational versus latitudinal gradients of diversity and species turnover;
- Identifying regional and elevational context-dependent response of multiple taxa to land use and climate change;
- Implementing alternative land use strategies, with a focus on agroecology, that maximize insect biodiversity conservation;
- Adopting strategies to mitigate impacts of climate change on insects, such as increasing landscape connectivity and habitat protection across altitudinal gradients;
- Determining mechanisms underlying insect response to global change;
- Identifying traits of extinction-prone species (drawing generalizations is particularly important for insects for which not all species can be measured)
- Understanding the synergistic influence of habitat loss and climate change;
- Assessing cascading ecological consequences of climate change and habitat loss for biodiversity (especially due to shifts in trophic dynamics) and for people (loss of ecosystem services such as pollination, pest control and disease regulation);
- Advancing taxonomy, training parataxonomists, and increasing availability of user-friendly species keys (this is especially important for facilitating comparisons among studies that otherwise include many morphospecies).

Acknowledgments

We thank Finbarr Horgan and Gunnar Brehm for valuable comments which improved this manuscript.

Literature Cited

Amat-García, E. C., G. D. Amat-García, and L. G. Henao-M. 2004. Taxonomic and ecologic diversity of mycophagic entomofauna in a high Andean forest of the eastern Colombian mountain range. *Revista de la Academia Colombiana de Ciencias Exactas Fisicas y Naturales* 28:223-231.

Amat-García, G. 1999. The scaraboid-passalid beetles (Coleoptera: Passalidae) of Colombia. 6. Their relationship to the landscape of the Eastern Cordillera of Colombia. *Revista de la Academia Colombiana de Ciencias Exactas Fisicas y Naturales* 23:163-170.

Armbrecht, I., L. Rivera, and I. Perfecto. 2005. Reduced diversity and complexity in the leaf-litter ant assemblage of Colombian coffee plantations. *Conservation Biology* 19:897-907.

Balint, Z., P. Boyer, H. W. Dahners, J. A. Salazar-Escobar, and K. Kertesz. 2006. Comments on the systematics and natural history of *Aveexcrenota*, a genus of rare Andean eumaeine Lycaenidae (Lepidoptera). *Acta Zoologica Academiae Scientiarum Hungaricae* 52:331-352.

Botes, A., M. A. McGeoch, H. G. Robertson, A. van Niekerk, H. P. Davids, and S. L. Chown. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* 33:71-90.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 302:1755-1756.

Brehm, G., and K. Fiedler. 2004. Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest. *Global Ecology and Biogeography* 13:7-14.

Brehm, G., L. M. Pitkin, N. Hilt, and K. Fiedler. 2005. Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography* 32:1621-1627.

Brehm, G., D. Süssenbach, and K. Fiedler. 2003. Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography* 26:456-466.

Brook, B. W. 2009. Global warming tugs at trophic interactions. *Journal of Animal Ecology* 78:1-3.

Brown, K. S. 1991. Conservation of Neotropical environments: insects as indicators. Pp. 349-404 in *The conservation of insects and their habitats*, edited by N. M. Collins and J. A. Thomas. London: Academic Press.

Bustos-H., J., and P. Ulloa-Chacon. 1996. Myrmecofauna and perturbation in a Neotropical cloud forest (Reserva Natural Hato Viejo, Valle del Cauca, Colombia). *Revista de Biologia Tropical* 44-45:259-266.

Cadena, C. D. 2007. Testing the role of interspecific competition in the evolutionary origin of elevational zonation: an example with *Buarremon* brush-finches (Aves, Emberizinae) in the Neotropical mountains. *Evolution* 61:1120-1136.

Celi, J., E. Terneus, J. Torres, and M. Ortega. 2004. Dung beetles (Coleoptera: Scarabaeinae) diversity in an altitudinal gradient in the Cutucu Range, Morona Santiago, Ecuadorian Amazon. *Lyonia* 7:37-52.

Chalumeau, F., and B. Brochier. 2007. *Chiasognathinae of the Andes: taxonomy, ethology, biogeography.* Hradec Králové: Taita Publisher.

Chen, I. C., H. J. Shiu, S. Benedick, J. D. Holloway, V. K. Cheye, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America* 106:1479-1483.

Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261.

Cook, J. 2002. A revision of the Neotropical genus *Cryptocanthon* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopterists Bulletin* 56:3-96.

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* 18:1795-1809.

Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* 75:247-256.

Davis, A. L. V., S. L. Chown, M. A. McGeoch, and C. H. Scholtz. 2000. A comparative analysis of metabolic rate in six *Scarabaeus* species (Coleoptera: Scarabaeidae) from southern Africa: further caveats when inferring adaptation. *Journal of Insect Physiology* 46:553-562.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105:6668-6672.

DeVries, P. J., T. R. Walla, and H. F. Greeney. 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society* 68:333-353.

Dourojeanni, M. J. 1990. Entomology and biodiversity conservation in Latin America. *American Entomologist* 36:88-93.

Duncan, F. D., and M. J. Byrne. 2000. Discontinuous gas exchange in dung beetles: patterns and ecological implications. *Oecologia* 122:452-458.

Dyer, L. A., M. S. Singer, J. T. Lill, J. O. Stireman, G. L. Gentry, R. J. Marquis, R. E. Ricklefs, H. F. Greeney, D. L. Wagner, H. C. Morais, I. R. Diniz, T. A. Kursar, and P. D. Coley. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448:696-699.

Erwin, T. L. 1982. Tropical forests their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36:74-75.

Escobar, F. 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Tropical Zoology* 17:123-136.

Escobar, F., and P. C. de Ulloa. 2000. Space and time distribution along a succesional gradient of coprofagous coleopterans (Scarabaeinae, Aphodiinae) in a tropical montane forest, Nariño Colombia. *Revista de Biologia Tropical* 48:961-975.

Escobar, F., G. Halffter, and L. Arellano. 2007. From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. *Ecography* 30:193-208.

Escobar, F., J. M. Lobo, and G. Halffter. 2005. Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes. *Global Ecology and Biogeography* 14:327-337.

Etter, A., C. McAlpine, K. Wilson, S. Phinn, and H. Possingham. 2006. Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture Ecosystems and Environment* 114:369-386.

Etter, A., and W. van Wyngaarden. 2000. Patterns of landscape transformation in Colombia, with emphasis in the Andean region. *Ambio* 29:432-439.

Fandiño-Lozano, M., and W. van Wyngaarden. 2005. *Prioridades de conservación biológica para Colombia*. Bogotá: Grupo ARCO. 188 pp.

Fossati, O., J. G. Wasson, C. Hery, G. Salinas, and R. Marin. 2001. Impact of sediment releases on water chemistry and macroinvertebrate communities in clear water Andean streams (Bolivia). *Archiv für Hydrobiologie* 151:33-50.

Franco, A. M. A., J. K. Hill, C. Kitschke, Y. C. Collingham, D. B. Roy, R. Fox, B. Huntley, and C. D. Thomas. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* 12:1545-1553.

González, V. H., and M. S. Engel. 2004. The tropical Andean bee fauna (Insecta: Hymenoptera: Apoidea), with examples from Colombia. *Entomologische Abhandlungen (Dresden)* 62:65-75.

Guevara Cardona, G., G. Reinoso Florez, and F. Villa Navarro. 2007. Caddisfly larvae (Insecta: Trichoptera) of the Coello River basin in central Colombia. *Trichopteron* 24:8-12.

Hall, J. P. W. 2005. Montane speciation patterns in *Ithomiola* butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? *Proceedings of the Royal Society of London B, Biological Sciences* 272:2457-2466.

Hamel-Leigue, A. C., S. K. Herzog, and D. J. Mann. 2008). Composition and species richness of a dung beetle (Coleoptera: Scarabaeinae) community in the lower Yungas of Cordillera Mosetenes, Bolivia. *Revista Boliviana de Ecologia y Conservacion Ambiental* 23:39-49.

Hernández-Camacho, J., R. Ortiz-Quijano, T. Walschburger, and A. Hurtado-Guerra. 1992. Estado de la biodiversidad en Colombia. Pp. 41-238 in *La diversidad biológica en Iberoamérica I*, edited by G. Halffter. Xalapa: Instituto de Ecología, A.C.

Herzog, S. K., S. R. Ewing, K. L. Evans, A. Maccormick, T. Valqui, R. Bryce, M. Kessler, and R. MacLeod. 2009. Vocalizations, distribution, and ecology of the Cloud-forest Screech-Owl (*Megascops marshalli*). *Wilson Journal of Ornithology* 121:240-252.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12:450-455.

Hilt, N., G. Brehm, and K. Fiedler. 2006. Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes. *Journal of Tropical Ecology* 22:155-166.

Hilt, N., G. Brehm, and K. Fiedler. 2007. Temporal dynamics of rich moth ensembles in the montane forest zone in southern Ecuador. *Biotropica* 39:94-104.

Hilt, N., and K. Fiedler. 2005. Diversity and composition of Arctiidae moth ensembles along a successional gradient in the Ecuadorian Andes. *Diversity and Distributions* 11:387-398.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489-513.

Hooghiemstra, H., V. M. Wijninga, and A. M. Cleef. 2006. The paleobotanical record of Colombia: implications for biogeography and biodiversity. *Annals of the Missouri Botanical Garden* 93:297-324.

Horgan, F. G. 2005. Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slopes of the Peruvian Andes. *Forest Ecology and Management* 216:117-133.

Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. A. Perez, and T. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B, Biological Sciences* 276:1939-1948.

IAASTD. 2009. *Agriculture at a crossroads. International assessment of agricultural knowledge, science and technology for development: Latin America and the Caribbean (LAC) report*. Washington, DC: Island Press.

Jacobsen, D. 2003. Altitudinal changes in diversity of macroinvertebrates from small streams in the Ecuadorian Andes. *Archiv für Hydrobiologie* 158:145-167.

Jacobsen, D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* 49:1293-1305.

Jacobsen, D. 2007. Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* 154:795-807.

Jacobsen, D., and A. Encalada. 1998. The macroinvertebrate fauna of Ecuadorian highland streams in the wet and dry season. *Archiv für Hydrobiologie* 142:53-70.

Jacobsen, D., and R. Marin. 2008. Bolivian Altiplano streams with low richness of macroinvertebrates and large diel fluctuations in temperature and dissolved oxygen. *Aquatic Ecology* 42:643-656.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233-249.

Jiménez, E., F. H. Lozano-Zambrano, J. Rodríguez, and D. P. Ramírez. 2007. Conservación de hormigas cazadoras: rareza y endemismo. Pp. 407-421 in *Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia*, edited by F. H. Lozano-Zambrano and E. Jiménez. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography* 31:1829-1839.

Kessler, M., and T. Krömer. 2000. Patterns and ecological correlates of pollination modes among bromeliad communities of Andean forests in Bolivia. *Plant Biology* 2:659-669.

Körner, C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* 22:569-574.

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters* 8:468-479.

Lamas, G. 1999. Perú: país de mariposas. *Rumbos* 14:6. Available at: http://www.rumbosonline.com/articles/14-06-specialbutterfly.htm.

Larsen, T. H. 2004. Dung beetles / escarabajos peloteros. Pp. 77-84, 185-192 in *Peru: Megantoni. Rapid Biological Inventories Report*, edited by C. Vriesendorp, L. Rivera Chavez, D. Moskovits, and J. Shopland. Chicago: The Field Museum.

Larsen, T. H., A. Lopera, and A. Forsyth. 2006. Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopterists Bulletin* 60:315-324.

Le Pont, F., J. Mouchet, and P. Desjeuz. 1990. Geographical and ecological distribution of anthropophilic sandflies (Diptera: Psychodidae) in Bolivia on a transect Andes-Amazonia. *Annales de la Societe Entomologique de France* 26:159-172.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters* 12:550-560.

McCoy, E. D. 1990. The distribution of insects along elevational gradients. *Oikos* 58:313-322.

Medina, C. A., F. Escobar, and G. H. Kattan. 2002. Diversity and habitat use of dung beetles in a restored Andean landscape. *Biotropica* 34:181-187.

Menéndez, R. 2007. How are insects responding to global warming? *Tijdschrift voor Entomologie* 150:355-365.

Menéndez, R., A. G. Megias, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B. Roy, and C. D. Thomas. 2006. Species richness changes lag behind climate change. *Proceedings of the Royal Society of London B, Biological Sciences* 273:1465-1470.

Molau, U. 2004. Mountain biodiversity patterns at low and high latitudes. *Ambio* 13:24-28.

Moret, P. 2005. The carabid beetles of the paramo ecosystem in the Andes of Ecuador: taxonomy, ecology and biogeograpy (Insecta, Coleoptera, Carabidae). Quito: Pontificia Universidad Católica del Ecuador. 306 pp.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, and K. Vulinec. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation* 137:1-19.

Ochoa, J. A. 2005. Distribution patterns of scorpions of the Andean region of southern Peru. *Revista Peruana de Biologia* 12:49-68.

Odegaard, F. 2000. How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society* 71:583-597.

Onore, G., and L. Bartolozzi. 2008. Description of the larvae of *Sphaenognathus (Chiasognathinus) gaujoni* (Oberthur, 1885) and *S. (C.) xerophilus* Bartolozzi, and Onore, 2006 (Coleoptera: Lucanidae), with observations about their altitudinal range extension. *Memoirs on Biodiversity* 1:399-406.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

Pearson, D. L., and S. S. Carroll. 2001. Predicting patterns of tiger beetle (Coleoptera: Cicindelidae) species richness in northwestern South America. *Studies on Neotropical Fauna and Environment* 36:25-136.

Perfecto, I. 2003. Conservation biology and agroecology: de un pájaro las dos alas. *Endangered Species Update* 20:133-145.

Perfecto I., and J. Vandermeer. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. *Oecologia* 108:577-582.

Philpott, S. M., W. J. Arendt, I. Armbrecht, P. Bichier, T. V. Dietsch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams-Linera, J. Valenzuela, and J. M. Zolotoff. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conservation Biology* 22:1093-1105.

Price, D. L. 2009. Phylogeny and biogeography of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae). *Systematic Entomology* 34:137-150.

Pyrcz, T. W. 2004. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus (Wroclaw)* 15:455-622.

Quinteros, R., L. A. Paz-Soldan, C. F. Pinto, L. F. Aguirre, O. Ruiz, and D. Tacachiri. 2006. Influence of human activities on butterfly communities of *Polylepis besseri* forests of Cochabamba - Bolivia. *Revista Boliviana de Ecologia y Conservacion Ambiental* 20:43-64.

Rahbek, C. 1995. The elevational gradient of species richness – a uniform pattern? *Ecography* 18:200-205.

Rivera, L. F., M. Botero Gomez, S. Escobar Ramirez, and I. Armbrecht. 2008. Diversidad de hormigas en sistemas ganaderos. Pp. 227-244 in *Ganadería del futuro: investigación para el desarrollo*, edited by E. Murgueitio, C. Cuartas, and J. Naranjo. Cali: Fundación CIPAV.

Robbins, R. K., and R. C. Busby. 2008. Phylogeny, taxonomy, and sympatry of *Timaeta* (Lycaenidae: Theclinae: Eumaeini): an Andean montane forest endemic. *Tijdschrift voor Entomologie* 151:205-233.

Rodríguez, L. O. 1996. *Diversidad biológica del Peru: zonas prioritarias para su conservación*. Lima: Proyecto FANPE GTZ-INRENA. 191 pp.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57-60.

Samways, M. J. 2005. *Insect diversity conservation*. Cambridge: Cambridge University Press.

Sanabria, C., I. Ambrecht, and C. Gutierrez-Chacon. 2008. Staphylinid diversity (Coleoptera: Staphylinidae) in five productive systems in the Colombian Andes. *Revista Colombiana de Entomologia* 34:217-223.

Schroth, G., G. A. Fonseca, C. A. Harvey, C. Gascon, H. L. Vasconcelos, and A. M. N. Izac. 2004. *Agroforestry and biodiversity conservation in tropical landscapes*. Washington, DC: Island Press.

Schrumpf, M., G. Guggenberger, C. Valarezo, and W. Zech. 2001. Tropical montane forest soils, development and nutrient status along an altitudinal gradient in the South Ecuadorian Andes. *Die Erde* 132:43-59.

Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kuhn. 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89:3472-3479.

Sites, R. W., M. R. Willig, and M. J. Linit. 2003. Macroecology of aquatic insects: a quantitative analysis of taxonomic richness and composition in the Andes mountains of northern Ecuador. *Biotropica* 35:226-239.

Spector, S. 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *Coleopterists Bulletin* 60:71-83.

Terborgh, J. 1977. Bird species-diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.

Terborgh, J. W., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562-576.

Thomas, C. D., A. M. A. Franco, and J. K. Hill. 2006. Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution* 21:415-416.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B, Biological Sciences* 270:467-473.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363.

Van Damme, P. A., C. Hamel, A. Ayala, and L. Bervoets. 2008. Macroinvertebrate community response to acid mine drainage in rivers of the high Andes (Bolivia). *Environmental Pollution* 156:1061-1068.

van der Hammen, T., and P. S. Ward. 2005. Ants from the Ecoandes expedition: diversity and distribution. *Studies on Tropical Andean Ecosystems* 6:239-248.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss, and C. D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65-69.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273-309.

Wilson, R. J., D. Gutierrez, J. Gutierrez, and V. J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* 13:1873-1887.

Wolda, H. 1987. Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* 30:313-323.

Wolda, H. 1988. Insect seasonality: why? *Annual Review of Ecology and Systematics* 19:1-18.

18

Patterns of Diversity and Endemism in the Birds of the Tropical Andes

Sebastian K. Herzog and Gustavo H. Kattan

Well over 2000 bird species, ca. 22% of all known species, inhabit the Andes of Colombia, Ecuador, Peru, and Bolivia from foothills (500 m) to snowline. Almost 600 (28%) of them occur nowhere else on Earth. The northern portion of the tropical Andes, extending from the Huancabamba depression in Peru to the Cordillera de Mérida of Venezuela, holds approximately the same number of bird species as the Amazon basin even though its surface area is 14 times smaller (Kattan et al. 2004). At a continental scale, bird species richness correlates with topographical complexity and ecosystem diversity, which are highest in the Andes. Species richness in 1°×1° latitude-longitude quadrats is 30-250% higher in the Andes (peaking at 850 species) than in the Amazon basin (Rahbek and Graves 2001). The tropical Andes are geologically young: Andean cloud forests are estimated to have evolved during the last 20 million years (Sempere et al. 2005), and the region's rich avifauna is undergoing active radiation and speciation since the Miocene (Fjeldså and Rahbek 1997). Therefore, large-scale human impacts such as landscape transformation and climate change are not only a threat to the diversity and uniqueness of the region's avifauna, but also to the evolutionary processes that have generated and maintain this diversity.

Higher-taxon richness in the tropical Andes is exceptional as well. Of the 28 orders and 96 families currently recognized as native to South America (Remsen et al. 2009), 25 orders (89%) and 75 families (78%) occur in the Andes. When excluding three orders and nine families of seabirds, representation increases to 100% and 86%, respectively. A recent taxonomic reference on the birds of the world (Dickinson 2003) recognized 194 families, 36% of which are found in the tropical Andes.

Of the global total of 218 Endemic Bird Areas (EBAs; Stattersfield et al. 1998, BirdLife International 2003), 47 (22%) are situated in continental South America, and 24 of these (51%) are partially or entirely located in the tropical Andes from Bolivia to the Cordillera de Mérida of Venezuela. A total of 355 restricted-range species (whose breeding ranges do not exceed 50,000 km^2) distributed in 43 families (45% of all South American families) occur in the tropical Andes (366 species when including the Cordillera de Mérida) (Table 18.1), corresponding to 62 % (64%) of all restricted-range species in continental South America (http://www.birdlife.org/datazone/). The prevalence of restricted-range species is a widespread phenomenon in montane areas of the northern Neotropics (Renjifo et al. 1997). In addition to high levels of endemism, montane avifaunas are also unique in terms of ecological roles, as evidenced by the richness of nectarivorous birds and bird-pollinated plants (Renjifo et al. 1997, Krömer et al. 2006).

Table 18.1. Distribution by family of 366 restricted-range species (species whose breeding ranges do not exceed 50,000 km^2) in the tropical Andes compared to the total number of species per family in continental South America, all islands within 1200 km of its shores in the Atlantic and Pacific oceans, and several islands in the Carribbean Sea (see Remsen et al. 2009). Eleven restricted-range species endemic to the Cordillera de Mérida in Venezuela are included.

Family	**No. of restricted-range species tropical Andes**	**Total no. of species South America**	**Percent restricted-range species**
Trochilidae (Hummingbirds)	57	254	22.4
Furnariidae (Ovenbirds)	43	283	15.2
Thraupidae (Tanagers)	38	195	19.5
Emberizidae (Sparrows)	33	162	20.4
Grallariidae (Antpittas)	25	49	51.0
Tyrannidae (Tyrant flycatchers)	25	348	7.2
Rhinocryptidae (Tapaculos)	20	53	37.7
Psittacidae (Parrots)	19	126	15.1
Cotingidae (Cotingas)	9	58	15.5
Thamnophilidae (Antbirds)	9	217	4.1
Cracidae (Guans)	8	43	18.6
Troglodytidae (Wrens)	8	47	17.0
Strigidae (Owls)	7	43	16.3
Parulidae (New World wood-warblers)	6	36	16.7
Odontophoridae (Wood-quail)	5	14	35.7
Picidae (Woodpeckers)	5	82	6.1
Turdidae (Thrushes)	4	32	12.5
Tinamidae (Tinamous)	4	45	8.9
Rallidae (Rails)	4	46	8.7
Ramphastidae (Toucans)	3	33	9.1
Fringillidae (Finches)	3	34	8.8
Columbidae (Pigeons and doves)	3	48	6.3
Podicipedidae (Grebes)	2	9	22.2
Capitonidae (Barbets)	2	14	14.3
Vireonidae (Vireos)	2	24	8.3
Pipridae (Manakins)	2	47	4.3
Accipitridae (Hawks)	2	54	3.7
Icteridae (New World blackbirds)	2	60	3.3
Semnornithidae (Toucan-barbet)	1	1	100.0
Cinclidae (Dippers)	1	2	50.0
Melanopareiidae (Crescentchests)	1	4	25.0
Nyctibiidae (Potoos)	1	6	16.7
Formicariidae (Antthrushes)	1	11	9.1
Corvidae (Jays)	1	15	6.7
Trogonidae (Trogons)	1	17	5.9
Galbulidae (Jacamars)	1	18	5.6
Cuculidae (Cuckoos)	1	21	4.8
Cardinalidae (Cardinal grosbeaks)	1	22	4.5
Apodidae (Swifts)	1	23	4.3
Falconidae (Falcons)	1	24	4.2
Tityridae (Tityras)	1	26	3.8
Caprimulgidae (Nightjars)	1	30	3.3
Bucconidae (Puffbirds)	1	35	2.9
Incertae Sedis*	1	—	—

* Species whose familial affinities are uncertain.

Birds are probably the best known group of organisms with respect to their taxonomy, natural history, biogeography, ecology, and conservation. Numerous studies have analyzed diversity patterns of tropical Andean birds at local and regional scales, but no comprehensive review of geographic patterns of species richness and endemism in tropical Andean birds has been published to date. In this chapter we synthesize current knowledge on such patterns in the region and briefly present the most prominent hypotheses on causal factors that underlie the most important patterns. Finally, we point out major knowledge gaps that need to be addressed by future studies. We use the terms 'species diversity' and 'species richness' interchangeably for the number of species present in a given unit of area. Analyses of restricted-range species are based on information extracted from BirdLife International's 2009 species factsheets (http://www.birdlife.org/datazone/).

Species Richness and Spatial Differentiation Patterns

Species diversity can be partitioned into three components that are defined at different spatial scales (Schluter and Ricklefs 1993). Alpha diversity refers to the number of species in a sample or locality (also termed within-habitat diversity), whereas beta diversity is the spatial turnover in species composition between samples or localities (also termed between-habitat diversity). Gamma diversity is the total species diversity in all samples or in a given region or landscape. The exceptional bird species richness of the tropical Andes is a reflection of high beta diversity or spatial turnover in species composition at all spatial scales (local to regional). Although alpha diversities are relatively low in the tropical Andes when compared to the Amazon basin (see below), beta and gamma diversities are extraordinarily high (Fjeldså 1994, Stotz 1998, Rahbek and Graves 2001, Kattan et al. 2004, McKnight et al. 2007, Melo et al. 2009): as one moves farther from a point of origin, species composition in the tropical Andes changes much faster than it does in the Amazon basin.

Observed patterns of species richness vary with the spatial scale or resolution (e.g., local plots *versus* 1°×1° latitude-longitude grids) of the analysis (Rahbek and Graves 2000) and the spatial extent examined (e.g., partial *versus* complete elevational gradients; McCain 2005, 2009). Methodological approaches to studying patterns of species richness also vary from local field-based studies (e.g., Kessler et al. 2001) to regional meta-data analyses (e.g., Kattan and Franco 2004, Herzog et al. 2005b) to continent-wide grid-based analyses using inter- and extrapolation of species occurrence data from a wide range of primary sources (e.g., Rahbek and Graves 2000, 2001). These different methodologies may produce contrasting results because they rely on different assumptions and have different biases.

Habitat Patterns

In general, bird species richness correlates positively with habitat complexity and rainfall. Humid forested sites at 1800 m in the Colombian Andes harbor >130 species (Kattan et al. 1994, Naranjo 1994), whereas anthropogenic pasturelands at the same elevation have <80 species (Munves 1975). Humid (evergreen) forests, in turn, tend to hold more species per unit area than seasonally dry forests. For example, Schmitt et al. (1997) reported 50 breeding species at 1500 m in an arid valley in the Bolivian Andes, whereas at least twice as many species occur at the same elevation in humid montane forest at similar latitudes (Herzog et al. 2005a). In very wet rainforest on the Pacific slope of Colombia at 1000 m, 271 species have been recorded in 80 ha (Hilty 1997). In some cases, however, excessive precipitation may lead to a reduction in bird species richness (Herzog 2008).

Anthropogenically disturbed or degraded Andean forests are often characterized by lower bird diversity than ecologically equivalent undisturbed forests nearby (Aben et al. 2008). Andean forest bird communities are similarly affected by habitat fragmentation, which has reduced species richness by 30% in two Colombian cloud forests (Kattan et al. 1994, Renjifo 1999). Well matured secondary forest, on the other hand, may harbor greater bird species richness than comparable primary forest (O'Dea and Whittaker 2007), and early to mid-successional forest stages may be species-poor but contain unique species (G.H. Kattan, unpubl. data).

Elevational Patterns at Local Scales

Current knowledge on elevational patterns of tropical Andean bird diversity at local scales is largely derived from a surprisingly small number of empirical studies, particularly from the east Andean slope in Peru and Bolivia (Terborgh 1977, Graham 1990, Patterson et al. 1998, Kessler et al. 2001, Herzog et al. 2005a). Along complete humid forest transects that extend from foothills and adjacent Amazonian lowlands up to the current closed timberline or to the treeline, species richness tends to decrease steadily and linearly with elevation (Terborgh 1977, Patterson et al. 1998). Herzog et al. (2005a) found some deviations from this pattern in the wet Yungas of Cochabamba, Bolivia, where bird diversity peaks around 1000 m and remains fairly constant from about 1800 m to timberline. However, elevation (as a proxy for temperature and ecosystem productivity) is the best single-predictor variable of species richness. The Amazonian *terra firme* forest avifauna in this region is poor due to its semi-isolation at the southwestern terminus of humid lowland forest (Herzog et al. 2005a), which explains the upslope shift of the diversity peak.

In contrast to slopes comprised entirely of humid forest, a peak in bird diversity at some mid-elevation point appears to be the general rule for rain-shadowed inter-Andean valleys (Naranjo 1994, Stiles and Bohórquez 2000, Kessler et al. 2001). These often very steep valleys are truncated at their lower elevational end and characterized by seasonally dry forest on lower slopes, fairly dry evergreen forest on upper slopes, and semi-deciduous forest in the transition between the two. In two such valleys in Bolivia, the location of the bird diversity peak varies between about 2500 m and 3000 m according to local ecoclimatic conditions (Kessler et al. 2001). A hump-shaped relationship between species richness and elevation is also apparent when considering only seasonally dry forest in Bolivia, with maximum species richness at about 1000-1200 m (based on data in Herzog and Kessler 2006).

Bird diversity patterns on the much drier western slope of the central Andes are even more poorly known. In southwest Peru, an extensive mid-elevation section may be so arid that it holds no resident breeding bird species at all, and species richness (and abundance) peaks at an exceptionally high elevation of about 3500 m (Pearson and Pearson Ralph 1978).

Despite these contrasting elevational patterns of bird diversity, the main causes for them are the same. In a global meta analysis of elevational transects McCain (2009) found strong support for current climatic conditions as the main driver of bird diversity. Temperature in combination with water availability were particularly important factors (McCain 2009), resulting in gradients of increasing bird diversity from elevations with cold and dry to those with warm and humid conditions.

Elevational Patterns at Larger Spatial Scales

We know only two studies that examined elevational diversity patterns at regional to continental scales (Rahbek 1997, Kattan and Franco 2004). Both take into account the effect that area has on species richness: an increase in species richness with increasing area is one of the fundamental rules in ecology (Lawton 1999). Because the area of elevational bands decreases strongly as one ascends from Amazonian or Pacific lowlands to páramo or puna, comparisons of regional species richness at different elevations should account for this effect. After controlling for area, Rahbek (1997) found that species richness of South American land birds peaks in the upper foothills around 1000 m, decreasing by about 14% in the lowlands and by about 86% above treeline (4500 m). However, when restricting his analysis to the four tropical Andean countries considered here, species richness remained essentially constant from lowlands up to 1500 m, forming a low-elevation plateau rather than a mid-elevation hump, from where it decreased significantly towards the treeline (see Figure 2C in Rahbek 1997).

Kattan and Franco (2004) examined elevational diversity patterns for eight regions in the Colombian Andes and peripheral mountain ranges. Without controlling for area, species richness decreases linearly with elevation on external slopes that are directly connected to adjacent lowlands, whereas internal Andean slopes where characterized by a slightly hump-shaped relationship between species richness and elevation, with diversity peaks between 1000 m and 2000 m. After controlling for area, a different pattern emerged: similar to the results of Rahbek (1997), species richness remained essentially constant from lowlands up to 2600 m, forming a low- to mid-elevation plateau, from where it decreased significantly towards the treeline.

Latitudinal Patterns

Although the latitudinal gradient of species richness is ecology's longest recognized and one of its best documented diversity patterns (Rohde 1992, Rosenzweig 1995, Willig et al. 2003), latitudinal patterns in avian diversity have largely been neglected in the tropical Andes. We know only four publications that specifically address the topic, three of which examined a rather limited latitudinal gradient (370-530 km). Poulsen and Krabbe (1997, 1998) found essentially constant species richness (alpha diversity) along two trans-equator transects in cloud forest (3000-3350 m) on the east and west Andean slope in Ecuador. Herzog (2008) compared three localities in lower Bolivian Yungas forest (1150-1600 m), finding almost identical species richness at two sites and 28% lower richness at the third, which may be attributable to variations in habitat characteristics and precipitation levels. However, all studies reported considerable turnover in species composition (beta diversity) and community structure despite the limited extension of the gradients. At a much smaller scale, Kattan et al. (2006) found significant turnover in species composition among localities at the same elevation in neighboring watersheds in the Colombian Andes.

Comparisons of alpha-diversity values from more extensive latitudinal gradients are problematic because of differences in survey methods, effort, area, and elevational range employed by different studies. For example, the almost 50 species recorded by Remsen (1985) in a Bolivian cloud forest (3300 m) are not comparable to the 83-92 species in five east Andean cloud forests of Ecuador (Poulsen and Krabbe 1997) for all of the above reasons. However, a survey from another Bolivian cloud forest area (Herzog et al. 2005a) is much more comparable to those of Poulsen and Krabbe (1997). In the same elevational range (3000-3350 m), 76 species were recorded in Bolivia in approximately half the area and with twice the survey effort, a value similar to the species richness found by Poulsen and Krabbe (1997) in five west Andean sites in Ecuador (65-80 species), but lower than alpha diversity in east Andean cloud forests of Ecuador. Whether this reflects a true latitudinal signal of decreasing alpha diversity with increasing latitude can not be ascertained without further field studies.

Fjeldså et al. (1999: figure 2) did not find a latitudinal pattern of gamma diversity for high-Andean birds that have breeding populations above 2500 m. An updated version of figure 2 in Fjeldså et al. (1999) is shown in Figure 18.1. Species richness in 15’×15’ latitude-longitude grid cells is highest on the east Andean slope from northern Ecuador to central Bolivia, where it decreases sharply south of 18°S, with three marked peaks: in Ecuador just south of the equator (southeast of Quito, 265 species), in northern Peru in the Tabaconas Namballe area just south of the Ecuadorian border (257), and in central Bolivia in Carrasco National Park (253). On the west Andean slope gamma diversity is highest around the equator.

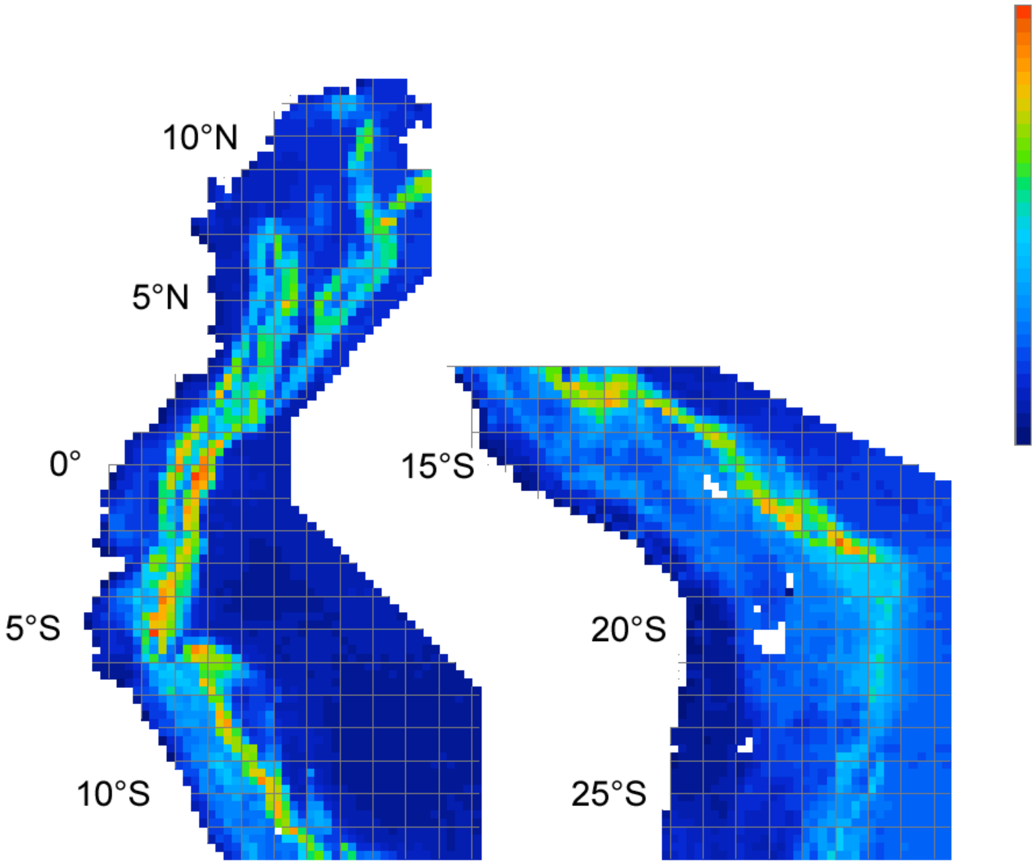

Figure 18.1. Species richness in 15’×15’ latitude-longitude grid cells of high-Andean birds that have breeding populations above 2500 m. Red color indicates maximum species richness (265 species just south of the equator). Figure provided by J. Fjeldså in November 2009 (data derived from the distributional data base of the Zoological Museum, University of Copenhagen).

Environmental Drivers of Gamma Diversity Patterns

As for the elevational distribution of bird species richness (McCain 2009), gamma diversity (1°×1° latitude-longitude grid cells) patterns in South American birds are largely explained by contemporary climate, particularly precipitation and energy availability (Rahbek and Graves 2001, Rahbek et al. 2007, although surface area (Rosenzweig 1995), regional and evolutionary history (Ricklefs 2004), as well as interactions between climate and evolutionary history (Rahbek and Graves 2001) can also play a role. It has become clear only recently, however, that the overriding influence of climate is not homogeneous for all groups of species. Rahbek et al. (2007) found that water and energy availability only explain diversity patterns of species with the largest geographical ranges, but not of species with small to moderately large ranges. Because widespread species contribute the largest number of data points they mask patterns of species with small ranges, which contribute little to the overall data. Richness patterns of narrowly distributed species appear to be influenced by topographic complexity and ecosystem diversity (Rahbek et al. 2007).

Endemism: Concepts and Patterns

The concept of endemism has been used in different ways in the biogeographic and conservation literature, but it generally refers to species whose geographic ranges are restricted in their spatial extent. Species with comparatively small ranges constitute an important component of biodiversity and its conservation because they are inherently vulnerable to habitat transformation and climate change. The term endemism has been applied to *political endemics*, i.e., species whose ranges are confined within the borders of a given country (or *near-endemics* when most of a species's range is confined to one country). The term has also been used to refer to species restricted to a biogeographic region such as the Andes. Stotz et al. (1996) divided the Neotropics into zoogeographic regions (dividing the tropical Andes into 'Northern Andes' and 'Central Andes'), and bird species found in only one such region were considered *zoogeographic endemics*. Young et al. (2009) similarly used the term to refer to 115 species restricted to the southwest Amazon watershed of eastern Peru and northern Bolivia.

Endemics are also defined as *restricted-range species* whose global breeding distributions do not exceed 50,000 km^2 (Stattersfield et al. 1998). Stattersfield et al. (1998) further identified Endemic Bird Areas (EBAs) that encompass the overlapping breeding ranges of at least two restricted-range species. A similar approach to defining areas of endemism in South America, albeit without a range size threshold, was used by Cracraft (1985), who identified 33 areas of bird endemism, including six in the Andes. However, knowledge about the distribution and species-level taxonomy of Neotropical birds has improved so much over the past 25 years that we will not discuss Cracraft's areas of endemism further.

In macroecological studies endemism is often expressed by two different quantitative measures. First, the lower *range-size quartile* of a species assemblage (the 25% of species with the smallest global ranges; Gaston 1994) is considered to be 'endemic', and the spatial distribution in the number of these 'endemic' species is examined. Second, a *range-size rarity* index is calculated as the mean inverse range size of all species combined in a given unit of analysis (Williams and Humphries 1994, Fjeldså et al. 1999), which represents a metric for the community or species pool as a whole.

Large-Scale Patterns of Endemism

Avian endemism in the tropical Andes is higher than anywhere else in continental South America as almost two thirds of the continent's restricted-range species occur in the tropical Andes. The Northern and Central Andes as defined by Stotz et al. (1996) each hold higher numbers of zoogeographic endemics (around 220 species each) than any other Neotropical zoogeographic region. This is partly a result of the peculiar shape of the distributional ranges of many Andean birds. These ranges, which extend along narrow elevational belts over fairly wide latitudinal gradients, favor population isolation and speciation processes (Graves 1985, 1988; Brumfield and Remsen 1996; Johnson 2002).

It can be argued that almost the entire tropical Andes constitute one large area of endemism. Latitudinally, areas of high endemism, as determined by an analysis of the number of lower range-size quartile species in 15'×15' latitude-longitude grid cells, are distributed fairly continuously and evenly from the Sierra Nevada de Santa Marta in northern Colombia south to central Bolivia (figure 4 in Fjeldså and Irestedt 2009; see also figure 1B in Fjeldså et al. 2005). Seven larger areas of peak endemism in the tropical Andes can be identified based on Fjeldså and Irestedt (2009), which overlap to varying degrees with 12 of the 24 EBAs found in the tropical Andes (Table 18.2). The other 12 EBAs cover much of the remaining area of the tropical Andes, the major exception being the Altiplano of Bolivia and southern Peru, which has very low levels of endemism. The top EBAs with the highest numbers of restricted-range species are: (1) Chocó in western Colombia and west-central Ecuador (EBA 041, 49 Andean restricted-range species); (2) Colombian East Andes (EBA 038, 34 restricted-range species); (3) Tumbesian region in western Ecuador and northwest Peru (EBA 045, 30 Andean restricted-range species). These are followed by the Santa Marta Mountains, Cordillera de Mérida, Peruvian high Andes, Colombian inter-Andean slopes, and North-east Peruvian cordilleras, each harboring 20-22 restricted-range species.

Young et al. (2009) identified three areas of endemism in the southwest Amazon watershed of eastern Peru and northern Bolivia, all of them in the Andes: southern Huánuco and central Cusco in Peru and the upper Yungas of northern Bolivia. They coincide at least partly with four Andean EBAs (North-east Peruvian cordilleras, Peruvian East Andean foothills, Bolivian and Peruvian lower Yungas, Bolivian and Peruvian upper Yungas), but due to the fine resolution of their study, Young et al. (2009) were able to identify which portions of a particular EBA likely harbor the largest number of endemic species. In addition, parts of the two Peruvian areas of endemism do not overlap with any EBA, including most of the Southern Huánuco area. In the central Cusco area of endemism, the southwestern Cordillera de Vilcabamba and the region along the Río Mapacho-Yavero east of Cusco do not coincide with an EBA.

Elevational (Local Scale) Patterns of Endemism

Along elevational gradients, endemism as expressed by both the lower range-size quartile and the range-size rarity index generally increases with elevation and peaks near the current closed timberline and, in Peru and Bolivia, in often isolated *Polylepis* forest fragments above timberline (Graves 1985, 1988; Fjeldså and Kessler 1996; Kessler et al. 2001; Fjeldså 2002; Fjeldså and Irestedt 2009). This is likely a consequence of the more fragmented topography and increased climatic harshness at higher elevations, which result in greater risks of stochastic local extinction, more scattered, isolated populations, and correspondingly faster rates of population differentiation (Kessler et al. 2001). Fjeldså and Irestedt (2009) further pointed out that the timber- and treeline zone plays a special role in diversification processes

Table 18.2. Qualitative comparison of the degree of spatial overlap between seven endemism hotspots (taken from figure 4 in Fjeldså and Irestedt 2009) and 12 Endemic Bird Areas (EBAs; Stattersfield et al. 1998, BirdLife International 2003) in the tropical Andes (from north to south). Figure 4 in Fjeldså and Irestedt (2009) is based on the lower range-size quartile of all South American breeding bird species with a spatial resolution of 15’×15’ latitude-longitude grid cells (729-775 km^2). See text for definition of EBAs.

Endemism hotspots	Endemic Bird Area	Degree of overlap
Sierra Nevada de Santa Marta, Colombia	Santa Marta mountains (EBA 036)	Very high
Cordillera de Mérida, Venezuela	Cordillera de Mérida (EBA 034)	Very high
Pacific slope from southern Cali department, Colombia, to just north of Quito, Ecuador	Chocó (EBA 041)	Moderate
East Andean slope at the equator, Ecuador	Ecuador-Peru East Andes (EBA 044)	Low
Southern Eucador (Loja and Zamora Chinchipe provinces) and adjacent Peru (Cordillera del Condor to northern Cajamarca and eastern Piura departments)	Central Andean páramo (EBA 043)	Very low
	Ecuador-Peru East Andes (EBA 044)	Low
	Tumbesian region (EBA 045)	Very low
	Southern Central Andes (EBA 046)	Very low
	Marañon valley (EBA 048)	Very low
Cordillera Vilcabamba north of Cuzco, Peru	Peruvian high Andes (EBA 051)	Very low
	Peruvian East Andean foothills (EBA 053)	Very low
Upper Bolivian Yungas (Cordillera de Apolobamba to Cordillera de Tiraque)	Bolivian and Peruvian upper yungas (EBA 055)	High
	High Andes of Bolivia and Argentina (EBA 056)	Very low

(see also Graves 1985, 1988), which underlines the conservation importance of timberline areas. Endemism drops sharply in adjacent puna habitats, where most species are widespread (Fjeldså and Kessler 1996), especially on the Altiplano of Bolivia and southern Peru (see figure 2 in Fjeldså et al. 1999, and figure 4 in Fjeldså and Irestedt 2009); whether this pattern also applies to the northern Andean páramo has not been analyzed. Thus, areas of high endemism usually do not coincide with areas of high species richness.

By contrast, when taking those species that are restricted to the Andes as our measure of endemism (some of which have fairly large ranges), richness of endemic species peaks at mid-elevations and decreases both toward higher and lower elevations (Kattan and Franco 2004).

Environmental Drivers of Endemism Patterns

Patterns of endemism essentially are diversity patterns of species with small geographic ranges. Based on the range-size rarity index, Fjeldså et al. (1999) showed that peak endemism areas in the Andes are characterized by high ecoclimatic stability, i.e., areas where particular topographic conditions moderate the impacts of extreme weather conditions. Such orographic moderation of climatic extremes is thought to have provided refugia for species during Pleistocene climate cycles, which suggests that many endemic species represent relict populations that survived periods of past global climatic change in theses stable areas (Fjeldså et al. 1999). Therefore, these same areas may be important conservation targets in the light of ongoing anthropogenic climate change.

As mentioned above, Rahbek et al. (2007) determined that gamma diversity patterns of South American species with small to moderately large ranges (first three range-size quartiles) appear to be influenced by topographic complexity (measured as the elevational range of each grid cell) and, to a lesser degree, ecosystem diversity, rather than climatic factors such as precipitation or energy availability. Thus, topographically and ecologically complex landscapes are conducive to the historical persistence of local populations. However, Rahbek et al. (2007) failed to take into account climatic complexity. On the east Andean slope in southern Peru and Bolivia, climatic complexity (precipitation range and, to a lesser degree, temperature range) explains diversity patterns of first- and second-quartile species better than topographic complexity for the same 1°×1° latitude-longitude grids as used by Rahbek et al. (2007) (S.K. Herzog et al., unpubl. data). Thus, whether topographic complexity or climatic complexity is the driving force behind patterns of endemism still needs to be resolved.

Knowledge Gaps: Challenges for Future Research

Although birds probably are the best known higher group of organisms in the Andes, our knowledge is still rather incomplete. Avian systematics currently are very much in flux and far from resolved (see Remsen et al. 2009). Taxonomic changes are unlikely to alter diversity patterns, but they may lead to a refinement of the details of geographical endemism patterns, especially at larger spatial scales. Quite a number of Neotropical birds that were considered fairly widespread, polytypic species not too long ago have been split recently and some of their subspecies raised to species level (e.g., Brumfield and Remsen 1996, Krabbe and Schulenberg 1997, García-Moreno and Fjeldså 1999, Isler et al. 2007), some of which are now considered restricted-range species (e.g., *Atlapetes melanolaemus* and *A. rufinucha*). Patterns of endemism are further influenced by recently discovered species, which are constantly being described from the tropical Andes and generally have restricted ranges (e.g., O'Neill et al. 2000, Cuervo et al. 2005, Herzog et al. 2008). In fact, the most likely scenario for species still waiting to be discovered is that they have small ranges restricted to particular mountain chains or regions that are poorly (or not at all) studied. Nonetheless, although new species are often found in poorly studied sites, they often occur within areas that are already well known for their high endemism (e.g., Fjeldså 2000) and tend to strengthen known endemism patterns.

Large areas in the Andes have not yet been surveyed, resulting in incomplete knowledge of the distribution of many species. First explorations of such areas often result in numerous new distributional records (e.g., Herzog et al. 1999, MacLeod et al. 2005). Restricted-range species illustrate this: the 24 EBAs that are at least partly located in the tropical Andes were considered to hold 385 restricted-range species by Stattersfield et al. (1998). Just over 10 years later, 96 (25 %) of these are known to have range sizes > 50,000 km^2, in some cases much greater, and hence no longer qualify as restricted-range species. Although this does not influence the validity of those EBAs themselves, nor questions the EBA concept, it illustrates how much more there is to learn about Andean birds.

Current understanding of local elevational diversity patterns is based on surprisingly few studies, almost exclusively along forested gradients (excluding puna and páramo grasslands), and regional variations in the pattern are thus poorly known. A major obstacle to improving our knowledge are logistical difficulties of accessing entire elevational gradients from treeline to foothills and adjacent lowlands that are reasonably well preserved throughout. The factors and mechanisms that cause elevational patterns of diversity are still debated, especially with respect to the mid-domain effect (e.g., Colwell et al. 2004, 2005, 2009; Hawkins et al. 2005; Zapata et al. 2005; Kerr et al. 2006; McCain 2009). To further our understanding of the mechanisms underlying the observed diversity patterns, more quantitative studies using robust sampling methods along complete or almost complete altitudinal gradients spanning a range of ecoclimatic conditions (e.g., dry to wet) are needed (McCain 2009). The study of latitudinal patterns has fared much worse than that of elevational patterns in the tropical Andes, because there is not a single comprehensive quantitative analysis of large-scale latitudinal patterns.

Studies on historical population structures (phylogeography; e.g., Cadena et al. 2007) to identify places of maximum lineage persistence within the habitat mosaics of the tropical Andes are needed, and the identification of such places is particularly crucial in the face of climate change. Finally, although not directly related to biodiversity patterns, the natural history, ecological requirements, interspecific ecological interactions (see Aguirre et al. Chapter 4, this volume), and dispersal abilities of most species are very poorly known, making it difficult to predict the exact current ranges of species and their responses to environmental changes and habitat disturbance. This is important because local ecological factors significantly shape community composition and species richness patterns (e.g., Herzog and Kessler 2006, McCain 2009).

Acknowledgments

We thank J. Fjeldså, who also kindly provided Figure 18.1, and M. Kessler for comments on the manuscript.

Literature Cited

Aben, J., M. Doerenbosch, S. K. Herzog, A. J. P. Smolders, and G. Van der Velde. 2008. Human disturbance affects a deciduous forest bird community in the Andean foothills of central Bolivia. *Bird Conservation International* 18:363-380.

BirdLife International. 2003. *BirdLife's online World Bird Database: the site for bird conservation*. Version 2.0. Cambridge: BirdLife International. Available: http://www.birdlife.org (accessed 16/6/2009)

Brumfield, R. T., and J. V. Remsen, Jr. 1996. Geographic variation and species limits in *Cinnycerthia* wrens of the Andes. *Wilson Bulletin* 108:205-227.

Cadena, D. A., J. Klicka, and R. E. Ricklefs. 2007. Evolutionary differentiation in the Neotropical montane region: Molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Molecular Phylogenetics and Evolution* 44:993-1016.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163:E1-E23.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2005. The mid-domain effect: there's a baby in the bathwater. *American Naturalist* 166:E149-E154.

Colwell, R. K., N. J. Gotelli, C. Rahbek, G. L. Entsminger, C. Farrell, and G. R. Graves. 2009. Peaks, plateaus, canyons, and craters: the complex geometry of simple mid-domain effect models. *Evolutionary Ecology Research* 11:355-370.

Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs* 36:49-84.

Cuervo, A. M., C. D. Cadena, N. Krabbe, and L. M. Renjifo. 2005. *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. *Auk* 122:445-463.

Dickinson, E. C. (ed.). 2003. *The Howard and Moore complete checklist of the birds of the world*. London: Christopher Helm.

Fjeldså, J. 1994. Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation* 3:207-226.

Fjeldså, J. 2000. The relevance of systematics in choosing priority areas for global conservation. *Environmental Conservation* 27:67-75.

Fjeldså, J. 2002. *Polylepis* forests – vestiges of a vanishing ecosystem in the Andes. *Ecotropica* 8:111-123.

Fjeldså, J., M. D. Álvarez, J. M. Lazcano, and B. León. 2005. Illicit crops and armed conflict as constraints on biodiversity conservation in the Andes region. *Ambio* 34:205-211.

Fjeldså, J., and M. Irestedt. 2009. Diversification of the South American avifauna: patterns and implications for conservation in the Andes. *Annals of the Missouri Botanical Garden* 96:398-409.

Fjeldså, J., and M. Kessler. 1996. Conserving the biological diversity of *Polylepis* woodlands of the highlands of Peru and Bolivia – a contribution to sustainable natural resource management. Copenhagen: NORDECO.

Fjeldså, J., E. Lambin, and B. Mertens. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography* 22:63-78.

Fjeldså, J., and C. Rahbek. 1997. Species richness and endemism in South American birds: implications for the design of networks of nature reserves. Pp. 466-482 in *Tropical forest remnants: ecology, management and conservation of fragmented communities*, edited by W. F. Laurance and R. O. Bierregaard. Chicago: University of Chicago Press.

García-Moreno, J., and J. Fjeldså. 1999. Re-evaluation of species limits in the genus *Atlapetes* based on mtDNA sequence data. *Ibis* 141:199-207.

Gaston, K. J. 1994. *Rarity*. London: Chapman and Hall.

Graham, G. L. 1990. Bats versus birds: comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *Journal of Biogeography* 17:657-668.

Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in plumage in Andean birds. *Auk* 102:556-579.

Graves, G. R. 1988. Linearity of geographic range and its possible effect on the population structure of Andean birds. *Auk* 105:47-52.

Hawkins, B. A., J. A. F. Diniz-Filho, and A. E. Weis. 2005. The mid-domain effect and diversity gradients: is there anything to learn? *American Naturalist* 166:E140-E143.

Herzog, S. K. 2008. First ornithological survey of Cordillera Mosetenes, with a latitudinal comparison of lower Yungas bird communities in Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 23:59-71.

Herzog, S. K., J. Fjeldså, M. Kessler, and J. A. Balderrama. 1999. Ornithological surveys in the Cordillera Cocapata, depto. Cochabamba, Bolivia, a transition zone between humid and dry intermontane Andean habitats. *Bulletin of the British Ornithologists' Club* 119:162-177.

Herzog, S. K., and M. Kessler. 2006. Local versus regional control on species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography* 15:163-172.

Herzog, S. K., M. Kessler, and K. Bach. 2005a. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography* 28:209-222.

Herzog, S. K., M. Kessler, and J. A. Balderrama. 2008. A new species of tyrannulet (Tyrannidae: *Phyllomyias*) from Andean foothills in northwest Bolivia and adjacent Peru. *Auk* 125:265-276.

Herzog, S. K., R. Soria Auza, and A. B. Hennessey. 2005b. Patrones ecorregionales de la riqueza, endemismo y amenaza en la avifauna boliviana: prioridades para la planificación ecorregional. *Ecología en Bolivia* 40(2):27-40.

Hilty, S. L. 1997. Seasonal distribution of birds at a cloud forest locality, the Anchicayá Valley, in western Colombia. *Ornithological Monographs* 48:321-343.

Isler, M. L., P. R. Isler, and B. M. Whitney. 2007. Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. *Auk* 124:11-28.

Johnson, N. K. 2002. Leapfrogging revisited in Andean birds: geographical variation in the Tody-tyrant superspecies *Poecilotriccus ruficeps* and *P. luluae*. *Ibis* 144:69-84.

Kattan, G. H., H. Alvarez-López, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. *Conservation Biology* 8:138-146.

Kattan, G. H., and P. Franco. 2004. Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. *Global Ecology and Biogeography* 13:451-458.

Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography* 31:1829-1839.

Kattan, G., P. Franco, C. A. Saavedra, C. Valderrama, V. Rojas, D. Osorio and J. Martínez. 2006. Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. *Conservation Biology* 20:1203-1211.

Kerr, J. T., M. Perring, and D. J. Currie. 2006. The missing Madagascan mid-domain effect. *Ecology Letters* 9:149-159.

Kessler, M., S. K. Herzog, J. Fjeldså, and K. Bach. 2001. Diversity and endemism of plants and birds along two gradients of elevation, humidity, and human land-use in the Bolivian Andes. *Diversity and Distributions* 7:61-77.

Krabbe, N., and T. S. Schulenberg. 1997. Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. *Ornithological Monographs* 48:47-88.

Krömer, T., M. Kessler, and S. K. Herzog. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica* 38:183-195.

Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177-192.

MacLeod, R., S. Ewing, S. K. Herzog, K. Evans, R. Bryce, and A. Maccormick. 2005. First ornithological inventory and conservation assessment for the Yungas forests of the Cordilleras Cocapata and Mosetenes, Cochabamba, Bolivia. *Bird Conservation International* 15:361-382.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86:366-372.

McCain, C. M. 2009. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* 18:346-360.

McKnight, M. W., P. S. White, R. I. McDonald, J. F. Lamoreux, W. Sechrest, R. S. Ridgely, and S. N. Stuart. 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS Biology* 5:e272.

Melo, A. S., T. F. L. V. B. Rangel, and J. A. F. Diniz-Filho. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* 32:226-236.

Munves, J. 1975. Birds of a highland clearing in Cundinamarca, Colombia. *Auk* 92:307-321.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

Naranjo, L. G. 1994. Composición y estructura de la avifauna del Parque Regional Natural Ucumarí. Pp. 305-325 in *Ucumarí: un caso típico de la diversidad biótica andina*, edited by J. O. Rangel. Pereira, Colombia: Corporación Autónoma Regional de Risaralda.

O'Dea, N., and R. J. Whittaker. 2007. How resilient are Andean montane forest bird communities to habitat degradation? *Biodiversity and Conservation* 16:1131-1159.

O'Neill, J. P., D. F. Lane, A. W. Kratter, A. P. Capparella, and C. Fox Joo. 2000. A striking new species of barbet (Capitoninae: *Capito*) from the eastern Andes of Peru. *Auk* 117:569-577.

Patterson, B. C., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593-607.

Pearson, O. P., and C. Pearson Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias del Museo de Historia Natural "Javier Prado"* 18:1-97.

Poulsen, B. O., and N. Krabbe. 1997. The diversity of cloud forest birds on the eastern and western slopes of the Ecuadorian Andes: a latitudinal and comparative analysis with implications for conservation. *Ecography* 20:475-482.

Poulsen, B. O., and N. Krabbe. 1998. Avifaunal diversity of five high-altitude cloud forests on the Andean western slope of Ecuador: testing a rapid assessment method. *Journal of Biogeography* 25:83-93.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist* 149:875-902.

Rahbek, C., N. J. Gotelli, R. K. Colwell, G. L. Entsminger, T. F. L. V. B. Rangel, and G. R. Graves. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society of London B, Biological Sciences* 274:165-174.

Rahbek, C., and G. R. Graves. 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proceedings of the Royal Society of London B, Biological Sciences* 267:2259-2265.

Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Science of the United States of America* 98:4534-4539.

Remsen, J. V. Jr. 1985. Community organization and ecology of birds of high elevation humid forest of the Bolivian Andes. *Ornithological Monographs* 36:733-756.

Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, D. F. Stotz, and K. J. Zimmer. 2009. *A classification of the bird species of South America*. Version 06/12/2009. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.html

Renjifo, L. M. 1999. Composition changes in a sub-Andean avifauna after long-term forest fragmentation. *Conservation Biology* 13:1124-1139.

Renjifo, L. M., G. P. Servat, J. M. Goerck, B. A. Loiselle, and J. G. Blake. 1997. Patterns of species composition and endemism in the northern Neotropics: a case for conservation of montane avifaunas. *Ornithological Monographs* 48:577-594.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1-15.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514-527.

Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.

Schluter, D., and R. E. Ricklefs. 1993. Species diversity: an introduction to the problem. Pp. 1-10 in *Species diversity in ecological communities: historical and geographical perspectives*, edited by R. E. Ricklefs and D. Schluter. Chicago: University of Chicago Press.

Schmitt, C. G., D. C. Schmitt, and J. V. Remsen, Jr. 1997. Birds of the Tambo area, an arid valley in the Bolivian Andes. *Ornithological Monographs* 48:701-716.

Sempere, T., D. Picard, and O. Plantard. 2005. Assessing and dating Andean uplift by phylogeography and phylochronology: early Miocene emergence of Andean cloud forest. Pp. 663-665 in *6th International Symposium on Andean Geodynamics, extended abstracts*. Barcelona: SAG 2005.

Stattersfield A. J., M. J. Crosby, A. J. Long, and D. C. Wege. 1998. *Endemic bird areas of the world: Priorities for biodiversity conservation. BirdLife Conservation Series No. 7.* Cambridge: BirdLife International.

Stiles, F. G., and C. I. Bohórquez. 2000. Evaluando el estado de la biodiversidad: el caso de la avifauna de la serranía de Las Quinchas, Boyacá, Colombia. *Caldasia* 22:61-92.

Stotz, D. F. 1998. Endemism and species turnover with elevation in montane avifaunas in the Neotropics: implications for conservation. Pp. 161-180 in *Conservation in a changing world*, edited by G. M. Mace, A. Balmford, and J. R. Ginsberg. Cambridge, MA: Cambridge University Press.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. *Neotropical birds: ecology and conservation*. Chicago: University of Chicago Press.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.

Williams, P. H., and C. J. Humphries. 1994. Biodiversity, taxonomic relatedness and endemism in conservation. Pp. 269-287 in *Systematics and conservation evaluation*, edited by P. L. Forey, C. J. Humphries, and R. I. Vane-Wright. Oxford: Clarendon Press.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273-309.

Young, B. E., I. Franke, P. A. Hernandez, S. K. Herzog, L. Paniagua, C. Tovar, and T. Valqui. 2009. Using spatial models to predict areas of endemism and gaps in the protection of Andean slope birds. *Auk* 126:554-565.

Zapata, F. A., K. J. Gaston, and S. L. Chown. 2005. The mid-domain effect revisited. *American Naturalist* 166:E144-E148.

19

Small Mammal Diversity in the Tropical Andes: An Overview

José Luis Mena, Sergio Solari, Juan Pablo Carrera, Luis Fernando Aguirre, and Humberto Gómez

The tropical Andes constitute one of the most important regions globally of mammal diversity and endemism (Ceballos and Ehrlich 2006; Mittermeier et al. 1998; Schipper et al. 2008). Nevertheless, taxonomy and distribution of most of mammals there remain inadequately known and revisions of most groups are needed (Gardner 2007). In South America, mammal species new to science are still being discovered at high rates and most species described in recent years are from the tropical Andes and Brazil (Patterson 2000; Reeder et al. 2007).

Small mammals (e.g., bats and rodents) are the most diverse group and account for more than half of the total mammal fauna in any given area. They affect the structure, composition, and dynamics of ecosystems through natural processes such as pollination, seed dispersal and depredation, mycorrhizal dispersal, insectivory, and as food for predators (DeMattia et al. 2004; Mangan and Adler 2002; Muchhala and Jarrín-V 2002; Napolitano et al. 2008; Naranjo et al. 2003; Steiner 1981; Vieira and de Moraes 2006; Walker et al. 2007; Williams-Guillén et al. 2008). Small mammals such as bats are good indicators of habitat disturbance (Castro-Luna et al. 2007; Medellín et al. 2000; Solari et al. 2002; Wilson et al. 1996). Likewise, small mammals have been particularly useful in the study of elevational gradients, mainly because they form well-defined assemblages (in contrast to medium-sized and large mammals) along such gradients (Lomolino 2001; Mena and Vázquez-Domínguez 2005; Patterson et al. 1998).

We here present an overview of the current knowledge about patterns of diversity and endemism for small mammals in the tropical Andes of Colombia, Ecuador, Peru, and Bolivia: marsupials (Didelphimorphia: Didelphidae and Paucituberculata: Caenolestidae), lagomorphs (Lagomorpha: Leporidae), rodents (Rodentia: Abrocomidae, Caviidae, Cricetidae, Ctenomyidae, Echimyidae, Heteromyidae, and Sciuridae), shrews (Soricomorpha: Soricidae), and bats (Chiroptera: Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae, Thyropteridae, and Vespertilionidae). Peru is the fifth most diverse country for mammals in the World (Pacheco et al. 2009) and Ecuador is listed as the ninth most diverse country despite its considerably small area compared to other megadiverse countries such as Brazil or Mexico (Tirira 2007). In order to assess and characterize small mammal diversity in the region, we conducted a survey of the literature (with special attention to elevational gradient studies), plus specimen records from US museum collections in the Mammal Networked Information System (MaNIS) data portals (http://manisnet.org/portals.html) and unpublished reports whenever these were available to us. Elevational gradient studies included here had to cover at least 70 % of the available elevational gradient and were grouped as local or regional (McCain 2007b), representing alpha or gamma diversity, respectively. They were evaluated based on the study group (bats or nonvolant small mammals), proportion of the entire elevational gradient that was sampled, species richness, and general geographic location (see Table 19.1). We follow Wilson and Reeder (2005) as a taxonomic reference.

Diversity and Distribution

At least 411 small mammal species inhabit the tropical Andes above 800 m. Marsupials are represented by 39 species, shrews by 7, bats by 166, rodents by 198, and lagomorphs by 1. Only 28 mammal species (6.2%) are endemic to Colombia, the majority of them are rodents and shrews (Alberico and Rojas-Díaz 2002), but a recent biogeographic analysis on bats added 5 endemic species, some of them restricted to the Andes (Mantilla-Meluk et al. 2009). In Ecuador, 38 species are recognized as endemic (Tirira 2007), although this number is decreasing due to extensive fieldwork and taxonomic revisions in neighboring Colombia and Peru (Mantilla-Meluk and Baker 2008; Pacheco et al. 2009). Most of the small nonvolant endemic species (1 shrew opossum, 2 shrews and 26 rodents) were collected on Andean slopes and highlands (1500 – 4000 m) (Voss 2003; Tirira 2007). Most of the Peruvian endemics (five genera and 65 species) are restricted to the Yungas of the east Andean slope (39 species), followed by the tropical lowland rainforest (14 species) (Pacheco et al. 2009). In Bolivia, one genus and 17 species are endemic, where the Altiplano has the highest degree of regional endemism (followed by the Yungas), and rodents contribute most to the endemism (Salazar-Bravo et al. 2002).

Highland Species Distributions

Among marsupials of the family Caenolestidae, shrew opossums (shrew equivalents or ecomorphs) of the genus *Caenolestes* are restricted to the northern Andes above 2000 m (Lunde and Pacheco 2003), whereas the genus *Lestoros* is restricted to the highlands of southern Peru and northwest Bolivia (Brown 2004). Short eared shrews (genus *Cryptotis*) are restricted to the Andes from Colombia to northern Peru above 1000 m (Eisenberg 1989; Eisenberg and Redford 1999; Gardner 2007), but knowledge about their taxonomy, distribution, and ecology is the most incomplete among Neotropical small mammals (Gardner 2007).

Two groups of rodents are associated with higher elevations in the tropical Andes. In the northern Andes, Ichthyomyini diversity reaches its peak on Andean slopes with nine species in four genera (Voss 1988): *Chibchanomys* (above 2400 m), *Anotomys* (2900 – 4000 m)*, Ichthyomys* (300 – 2700 m), and *Neusticomys* (up to 3700 m). By contrast, the Phyllotine genus *Galenomys*, the Akodontine genus *Necromys*, and the genera *Chinchillula, Neotomys*, and *Punomys* are restricted to the puna of the Altiplano in southern Peru and western Bolivia (Pearson 1951; Reig 1986). The genus *Thomasomys* is a smaller but still species-rich taxon that is endemic to tropical Andean cloud forests from Venezuela to Bolivia (Nowak 1999; Voss

Table 19.1. Elevational data sets of small mammal diversity in the tropical Andes. Elevational sample coverage is the percentage of the available gradient sampled (NVSM = nonvolant small mammals).

Location	**Country**	**Diversity**	**Lower elevational limit**	**Upper elevational limit**	**Elevational sample coverage (%)**	**Taxa**	**Spp**	**Richness peak**	**Reference**
La Libertad (Western slope)	Peru	Gamma	8	3962	99	NVSM	19	2800-3100	Osgood (1914)
South western Peru	Peru	Alpha	0	4500	98	NVSM	20	4000	Pearson and Ralph (1978)
Manu (Eastern slope)	Peru	Gamma	340	3450	95	NVSM	65	< 400	Solari et al (2006)
Manu (Eastern slope)	Peru	Gamma	340	3450	95	Bats	92	< 400	Solari et al (2006)
Eastern slope (8° to 17°S)	Peru	Gamma	0	3200	91	Bats	101	< 400	Graham (1983)
Eastern Cordillera	Colombia	Gamma	350	4000	90	Bats	42	1600-1900	Bejarano-Bonilla et al. (2007)
SW Choco	Colombia	Gamma	500	3500	85	Bats	36	1400	Fawcett (unpubl - 1994)
Central Cordillera	Colombia	Gamma	120	3160	75	Bats	39	500-600	Muñoz (1990, 1993)
Carrasco (Eastern slope)	Bolivia	Gamma	500	3500	70	Both	54	300-600	Vargas & Patterson (2007)
Yanachaga (Eastern slope)	Peru	Gamma	300	2800	68	Both	98	300-600	Vivar (2006)
Eastern Slopes	Ecuador	Gamma	600	3000	67	Bats	67	600 -1200	Carrera (unpubl - 2003)
Lima (Western slope)	Peru	Gamma	0	4400	67	NVSM	21	2400-2800	Unpublished data
Vilcabamba, (Eastern slope)	Peru	Gamma	850	3350	66	NVSM	22	?	Emmons et al. (2001) and Solari et al. (2001)
Eastern Cordillera	Colombia	Gamma	326	2640	55	Bats	29	600-1500	Tamsitt (1965)
Apurimac, (Eastern slope)*	Peru	Alpha	805	3500	53	Both	60	805	Pacheco et al. (2007)
Abiseo, (Eastern slope)	Peru	Gamma	2100	3850	45	NVSM	14	2100-3200	Leo & Romo (1992)
Central Cordillera	Colombia	Gamma	2200	3750	45	Both	42	?	Sanchez et al. (2004)
Sabana, Eastern Cordillera	Colombia	Gamma	2500	3600	31	Bats	10	2600	Tamsitt et al. (1964)
SW Choco	Colombia	Gamma	870	1950	30	Bats	28	900-1100	Alberico & Orejuela (1982) and Cadena et al. (1998)
Central Cordillera	Colombia	Gamma	2500	3500	25	NVSM	15	constant richness	Gomez-Valencia (unpublished - 2006)
Eastern Cordillera	Colombia	Gamma	2300	3100	22	NVSM	13	?	Lopez-A. & Montenegro-D. (1993)
Eastern Cordillera	Colombia	Gamma	1900	2600	17	NVSM	15	?	Gomez-Laverde (1994)

2003). Apparently, the center of diversity for this genus with at least seven species includes eastern Ecuador, where several species may occur sympatrically (Voss 2003).

Rodents are the only small mammals that inhabit elevations above 4000 m: Abrocomidae (1 species), Caviidae (2), Cricetidae (14), and Ctenomyidae (3). The rodent genus *Punomys* has records exclusively in localities above 4000 m (Eisenberg and Redford 1999; Pacheco and Patton 1995). The low partial pressure of oxygen and low ambient temperatures of high-elevation environments present a number of physiological challenges for endothermic animals. Camelids and some rodents (*Chinchilla* spp. and *Cavia porcellus*) of the high Andes are adapted to high-elevation hypoxia with hemoglobin that has high oxygen affinity (Ostojic et al. 2002; Storz 2007). Preliminary observations indicate that high-Andean rodents tolerate very low atmospheric oxygen concentrations, but the available data do not permit an analysis of the altitudinal limits of their distribution (McNab 2002; Morrison 1964). Lowland species may be limited by low barometric pressure at higher elevations, but highland species may face lower elevational limits to their distribution, which are unlikely to be related to high barometric pressures (McNab 2002).

There are few montane species among bats, including nectarivores (*Anoura aequatoris, A. fistulata, A. latidens, A. luismanueli*), frugivores (*Carollia manu, Stunira aratathomasi, S. bogotensis, S. nana,Platyrrhinus ismaeli*), and insectivores (*Eptesicus andinus, Histiotus humboldti, Mimon koepckeae, Mormopterus phrudus*). Reduced species richness and poorly developed endemism in Andean bat communities contrast with patterns shown by sympatric rodent faunas, which are diverse and strongly endemic on the Altiplano (see Figure 19.1) and markedly zoned along the eastern versant (Patterson et al. 1998). There are few records of bat species above 3500 m, with the probable exception of *Histiotus montanus* (up to 4000 m; Graham 1983, Gardner 2007). Koopman (1978) pointed out that Stenodermatinae bats have not been found at elevations higher than 3800 m. One of the species with records at higher elevations is the common vampire bat *Desmodus rotundus* (up to 3680 m) (Quintana and Pacheco 2007). In Costa Rica, LaVal (2004) found evidence of an upslope movement of *D. rotundus* as an apparent result of global warming; this has not been corroborated in the tropical Andes.

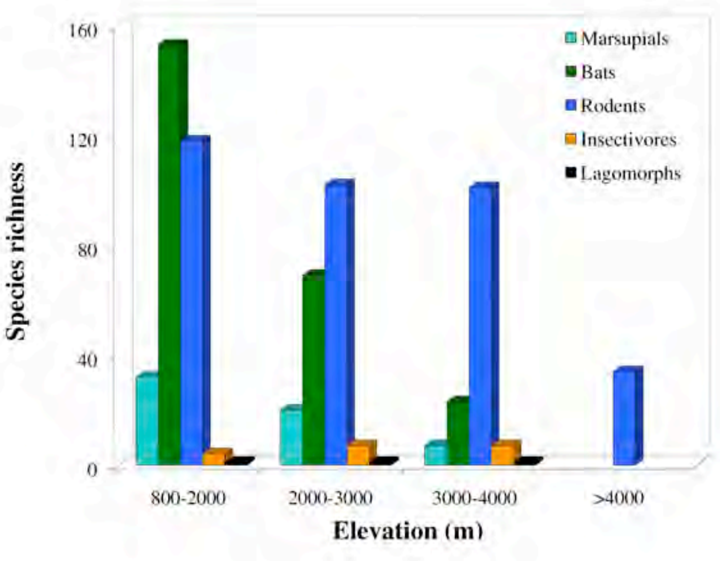

Figure 19.1. Species richness of mammals in elevational intervals along Tropical Andes (Colombia, Ecuador, Peru and Bolivia), including both eastern and western versants.

Biogeographic Role of the Andes

The high Andes have played a major role as "islands" where sigmodontine rodents (Cricetidae) experienced long periods of isolation and as a consequence evolved into several species, whereas lowland biomes contributed only secondarily to the process of diversification (Reig 1986). The number of rodent species endemic to the Andes supports the hypothesis that geographic isolation has been the most important cause of diversification among these mammals (Patton and Smith 1992). Although Koopman (1978) did not find evidence for any biogeographic role of the Andes for bats, concluding that bat distributions offer little support for a vicariance hypothesis, more recently, patterns similar to those of sigmodontines have been reported for the genera *Sturnira, Platyrrhinus* and *Carollia* (Ditchfield 2000; Mantilla-Meluk et al. 2009; Pacheco et al. 2004; Patterson et al. 1992; Velazco and Patterson 2008).

Puna and Paramo

The puna rodent fauna of Bolivia and Peru has more genera (at least 16) and species (at least 34) than the paramo rodent fauna of Colombia, Ecuador, and Peru (at least 8 genera and 16 species). This difference is probably the result of three main factors that have favored diversification in the puna (Reig 1986): the puna is older than the paramo biome (historical effect), it has greater environmental heterogeneity (ecological effect), and it has a larger and more continuous extension, especially on the extensive Altiplano (spatial effect).

Some studies suggest a biogeographical subdivision along the eastern border of the Lake Titicaca basin, with dry puna to the west and humid puna to the east. The dry highland zone of the Titicaca basin itself is characterized by the presence of *Phyllotis osilae osilae, Auliscomys boliviensis, Punomys lemminus, Akodon andinus, A. berlepschii, A. boliviensis, A. subfuscus arequipae, Necromys amoenus, Chroeomys jelskii pulcherrimus*, and *Galea musteloides* (Pacheco and Patton 1995; Ramirez et al. 2007). The humid puna of the Cordillera Oriental, on the other hand, is characterized by *Phyllotis osilae phaeus, Punomys kofordi, Chreomys jelskii cruceri, Auliscomys pictus, Oxymicterus paramensis, Akodon puer*, and *Akodon subfuscus subfuscus* (Pacheco and Patton 1995). A recent analysis by Ramirez et al.(2007) suggests that small mammal assemblages in the humid puna have greater similarity with those of the paramo than those of the dry puna.

The Elevational Gradient of Small Mammal Diversity

The Tropical Andes Scale

Available data on the elevational range size for species above 800 m shows that small mammal richness generally decreases with elevation for the tropical Andes as a whole (Figure 19.1; nonvolant small mammals: $R^2 = 0.84$, $P < 0.0001$; bats: $R^2 = 0.99$, $P < 0.0001$). Lomolino (2001) predicted that gamma diversity, the total richness of an entire elevational zone, should vary directly with the total area of each elevational zone, peaking in those zones that cover the largest area (e.g., the Amazon lowlands). Therefore, and because area decrease with elevation in the tropical Andes, the influence of area on this relationship should be considered (see Rahbek

1997). However, McCain (2007b) found evidence that area and spatial constraints (mid-domain effect) represent sources of error rather than mechanisms underlying mammalian diversity patterns. Indeed, the Amazonian lowlands have more species than the puna or paramo, which has been explained as a consequence of climatic, edaphic, spatial (area), and historical factors (Patton et al. 2000; Patton et al. 1997; Voss and Emmons 1996). However, especially at middle and higher elevations (puna, paramo, and yungas) the tropical Andes are richer in higher taxonomic levels such as tribes and genera (see previous sections).

The rodent tribes Akodontini, Phyllotini, and Thomasomyini (Cricetidae: Sigmodontinae) show highest species richness at mid elevations (Figure 19.2), a pattern not seen in marsupials and bats. A recent analysis of regional mammal endemism (mainly rodents) on the eastern versant of Bolivia and Peru showed a narrow elevational band with high numbers of endemic species (with ranges entirely confined to the area under consideration) occurring just below the treeline in upper Yungas forest (Pacheco et al. 2007). Nevertheless, it is important to highlight that these levels of endemism at middle elevations should be corroborated, especially because of our deficient knowledge about distribution, potentially misidentified specimens (see below), and lack of taxonomic syntheses.

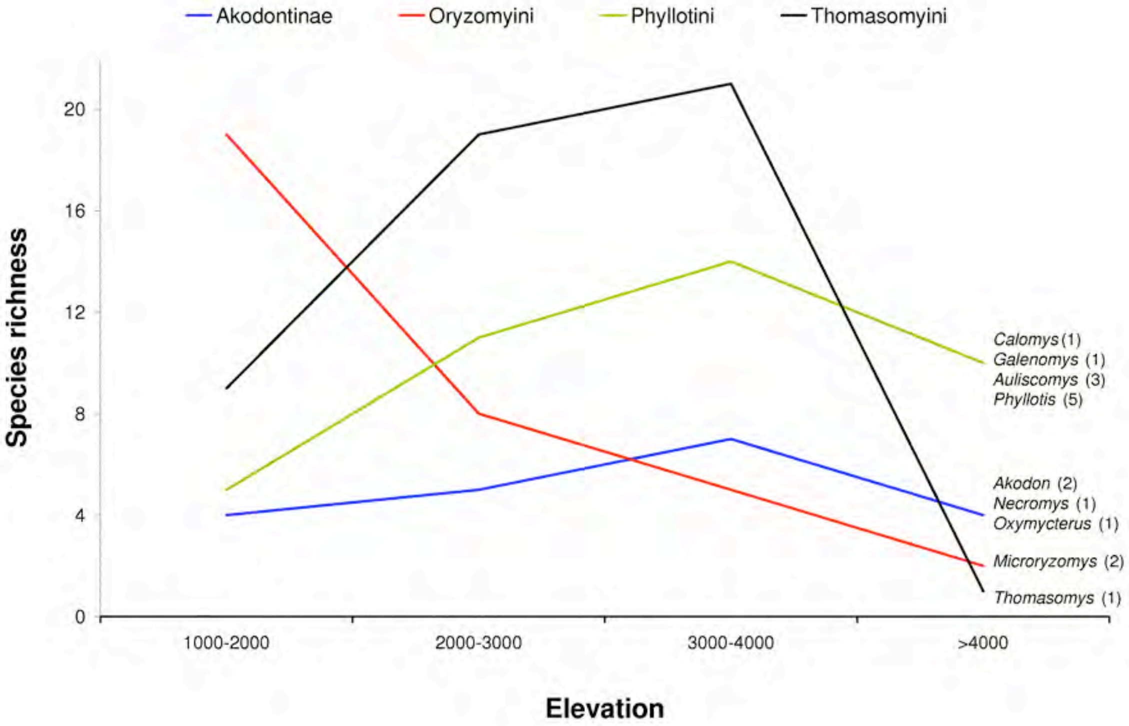

Figure 19.2. Species richness of Sigmodontinae tribes along elevation on the western versant of the Tropical Andes (species number in parentheses). The same pattern was recorded along the eastern slope (data not shown).

Regional and local scale

Our literature review shows that gradients along the eastern versant of the Andes have received the most attention: 14 out of 22 studies/localities (Table 19.1). Most studies from the tropical Andes suffer from incomplete elevational sampling (either covering only the mid-range or the upper part of the gradient), and most are characterized by insufficient sampling effort at each local survey site. Studies that sample only part of an elevational gradient often provide spurious results by excluding the lower (lowlands) or upper (highlands) end of the mountain from the analysis, so that they are impractical to identify elevational patterns. McCain (2007b) illustrated how difficult it is to obtain data from complete elevational gradients extending from lowlands to mountain peaks. As for insufficient sampling effort, most bat surveys, for example, depend on mist nets that are set at ground-level (despite the availability of other methods such as searching roost sites or identifying echolocation calls), and results thus are biased towards understory species, whereas canopy and open-area species remain underrepresented. We recognize that misidentifications of specimens represent a potential bias, especially in older literature (but we included only one "older" gradient study). Indeed, an update of these datasets based on current taxonomy is necessary.

Nonvolant Small Mammals

In general, there are few elevationally complete studies on both eastern and western slopes. We recorded only three studies with > 70% of the gradient sampled (Table 19.1). A study along the Peruvian eastern versant in Manu National Park shows a decrease of species richness with elevation (Figure 19.3; $R^2 = 0.82$, $P = 0.0001$). This result contrasts markedly with the pattern of a mid-elevation peak in nonvolant small mammal richness (McCain 2005). Manu has particular rodent assemblages restricted to elevational zones with replacements at species, genus, and even tribal levels (Patterson et al. 1998). A similar pattern of decreasing species richness with elevation occurs in both Yanachaga (Figure 19.3), Peru, with the 68% of gradient sampled ($R^2 = 0.48$, $P = 0.0001$), and Carrasco National Park in Bolivia (Vargas and Patterson 2007; original data not available). Peru's Manu National Park (340 – 3675 m) has become the most intensively studied protected area in the tropical Andes with more than 20 years of mammalogical research (Pacheco et al. 1993; Patterson et al. 1998; Solari et al. 2006), but no similar efforts have occurred in other tropical countries (see below). There are no studies of complete elevational gradients in Bolivia, Ecuador, or Colombia. We did not consider the data of Osgood (1914) from Libertad, Peru, because they would require reanalysis based on reidentification of specimens using current taxonomy.

On the western slope of the Peruvian Andes (Pearson and Ralph 1978), diversity increases with elevation ($R^2 = 0.44$, $P = 0.0001$), probably as a result of increased precipitation (and vegetation) with elevation, and more speciation events in the puna than in coastal deserts (Marquet 1994; Pearson and Ralph 1978). No studies appear to have been conducted on the more humid and diverse Pacific slope of Colombia, Ecuador (the Chocó), and northern Peru (Pacific tropical forest). Detailed studies testing both historical and environmental hypotheses should be conducted to improve our knowledge of the relationship between nonvolant small mammal richness and elevation along the latitudinal extension of the western slope of the tropical Andes, which presents contrasting lowlands such as the Pacific desert and Pacific tropical rainforests, and highlands such as dry puna and humid páramo, and even inter-Andean valleys. For example, the Peruvian eastern versant is more species rich in small mammals than the western versant (Pacheco et al. 2009), whereas the western and eastern versants of the Colombian Andes have similarly high diversity (Kattan et al. 2004). In general, there are very few studies on elevational gradients in nonvolant small mammals. Published general inventories of nonvolant mammals at elevations above 800 m are scarce (Gómez-Valencia 2006; Mena and Medellín 2010; Ramirez et al. 2007; Sánchez et al. 2004; Vivar 2006).

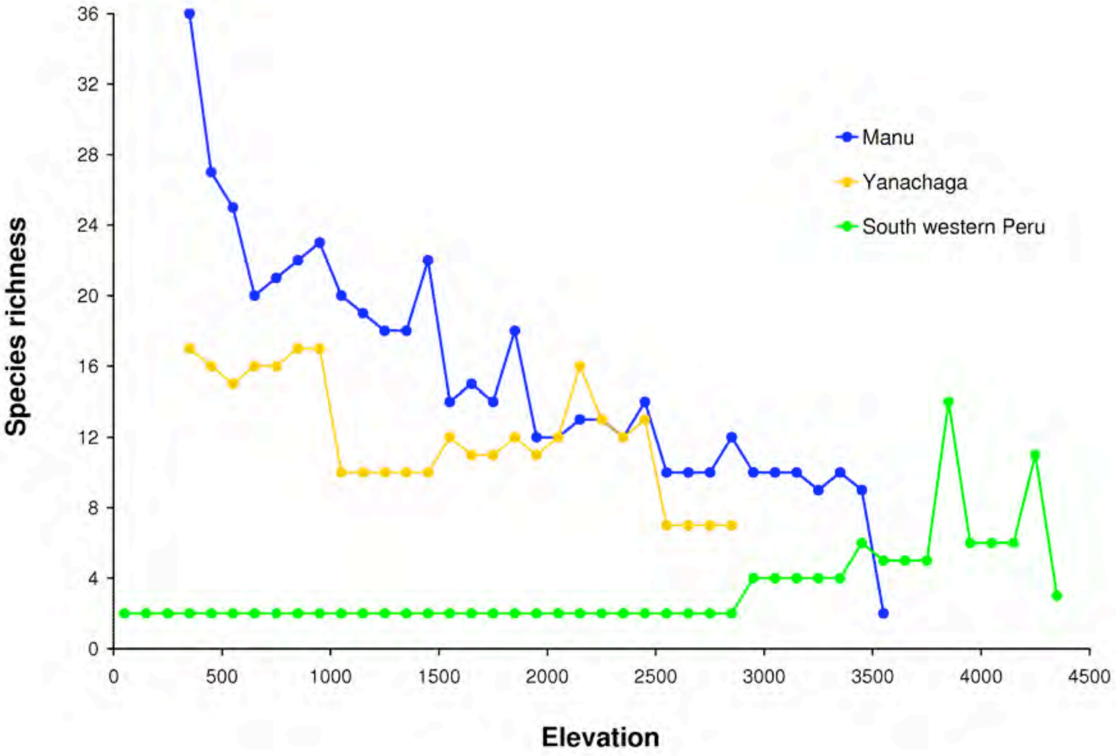

Figure 19.3. Elevational gradients in both western (WS) and eastern slopes (ES) of the Peruvian Andes: Manu (Solari et al. 2006), Yanachaga (Vivar 2006) and South western Peru (Pearson and Ralph 1978). See Table 19.1 for sources and details.

Bats

We recorded five studies on elevational gradients with > 70 % of the gradient sampled (Table 19.1). Along the Peruvian eastern versant, bat faunas tend to show a monotonic decrease of diversity with elevation both for the region as a whole (Graham 1983; $R^2 = 0.92$, $P = 0.0001$) and for Manu (Solari et al. 2006; $R^2 = 0.83$, $P = 0.0001$). The decrease of bat diversity with increasing elevation has been linked to an inefficient thermoregulation of species with Neotropical origin (especially for Phyllostominae species) (Graham 1983, 1990; Soriano 2000; Soriano et al. 1999). Highland faunas generally are attenuated versions of those found in the lowlands (Patterson et al. 1996; Patterson et al. 1998). For example, species richness of bat assemblages in Manu decreases monotonically, from 77 species between 300-500 m to only seven above 3000 m.

In Colombia, two studies on the eastern slope of the Cordillera Central (Muñoz 1990, 1993) and in the Chocó (Fawcett 1994) showed higher bat species richness at mid-elevations (Table 19.1). This was explained by the presence of secondary forests at middle elevations, providing support for the intermediate disturbance hypothesis (Bejarano-Bonilla et al. 2007). Similarly, Carrera (2003) analyzed the effect of elevation on species richness of bats on the central eastern slopes of the Ecuadorian Andes and found evidence of a mid-elevation peak between 1000 - 1100 m, which may be mainly due to the presence of a complex system of caves located in this gradient and a considerable collecting effort performed in the area since the 1980's (Rageot and Albuja 1994).

In a global analysis, McCain (2007a) suggested that elevational patterns of bat richness are related to local climatic gradients (temperature and water availability), habitat complexity, and species composition. Thus, decreasing species richness with elevation will occur on mountains with wet and warm lowlands (e.g., Manu, Yanachaga), but mid-elevation peaks will occur on mountains with arid lowlands (e.g., western Peru). Whereas some studies along the eastern slope corroborate the first prediction, studies on alpha diversity along the dry western slope of Peru are necessary to test the second prediction. In general, despite an increasing number of studies on bat species assemblages in Colombia, Ecuador, Peru, and Bolivia (Aguirre 2002; Aguirre et al. 2003; Ascorra et al. 1993; Ascorra et al. 1996; Bejarano-Bonilla et al. 2007; Espinoza et al. 2008; Hice et al. 2004; Numa et al. 2005; Pacheco et al. 2007; Pérez-Torres and Ahumada 2004; Rex et al. 2008; Sánchez et al. 2007; Vargas and Patterson 2007), there are few studies on elevational gradients for bat faunas. For example, in Bolivia the only attempt to study patterns of bat distribution along an elevational gradient was conducted by Vargas and Patterson (2007) in a gradient from 400 to 3600 m in Carrasco National Park (Cochabamba).

Directions for future research

In general, the current knowledge of distributional limits (both ecological and geographic), population demography, basic life history parameters, and natural history is still inadequate for most species inhabiting the tropical Andes. This incomplete understanding does not allow for a realistic or objective analysis and comparison of alpha, beta, or gamma diversity patterns. It also is the main obstacle to understanding elevational gradients of diversity in the tropical Andes. For example, in the first assessment of elevational richness patterns in Manu, Patterson et al. (1998) determined that rodent richness was high both in the lowlands and in the highlands, with an apparent minimum at intermediate elevations. However, additional inventories in Manu (Solari et al. 2006) revealed a steady decline in rodent richness with elevation (Figure 19.3). This highlights the importance of complete and standardized inventories along elevational gradients to improve our knowledge about diversity patterns. In addition, the integration of databases of natural history collections and museums are a high-priority for investigators and future collaborations between institutions in the area.

The limited availability of information on elevational and latitudinal gradients from the tropical Andes impede a thorough understanding of how global warming and land use change are stressing mammal assemblages at local to regional scales. Undoubtedly, it is necessary to increase basic information, which can be obtained through standardized surveys along elevation gradients on eastern and western slopes, which will also allow for monitoring of potential upslope movements of species due to global warming. For example, the study of population dynamics of the common vampire bat can provide valuable information about global warming, spread of diseases, and destruction of natural environments.

In summary, detailed and accurate information about patterns of diversity in Andean mammals is needed to advance conceptual understanding in biogeography and ecology, as well as for the development of effective conservation strategies. This is a critical issue because recent climate change has already begun to affect species' geographic ranges around the world.

Literature Cited

Aguirre, L. F. 2002. Structure of a Neotropical savanna bat community. *Journal of Mammalogy* 83:775-784.

Aguirre, L. F., X. Velez-Liendo, A. Muñoz, and A. Selaya. 2003. Patrones de distribución y zoogeografía de los murciélagos de Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 14:3-17.

Alberico, M., and V. Rojas-Díaz. 2002. Mamíferos de Colombia. Pp. 185-226 in *Diversidad y conservación de los mamíferos neotropicales*, edited by G. Ceballos and J. A. Simonetti. México City: CONABIO-UNAM.

Alberico, M., and J. Orejuela. 1982. Diversidad específica de dos comunidades de murciélagos en Nariño, Colombia. *Cespedesia* 11 Sup. 3:31-40.

Ascorra, C. F., D. Gorchov, and F. Cornejo. 1993. The bats from Jenaro Herrera, Loreto, Peru. *Mammalia* 57:533-552.

Ascorra, C. F., S. Solari, and D. E. Wilson. 1996. Diversidad y ecología de los quirópteros en Pakitza. Pp. 593-612 in *Manu: the biodiversity of southeastern Peru*, edited by D. E. Wilson and A. Sandoval. Lima: Smithsonian Institution Press.

Bejarano-Bonilla, D. A., A. Yate-Rivas, and M. H. Bernal-Bautista. 2007. Diversidad y distribución de la fauna quiroptera en un transecto altitudinal en el departamento del Tolima, Colombia. *Caldasia* 29:297-308.

Brown, B. E. 2004. Atlas of the New World marsupials. *Fieldiana Zoology, New Series* 102:1-308.

Cadena, A., R. P. Anderson, and P. Rivas-Pava. 1998. Colombian mammals from the Chocoan slopes of Nariño. *Occasional Papers, Museum of Texas Tech University* 180:1-15.

Carrera, J. P. 2003. *Distribución de murciélagos (Chiroptera) a través de un gradiente altitudinal en las estribaciones orientales de los Andes ecuatorianos.* Licenciatura thesis. Quito: Pontificia Universidad Católica del Ecuador.

Castro-Luna, A. A., I. J. Sosa, and G. Castillo-Campos. 2007. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. *Acta Chiropterologica* 9:219-228.

Ceballos, G., and P. R. Ehrlich. 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences* 103:19374-19379.

DeMattia, E. A., L. M. Curran, and B. J. Rathcke. 2004. Effects of small rodents and large mammals on Neotropical seeds. *Ecology* 85:2161-2170.

Ditchfield, A. D. 2000. The comparative phylogeography of Neotropical mammals: patterns of intraspecific mitochondrial DNA variation among bats contrasted to nonvolant small mammals. *Molecular Ecology* 9:1307-1318.

Eisenberg, J. F. 1989. *Mammals of the Neotropics: the northern Neotropics. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana*. Chicago: University of Chicago Press.

Eisenberg, J. F., and K. H. Redford, eds. 1999. *Mammals of the Neotropics: the central Neotropics. Ecuador, Peru, Bolivia, Brazil*. Chicago: University of Chicago Press.

Emmons, L. H., L. Luna, and M. Romo. 2001. Mammals of the northern Vilcabamba mountain range, Peru. Pages 105-109 in *Biological and social assessments of the Cordillera de Vilcabamba, Peru. RAP Working Papers 12 and SI/MAB Series 6*, edited by L. E. Alonso, A. Alonso, T. S. Schulenberg, and F. Dallmeier. Washington, DC: Conservation International.

Espinoza, A., L. F. Aguirre, M. I. Galarza, and E. Gareca. 2008. Ensamble de murciélagos en sitios con diferente grado de perturbación en un bosque montano del Parque Nacional Carrasco, Bolivia. *Mastozoología Neotropical* 15:297-308.

Fawcett, D. 1994. Bats. Pp. 60-67 in *Surveys and conservation of biodiversity in the Chocó, south-west Colombia*, edited by P. G. W. Salaman. Cambridge: BirdLife International.

Gardner, A. L. (ed.). 2007. *Mammals of South America, volume 1*. Chicago: University of Chicago Press.

Gómez-Laverde, M. 1994. Los pequeños mamíferos no voladores del Parque Regional Ucumari. Pages 377-396 in J. O. Rangel-Churrio, editor. *Ucumari: un caso típico de la diversidad biótica andina*. Bogotá: CARDER-Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

Gómez-Valencia, B. 2006. *Estructura de la comunidad de pequeños mamíferos en un gradiente altitudinal, reserva Rio Blanco, Manizales, Caldas.* Tesis de pregrado. Bogotá: Departamento de Biologia, Universidad Nacional de Colombia.

Graham, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of Mammalogy* 64:559-571.

Graham, G. L. 1990. Bats versus birds: comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *Journal of Biogeography* 17:657-668.

Hice, C. L., P. M. Velazco, and M. R. Willig. 2004. Bats of the Reserva Nacional Allpahuayo-Mishana, northeastern Peru, with notes on community structure. *Acta Chiropterologica* 6:319-334.

Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography* 31:1829-1839.

Koopman, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *American Museum Novitates* 2651:1-33.

LaVal, R. K. 2004. Impact of global warming and locally changing climate on tropical cloud forest bats. *Journal of Mammalogy* 85:237-244.

Leo, M., and M. Romo. 1992. Distribución altitudinal de roedores sigmodontinos (Cricetidae) en el Parque Nacional río Abiseo, San Martin, Perú. *Memorias del Museo de Historia Natural UNMSM* 21:105-118

Lomolino, M. V. 2001. Elevational gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10:3-13.

López-Arévalo, H. F., and O. L. Montenegro-Díaz. 1993. Mamíferos no voladores de Carpanta. Pp. 165-187 in *Carpanta: selva nublada y páramo*, edited by G. I. Andrade. Fundación Natura, Bogotá.

Lunde, D. P., and V. Pacheco. 2003. Shrew opossums (Paucituberculata: *Caenolestes*) from the Huancabamba region of east Andean Peru. *Mammal Study* 28:145-146.

Mangan, S., and G. Adler. 2002. Seasonal dispersal of arbuscular mycorrhizal fungi by spiny rats in a Neotropical forest. *Oecologia* 131:587-597.

Mantilla-Meluk, H., and R. J. Baker. 2008. Mammalia, Chiroptera, Phyllostomidae, *Anoura fistulata*: distribution extension. *Check List* 4:427-430.

Mantilla-Meluk, H., A. M. Jiménez-Ortega, and R. J. Baker. 2009. Phyllostomid bats of Colombia: annotated checklist, distribution, and biogeography. *Special Publications, Museum of Texas Tech University* 56.

Marquet, P. A. 1994. Diversity of small mammals in the Pacific coastal desert of Peru and Chile and in the adjacent area: biogeography and community structure. *Australian Journal of Zoology* 42:527-542.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86:366-372.

McCain, C. M. 2007a. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* 16:1-13.

McCain, C. M. 2007b. Area and mammalian elevational diversity. *Ecology* 88:76-86.

McNab, B. K. 2002. *The physiological ecology of vertebrates: a view from energetics*. Ithaca, NY: Cornell University Press.

Medellín, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology* 14:1666-1675.

Mena, J. L., and E. Vázquez-Domínguez. 2005. Species turnover on elevational gradients in small rodents. *Global Ecology and Biogeography* 14:539-547.

Mena, J. L., and R. A. Medellín. 2010. Small mammal assemblages in a disturbed tropical landscape at Pozuzo, Peru. *Mammalian Biology* 75:83-91.

Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. Da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12:516-520.

Morrison, P. R. 1964. Wild animals at high altitudes. *Symposia of the Zoological Society of London* 13:49-57.

Muchhala, N., and P. Jarrín-V. 2002. Flower visitation by bats in cloud forests of western Ecuador. *Biotropica* 34:387-395.

Muñoz, J. 1993. Murciélagos del norte de Antioquia (Colombia). *Studies on Neotropical Fauna and Environment* 28:83-93.

Muñoz, J. 1990. Diversidad y hábitos alimenticios de murciélagos en transectos altitudinales a través de la Cordillera Central de los Andes en Colombia. *Studies on Neotropical Fauna and Environment* 25:1-17.

Napolitano, C., M. Bennett, W. E. Johnson, S. J. O'Brien, P. A. Marquet, I. Barría, E. Poulin, and A. Iriarte. 2008. Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. *Molecular Ecology* 17:678-690.

Naranjo, M. E., C. Rengifo, and P. J. Soriano. 2003. Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae). *Journal of Tropical Ecology* 19:19-25.

Nowak, R. M. 1999. *Walker's mammals of the world*. Baltimore, MD: Johns Hopkins University Press.

Numa, C., J. R. Verdú, and P. Sánchez-Palomino. 2005. Phyllostomid bat diversity in a variegated coffee landscape. *Biological Conservation* 122:151-158.

Osgood, W. H. 1914. Mammals of an expedition across northern Peru. Fieldiana Zoology 10:143-185.

Ostojic, H., C. Veronica, and C. Monge. 2002. Hemoglobin affinity in Andean rodents. *Biological Research* 35:27-30.

Pacheco, V., and J. L. Patton. 1995. A new species of the Puna mouse, genus *Punomys* Osgood, 1943 (Muridae, Sigmodontinae), from the southeastern Andes of Peru. *Zeitschrift für Säugetierkunde* 60:85-96.

Pacheco, V., S. Solari, and P. M. Velazco. 2004. A new species of *Carollia* (Chiroptera: Phyllostomidae) from the Andes of Peru and Bolivia. *Occasional Papers, Museum of Texas Tech University* 235:1-15.

Pacheco, V., R. Cadenillas, S. Velazco, E. Salas, and U. Fajardo. 2007. Noteworthy bat records from the Pacific Tropical rainforest region and adjacent dry forest in northwestern Peru. *Acta Chiropterologica* 9:409-422.

Pacheco, V., R. Cadenillas, E. Salas, C. Tello, and H. Zeballos. 2009. Diversidad y endemismo de los mamíferos del Perú. *Revista Peruana de Biología* 16:5-32.

Pacheco, V., B. D. Patterson, J. L. Patton, L. H. Emmons, S. Solari, and C. F. Ascorra. 1993. List of mammal species known to occur in Manu Biosphere Reserve, Peru. *Publicaciones del Museo de Historia Natural "Javier Prado" UNMSM, Serie A, Zoología* 44:1-12.

Pacheco, V., H. L. Quintana, P. A. Hernandez, L. Paniagua, J. Vargas, and B. E. Young. 2007. Mamíferos. Pp. 40-45 in *Distribución de las especies endémicas en la vertiente oriental de los Andes en Perú y Bolivia*, edited by B. E. Young. Arlington, VA: NatureServe.

Patterson, B. D. 2000. Patterns and trends in the discovery of new Neotropical mammals. *Diversity and Distributions* 6:145-151.

Patterson, B. D., V. Pacheco, and M. V. Ashley. 1992. On the origins of the western slope region of endemism: systematics of fig-eating bats, genus *Artibeus*. *Memorias del Museo de Historia Natural UNMSM* 21:189-205.

Patterson, B. D., V. Pacheco, and S. Solari. 1996. Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology* 240:637-658.

Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593-607.

Patton, J. L., and M. F. Smith. 1992. mtDNA Phylogeny of Andean mice: a test of diversification across ecological gradients. *Evolution* 46:174-183.

Patton, J. L., M. N. da Silva, and J. R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244:1-306.

Patton, J. L., M. N. F. da Silva, M. C. Lara, and M. A. Mustrangi. 1997. Diversity, differentiation, and the historical biogeography of nonvolant small mammals of the Neotropical forests. Pp. 455-465 in *Tropical forest remnants: ecology, management, and* *conservation of fragmented communities*, edited by W. F. Laurance and R. O. Bierregaard. Chicago: University of Chicago Press.

Pearson, O. P. 1951. Mammals in the highlands of southern Peru. *Bulletin of the Museum of Comparative Zoology* 106:117-174.

Pearson, O. P., and C. P. Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias del Museo de Historia Natural "Javier Prado"* 18:1-97.

Pérez-Torres, J., and J. A. Ahumada. 2004. Murciélagos en bosques alto-andinos, fragmentados y continuos, en el sector occidental de la sabana de Bogotá (Colombia). *Universitas Scientiarum* 9:33-46.

Quintana, H., and V. Pacheco. 2007. Identificación y distribución de los murciélagos vampiros del Perú. *Revista Peruana de Medicina Experimental y Salud Publica* 24:81-88.

Rageot, R., and L. Albuja. 1994. Mamíferos de un sector de la alta Amazonía ecuatoriana: Mera, provincia de Pastaza. *Revista Politécnica* 19:165-208.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist* 149:875-902.

Ramirez, O., M. Arana, E. Bazán, A. Ramirez, and A. Cano. 2007. Assemblages of bird and mammal communities in two major ecological units of the Andean highland plateau of southern Peru. *Ecologia Aplicada* 6:139-148.

Reeder, D. M., K. M. Helgen, and D. E. Wilson. 2007. Global trends and biases in new mammal species discoveries. *Occasional Papers, Museum of Texas Tech University* 269:1-35.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404-439 in *High altitude tropical biogeography*, edited by M. Monasterio and F. Vuilleumier. New York: Oxford University Press.

Rex, K., D. H. Kelm, K. Wiesner, T. H. Kunz, and C. C. Voigt. 2008. Species richness and structure of three Neotropical bat assemblages. *Biological Journal of the Linnean Society* 94:617-629.

Salazar-Bravo, J., T. L. Yates, and L. M. Zalles. 2002. Mamíferos de Bolivia. Pp. 65-113 in *Diversidad y conservación de los mamíferos neotropicales*, edited by G. Ceballos and J. A. Simonetti. México City: CONABIO-UNAM.

Sánchez, F., P. Sánchez-Palomino, and A. Cadena. 2004. Inventario de mamíferos en un bosque de los Andes centrales de Colombia. *Caldasia* 26:291-309.

Sánchez, F., J. Alvarez, C. Ariza, and A. Cadena. 2007. Bat assemblage structure in two dry forests of Colombia: composition, species richness, and relative abundance. *Mammalian Biology* 72:82-92.

Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A. S. L. Rodrigues, S. N. Stuart, H. J. Temple, J. Baillie, L. Boitani, T. E. Lacher Jr., R. A. Mittermeier, A. T. Smith, D. Absolon, J. M. Aguiar, G. Amori, N. Bakkour, R. Baldi, R. J. Berridge, J. Bielby, P. A. Black, J. J. Blanc, T. M. Brooks, J. A. Burton, T. M. Butynski, G. Catullo, R. Chapman, Z. Cokeliss, B. Collen, J. Conroy, J. G. Cooke, G. A. B. da Fonseca, A. E. Derocher, H. T. Dublin, J. W. Duckworth, L. Emmons, R. H. Emslie, M. Festa-Bianchet, M. Foster, S. Foster, D. L. Garshelis, C. Gates, M. Gimenez-Dixon, S. Gonzalez, J. F. Gonzalez-Maya, T. C. Good, G. Hammerson, P. S. Hammond, D. Happold, M. Happold, J. Hare, R. B. Harris, C. E. Hawkins, M. Haywood, L. R. Heaney, S. Hedges, K. M. Helgen, C. Hilton-Taylor, S. A. Hussain, N. Ishii, T. A. Jefferson, R. K. B. Jenkins, C. H. Johnston, M. Keith, J. Kingdon, D. H. Knox, K. M.

Kovacs, P. Langhammer, K. Leus, R. Lewison, G. Lichtenstein, L. F. Lowry, Z. Macavoy, G. M. Mace, D. P. Mallon, M. Masi, M. W. McKnight, R. A. Medellin, P. Medici, G. Mills, P. D. Moehlman, S. Molur, A. Mora, K. Nowell, J. F. Oates, W. Olech, W. R. L. Oliver, M. Oprea, B. D. Patterson, W. F. Perrin, B. A. Polidoro, C. Pollock, A. Powel, Y. Protas, P. Racey, J. Ragle, P. Ramani, G. Rathbun, R. R. Reeves, S. B. Reilly, J. E. Reynolds III, C. Rondinini, R. G. Rosell-Ambal, M. Rulli, A. B. Rylands, S. Savini, C. J. Schank, W. Sechrest, C. Self-Sullivan, A. Shoemaker, C. Sillero-Zubiri, N. De Silva, D. E. Smith, C. Srinivasulu, P. J. Stephenson, N. van Strien, B. K. Talukdar, B. L. Taylor, R. Timmins, D. G. Tirira, M. F. Tognelli, K. Tsytsulina, L. M. Veiga, J.-C. Vie, E. A. Williamson, S. A. Wyatt, Y. Xie, and B. E. Young. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322:225-230

Solari, S., J. J. Rodríguez, E. Vivar, and P. M. Velazco. 2002. A framework for assessment and monitoring of small mammals in a lowland tropical forest. *Environmental Monitoring and Assessment* 76:89-104.

Solari, S., V. Pacheco, L. Luna, P. M. Velazco, and B. D. Patterson. 2006. Mammals of the Manu Biosphere Reserve. *Fieldiana: Zoology, n.s.* 110:13-22.

Solari, S., E. Vivar, P. M. Velazco, and J. J. Rodríguez. 2001. Small mammals of southern Vilcabamba region, Peru. Pp. 110-116 in *Biological and social assessments of the Cordillera de Vilcabamba, Peru. RAP Working Papers 12 and SI/MAB Series 6*, edited by L. Alonso, A. Alonso, T. Schulenberg, and F. Dallmeier. Washington, DC: Conservation International.

Soriano, P. J. 2000. Functional structure of bat communities in tropical rainforests and Andean cloud forests. *Ecotropicos* 13:1-20.

Soriano, P. J., A. Díaz de Pascual, J. Ochoa, and M. Aguilera. 1999. Biogeographic analysis of the mammal communities in the Venezuelan Andes. *Interciencia* 24:17-25.

Steiner, K. E. 1981. Nectarivory and potential pollination by a Neotropical marsupial. *Annals of the Missouri Botanical Garden* 68:505-513.

Storz, J. F. 2007. Hemoglobin function and physiological adaptation to hypoxia in high-altitude mammals. *Journal of Mammalogy* 88:24-31.

Tamsitt, J. R. 1965. Aspects of altitudinal distribution of chiropterans in the eastern Cordillera of Colombia. *American Zoology* 5:1-492.

Tamsitt, J. R., D. Valdivieso, and J. Hernandez-Camacho. 1964. Bats of the Bogota savanna, Colombia, with notes on the altitudinal distribution of Neotropical bats. *Revista Tropical de Biología* 12:107-115.

Tirira, D. 2007. *Guía de campo de los mamíferos del Ecuador. Publicación Especial 6.* Quito: Ediciones Murciélago Blanco.

Vargas, A., and B. D. Patterson. 2007. Comunidades de murciélagos montanos en Bolivia. Pp. 82-86 in *Historia natural, distribución y conservación de los murciélagos de Bolivia*, edited by L. F. Aguirre. Santa Cruz de la Sierra: Editorial Centro de Ecología y Difusión Simón I. Patiño.

Velazco, P. M., and B. D. Patterson. 2008. Phylogenetics and biogeography of the broad-nosed bats, genus *Platyrrhinus* (Chiroptera: Phyllostomidae). *Molecular Phylogenetics and Evolution* 49:749-759.

Vieira, E. M., and D. A. de Moraes. 2006. Carnivory and insectivory in Neotropical marsupials. Pp. 271-284 in *Predators with pouches: the biology of carnivorous marsupials*, edited by M. Jones, C. Dickman, and M. Archer. Collingwood, Australia: CSIRO Publishing.

Vivar, E. 2006. *Análisis de distribución altitudinal de mamíferos pequeños en el Parque Nacional Yanachaga-Chemillén, Pasco, Perú*. Tesis de maestria. Lima: Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos.

Voss, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188:259-493.

Voss, R. S. 2003. A new species of *Thomasomys* (Rodentia: Muridae) from eastern Ecuador, with remarks on mammalian diversity and biogeography in the Cordillera Oriental. *American Museum Novitates* 3421:1-47.

Voss, R. S., and L. H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* 230:1-115.

Walker, R. S., A. J. Novaro, P. Perovic, R. Palacios, E. Donadio, M. Lucherini, M. Pia, and M. S. Lopez. 2007. Diets of three specie of Andean carnivores in high-altitude deserts of Argentina. *Journal of Mammalogy* 88:519-525.

Wilson, D. E., C. F. Ascorra, S. Solari, D. E. Wilson, and A. Sandoval. 1996. Bats as indicators of habitat disturbance. Pp. 613-625 in *Manu: the biodiversity of southeastern Peru*. Lima: Smithsonian Institution Press.

Wilson, D. E., and D. M. Reeder (eds.). 2005. *Mammal species of the world*. Baltimore, MD: Johns Hopkins University Press.

Williams-Guillén, K., I. Perfecto, and J. Vandermeer. 2008. Bats limit insects in a Neotropical agroforestry system. *Science* 320:70-70.

20

Biodiversity in Aquatic Systems of the Tropical Andes

Mabel Maldonado, Javier A. Maldonado-Ocampo, Hernán Ortega, Andrea C. Encalada, Fernando M. Carvajal-Vallejos, Juan Francisco Rivadeneira, Francisca Acosta, Dean Jacobsen, Álvaro Crespo, and Carlos A. Rivera-Rondón

Aquatic systems and their biodiversity are probably the environments that have received the least research attention in the tropical Andes. Current knowledge is limited and derived from studies that are relatively narrow in scope and restricted to specific systems and taxonomic groups of aquatic organisms. Thus, the information available to describe and interpret aquatic diversity patterns in the Andes is far from complete, and emerging patterns are therefore preliminary and still lack causal explanations. The present chapter reviews the current state of knowledge about Andean aquatic biodiversity with the primary goal of identifying present knowledge gaps.

Aquatic Systems of the Tropical Andes

Andean aquatic systems include a wide range of environments, including small to large lakes of different origins and with different characteristics, headwater streams that constitute part of South America's largest river basins, extensive associated wetlands, and extreme environments such as salt lakes and geothermal springs.

The greatest variety of aquatic environments is found in the high-Andean zone above 3000 m (Izurieta 2007) in the terrestrial ecoregions known as páramo and puna. The most representative wetlands in the páramos of Colombia, Venezuela, Ecuador, and northern Peru are glacial lakes and *Sphagnum* peat bogs (Flachier 2005, Rubio et al. 2005), whereas lakes and peat bogs without *Sphagnum* are characteristic of the puna of Peru, Bolivia, Argentina, and Chile (Arévalo 2005, Castro 2007, Navarro and Maldonado 2002). These environments can be characterized as follows:

- Lakes: Lakes are very numerous and primarily of glacial or tectonic origin, although lakes of volcanic and fluvial origin, among others, also exist. The largest lakes are found in the Altiplano of Peru and Bolivia. Many are deep, warm monomictic lakes, whose waters mix once a year from top to bottom during austral winter, but are thermally stratified throughout the rest of the year. The mesotrophic Lake Titicaca is characterized by intermediate levels of primary productivity (Iltis et al. 1991, Richerson et al. 1991) and support important fisheries. Farther south lies the shallow, highly mineralized, and eutrophic Lake Poopó with its high primary productivity, as well as the large salt lakes of Uyuni and Coipasa, which lack aquatic biota but support extensive wetlands on their shores (Navarro and Maldonado 2002). These three lakes cover a combined area of about 25,000 km^2 (Montes de Oca 2004). Throughout the high Andes, lakes with small surface areas are so numerous that, despite their limited individual size, cumulatively they account for large areas. In Ecuador, for example, all lakes > 25 ha cover a combined area of almost 500 km^2, whereas the salt lakes in the watershed of the southern Bolivian Altiplano add up to a total of about 2,000 km^2 (Montes de Oca 2004). Lakes of glacial origin are abundant in the páramo and humid puna. They are relatively deep, oligothermal (cold-adapted), and cold polymictic (their waters can mix from top to bottom throughout the ice-free period) (Aguilera et al. 2006). In the dry puna, shallow salt lakes with an extreme seasonality are more common (Castro 2007, Navarro and Maldonado 2002).

- River systems: The Andean hydrographic network includes open exorheic systems whose water constantly flows out of the system under almost all climatic circumstances and that drain to the Pacific or the Atlantic oceans. These include the major headwaters of the Amazon system. There are also closed, endorheic systems, the largest of which is the internal rivers and lakes of the Altiplano basin. Characteristic river environments include headwater streams, which are fed by glacial meltwater, precipitation, springs, lakes, and wetlands. They are highly variable in morphology, ranging from steep torrents to braided rivers on alluvial plains that consist of a network of small channels separated by small and often temporary islands (anastomizing rivers). Hydrological regimes of endorheic rivers are often highly unpredictable, and with the exception of the Rio Desaguadero on the Bolivian Altiplano, no rivers with important flow volumes exist (Jacobsen 2008).

- Wetlands: Peat bogs with or without *Sphagnum* are characteristic high-Andean environments. Peat bogs without *Sphagnum* (bofedales) of the puna are complex wetlands that harbor numerous ponds and streams, both permanent and seasonal, with highly variable degrees of mineralization (Navarro and Maldonado 2002). Geothermal springs are also common, but poorly known ecologically.

In the montane zone below 3000 m, lakes are less numerous, characterized by pronounced seasonality, and tend to be eutrophic with high primary productivity (Donato 2004, Navarro and Maldonado 2002). Typical montane rivers, generally have alternating sections of riffles, relatively deep pools, and narrow flow channels, have a fast overall current, and largely lack aquatic plants (Winemiller et al. 2008). They experience strong diurnal temperature variations (Lewis 2008), and their hydrological regime is often ‘flashy’ (i.e., experiencing rapid changes in discharge) and unpredictable, even in the most humid Andean regions (Boulton et al. 2008).

Aquatic Diversity Patterns

Aquatic diversity in the Andes has received less attention than terrestrial diversity from the research and conservation community, which has hampered the interpretation of patterns at regional scales. For South America as a whole, several biogeographic proposals exist that define freshwater faunistic regions (e.g., Gery 1969, Ringuelet 1975) or freshwater ecoregions (Abell et al. 2008) based on the continent's ichthyofauna. In all classifications, some exclusively Andean regions exist but in most cases Andean sections are integrated into more extensive watersheds that extend into the lowlands.

For the tropical Andes, few regional-scale efforts for interpreting diversity patterns exist. That of Rumrich et al. (2000) for Andean diatoms is a noteworthy exception. At the country level, efforts are largely centered on selected taxonomic groups, such as the algae of Colombia (Donato 2001), the fishes of the Colombian Andes (Maldonado-Ocampo et al. 2005), macroinvertebrates in Colombia (Rolan-Perez 1988), the fishes of Peru (Ortega and Hidalgo 2008), and the fishes of Bolivia (Sarmiento and Barrera 1997). For Bolivia, a preliminary synthesis based on integrated information on algae, aquatic plants, invertebrates, and fishes exists within the framework of Bolivian freshwater ecoregions (Navarro and Maldonado 2002).

With the goal of interpreting preliminary diversity patterns in the aquatic biota of the tropical Andes and integrating all groups of organisms, we compiled a hydrographic watershed map for northwest South America based on the Pfafstetter system with level 2 coding (see, e.g., Crespo et al. 2008 for details): 15 watersheds were delimited that coincide at least partly with the tropical Andes (Figure 20.1, Table 20.1). Two elevational zones were defined: the high-Andean zone (> 3000 m) and the montane zone (500-3000 m). Names and limits of these zones were defined arbitrarily by the authors because it was not possible to standardize criteria used in the different countries.

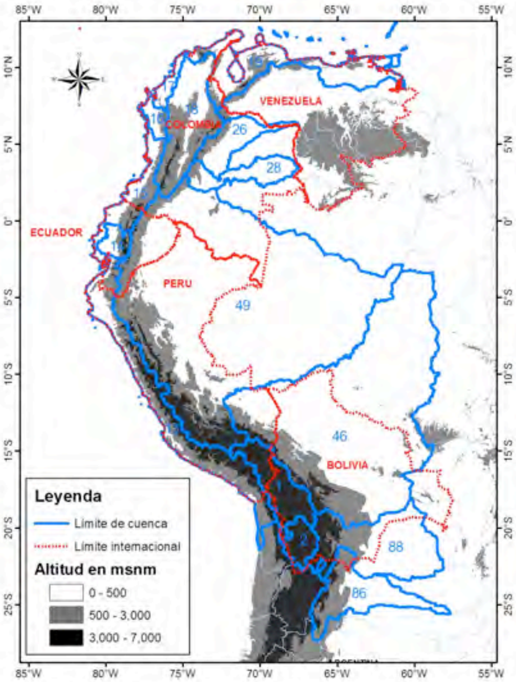

Figure 20.1. Watersheds in South America that coincide at least partly with the tropical Andes. Map compiled using the Pfafstetter system with level 2 (2-digit) coding. Names of watersheds are specified in Table 20.1. Map prepared by A. Crespo.

The countries with the largest Andean extension are Colombia, Ecuador, Peru, and Bolivia, and the high-Andean zone is most extensive in Peru and Bolivia (Figure 20.1). The Andean surface area of each watershed is shown in Table 20.1, adding up to a total of over 1.6 million km^2.

Within this geographical framework, we compiled background information on aquatic diversity with respect to species richness, endemism, and characteristic species and communities. This synthesis showed the scarcity of available information, the existence of serious geographic knowledge gaps, limited spatial resolution, and taxonomic uncertainties. We were able to compile data for all four countries (Colombia, Ecuador, Peru, Bolivia) only for fishes. For the remaining groups (algae, aquatic plants, invertebrates) only localized information could be identified.

Table 20.1. Names of watersheds shown in Figure 20.1, countries with which they coincide, and area of the Andean portion of each watershed.

No.	Name	Countries (in order of decreasing watershed area)	Andean area km^2	Main watershed or slope
1	Titicaca	Bolivia, Perú, Chile	153,677	Endorheic
2	Southern Altiplano	Bolivia, Chile	57,120	Endorheic
13	Southern Pacific	Perú, Ecuador	259,758	Pacific
14	Guayas	Ecuador	17,789	Pacific
15	Northern Pacific	Colombia, Ecuador	57,324	Pacific
16	Atrato	Colombia	10,924	Caribbean
17	Sinú	Colombia	2,985	Caribbean
18	Magdalena-Cauca	Colombia	159,124	Caribbean
19	Catatumbo	Colombia, Venezuela	66,341	Caribbean
26	Orinoco Drainage	Colombia	24,170	Orinoco
28	Guaviare	Colombia	13,218	Orinoco
46	Madera	Bolivia, Perú	238,781	Amazon
49	Upper Amazon	Perú, Ecuador, Colombia	417,106	Amazon
88	Pilcomayo	Bolivia	112,208	Plata
86	Bermejo	Bolivia, Argentina	91,468	Plata

Algae

The diversity and composition of algae communities is related to the dissolved mineral content of the water. Diversity is greater in weakly mineralized waters, where Chlorophyta predominate in lakes and Zygophyceae in cushion bogs. With increasing mineralization, Chromophyta and Cyanophyta become dominant in lakes, and Euglenophyceae in cushion bogs (Acosta et al. 2003, Cadima et al. 2005, Goitia et al. 2007, Navarro and Maldonado 2002). Virtually no information exists on endemism in algae for the tropical Andes.

In Colombia, most studies on algae have been conducted in the Magdalena watershed above 1500 m. To date, approximately 1300 species have been cited for Colombia (Table 20.2). More species of algae occur in generally oligotrophic (i.e., with low primary productivity) high-Andean lakes than at lower elevations, where lakes are found in small numbers and are primarily mesotrophic. The number of studies in lotic ecosystems (rivers, streams, springs) is lower than for lakes and therefore fewer lotic species have been recorded (Table 20.2). Some studies suggest elevational turnover in diatom species composition due to changes in pH and turbity of the water (Díaz y Rivera-Rondón 2004).

Donato (2001) reported a pattern in the structure of phytoplankton communities as a result of differences in geology: rich Desmidiaceae floras are typical of poorly mineralized lakes of Colombia's Cordillera Central, whereas their species richness is low and only widespread species occur in lakes of recent volcanic origin in the Cordillera Oriental.

In Ecuador, most studies on algae have been conducted in lakes, and approximately 1500 species of diatoms have been cited for the country, most of them from high-Andean lakes (M. Steinitz-Kannan pers. com.; Steinitz-Kannan, 1997). However, a handful of studies from Andean-Amazonian rivers suggest that diatom diversity could be greater here than in high-Andean lakes (De Oliveira and Steinitz-Kannan 1993, Steinitz-Kannan 2000).

In Bolivia, the greatest species richness of algae is found in the numerous high-Andean lakes and cushion bogs, especially in the Madera and Titicaca watersheds (Table 20.3). Lower diversity in the Southern Altiplano and Pilcomayo watersheds could be related to a predominance of salt lakes, which is typical of xeric climates.

Aquatic plants (macrophytes)

The submerged vegetation in streams of the Ecuadorian páramo is composed of only two species that belong to cosmopolitan genera (*Myriophyllum quitense*, *Potamogeton paramoanus*). Amphibian vegetation is more diverse and composed of genera such as *Callitriche, Ranunculus, Lilaea*, and *Isoetes*, the latter having received much interest due to its high species richness and levels of endemism, and because in addition it is an indicator of oligotrophic waters (Jacobsen and Terneus 2001).

Bolivian macrophytes have been fairly well studied from both phytosociological and ecological perspectives, and they were included in a description of the vegetation types of the country (Navarro and Ferreira 2007). Although available information on species richness patterns is limited (Table 20.3), it suggests that diversity is greatest in lake environments, including widespread genera such as *Myriophyllum, Potamogeton, Chara, Ranunculus*, *Lilaeopsis,* and *Lemna* (Navarro and Maldonado 2002). As in algae, diversity and composition of macrophyte communities is related to the degree of mineralization of the water (De la Barra 2003).

Table 20.2. Number of species of algae, zooplankton, and benthos (aquatic insects) recorded in Colombia by elevational zone. Sources: Hurlbert et al. (1981), Koste and De Paggi (1982), Muñoz-Quesada (2004), Zuñiga et al. (2004), Gaviria and Aranguren (2007), Sala et al. (2008), H. Aristizábal unpubl. data, S. Duque and M. Nuñez unpubl. data, C. Rivera unpubl. data.

Elevation (m)	Algae in lakes	Algae in rivers	Zooplankton	Benthos
> 3000	450	80	48	10
2000-3000	684	55	57	54
1000-2000	90	104	52	128
500-1000	0	24	18	105

Table 20.3. Number of species of algae and aquatic plants recorded in Bolivia by watershed and elevational zone. Sources: Navarro and Maldonado 2002, Acosta et al. 2003, De la Barra 2003, Cadima et al. 2005, Goitia et al. 2007. * = not recorded in the respective elevational zone or watershed; ? = no information available.

	ALGAE			**AQUATIC PLANTS**				
	Lakes		**Bogs**	**Lakes**		**Rivers**		**Bogs**
Elevation (m)	**500 - 3000**	**> 3000**	**> 3000**	**500 – 3000**	**> 3000**	**500 - 3000**	**> 3000**	**> 3000**
Titicaca								
Altiplano	*	259	144	*	20	*	?	?
Cordillera Oriental	*	177	?	*	22	*	?	?
Southern Altiplano								
Cordillera Occidental	*	65	126	*	1	*	?	8
Altiplano	*	?	?	*	5	*	5	?
Madera Basin								
Beni	?	459	437	?	10	?	?	10
Ichilo-Chapare	?	?	?	29	?	?	?	?
Grande	154	381	437	31	21	?	?	10
Pilcomayo River	?	154	?	?	3	?	?	?
Bermejo River	?	*	*	?	*	?	*	*

Planktonic invertebrates (zooplankton)

As in algae and aquatic plants, many zooplankton genera and species are cosmopolitan in distribution.

Zooplankton species richness in Colombia does not show a clear elevational trend (Table 20.2). However, some families exhibit regional-scale patterns, such as the Centropagidae (Copepoda), which are restricted to high-Andean lakes, and the Diaptomidae, which generally inhabit lakes and rivers at mid- to low elevations (Gaviria and Aranguren 2007).

In Bolivia, high-Andean lakes and cushion bogs, especially those in the Titicaca and Madera watersheds, harbor greater species numbers than the Southern Altiplano and Pilcomayo watersheds (Table 20.4). In all watersheds, zooplankton communities are dominated by *Boeckella* (Copepoda) species, a genus characteristic of the high-Andean zone.

The composition of zooplankton communities is influenced by the degree of mineralization of the water, and diversity increases with decreasing mineralization. In weakly mineralized lakes, rotifers and cladocerans (water fleas) are most diverse; with increasing mineralization, cladocerans are the first group to disappear, followed by copepods (Navarro and Maldonado 2002, Acosta et al. 2003). A similar pattern is found in cushion bogs (Coronel et al. 2007, Goitia et al. 2007). Limited information from high-Andean lakes in Peru also indicates that the degree of mineralization as well as the presence of fishes control zooplankton diversity. *Boeckella* and *Daphnia* dominate in lakes without fishes, cladocerans are absent from well mineralized lakes, and cladocerans of small size dominate in lakes with fishes (Hurlbert et al. 1986).

Table 20.4. Number of species of planktonic invertebrates and number of families and species (in parentheses) of benthic macroinvertebrates recorded in Bolivia by watershed and elevational zone. Sources: Navarro and Maldonado 2002, Acosta et al. 2003, Maldonado and Goitia 2003, Coronel et al. 2007, Goitia et al. 2007, E. Goitia unpubl. data. * = not recorded in the respective elevational zone or watershed; ? = no information available; (+) = excludes rotifers.

	ZOOPLANKTON			**BENTHOS**				
	Lakes		**Bogs**	**Lakes**		**Rivers**		**Bogs**
Elevation (m)	**500 - 3000**	**> 3000**	**> 3000**	**500 - 3000**	**> 3000**	**500 - 3000**	**> 3000**	**> 3000**
Titicaca								
Altiplano	*	46	?	*	35 (99)	*	12	?
Cordillera Oriental	*	71	?	*	39	*	20	?
Southern Altiplano								
Cordillera Occidental	*	22	32	*	19	*	18	20 (34)
Altiplano	*	?	?	*	?	*	?	?
Madera								
Beni	?	45	55	?	20	46	20	26 (37)
Ichilo-Chapare	?	?	?	?	?	29	17	?
Grande	46	85	55	21 (36)	20	24	22	26 (37)
Pilcomayo	?	11 (+)	?	?	12	25 (49)	?	?
Bermejo	?	*	*	?	*	25 (79)	*	*

Benthic macroinvertebrates

Although there is good general knowledge at the family level, this is the least known group at the species level mainly because the identification of tropical species requires expert knowledge given that few taxa have been treated in detailed revisions (Jacobsen et al. 2008). In general terms, the pattern of decreasing diversity with increasing elevation in Andean rivers is less clear in macroinvertebrates than in other groups such as fishes (Jacobsen 2008).

In rivers of the Ecuadorian páramo, dominant groups include Planariidae (Turbellaria), Oligochaeta, Hyalellidae (Amphipoda), Baetidae (Ephemeroptera), Hydroptilidae, Limnephilidae (Trichoptera), Chironomidae, Simuliidae (Diptera), and Elmidae (Coleoptera) (Jacobsen 2008). In general, diversity decreases with elevation for these orders, and this pattern is particularly pronounced in Hemiptera and Odonata, which do not occur in the high zone of Ecuador (Encalada 1997) despite being very diverse in the lowlands (Jacobsen 2004). Several important families, such as Gripopterygidae (Plecoptera), Anomalosychidae, and Limnephilidae (both Trichoptera), on the other hand are restricted to high-Andean elevations.

In Colombia, the orders Hemiptera, Ephemeroptera, and Trichoptera have been studied most the montane zone of the Magdalena-Cauca watershed. Table 20.2 shows the variation in species richness of aquatic insects, which is greatest in the montane zone, where especially Hemiptera have been recorded most frequently below 1500 m (Aristizabal 2002). Trichoptera and Ephemeroptera are also diverse groups in the Colombian Andes (Muñoz-Quesada 2004, Zuñiga et al. 2004).

In Bolivia (Table 20.4), Chironomidae, Baetidae, and Elmidae are dominant in high-Andean rivers, and Amphipoda, Conchostraca, and Anostraca are restricted to this elevational zone. In the montane zone new and numerically important families appear, including Leptophlebiidae, Leptohyphidae, Simuliidae, Culicidae, and Hydrophilidae, whereas Caenidae, Coenagrionidae, Naucoridae, and Corydalidae are present only at low elevations (Maldonado et al. 2007). The composition of benthic macroinvertebrate communities in the high-Andean zone is also affected by water salinity. Mollusks, ostracods, and amphipods are abundant in poorly mineralized lakes and absent from highly mineralized lakes, where primarily dipterans and species of *Artemia* persist (Navarro y Maldonado 2002). In cushion bogs, chironomids, oligochaets, gastropods, corixids, and amphipods are abundant, but with increasing mineral content the diversity of these aquatic insects decreases markedly (Coronel et al. 2007, Goitia et al. 2007).

Fishes

Estimating the total number of fish species that inhabit the tropical Andes is currently hampered by taxonomic uncertainties and geographic knowledge gaps. The number of Andean fish species recorded is greatest in Colombia (220), followed by Bolivia (162), Peru (125), and Ecuador (92).

Table 20.5 shows the composition of families and genera in the four countries for the high-Andean and mid-montane zones. In Colombia and Ecuador, fish diversity is rather low in these zones and characterized by the presence of Trichomycteridae, Astroblepidae, and Characidae. Fish diversity is much greater in Peru and Bolivia at the same elevations, with *Orestias* as a characteristic genus.

Among genera, *Astroblepus* is very species rich in Colombia, Ecuador, and Peru, but appears to be less diverse in the Madera watershed, and its southern distributional limit is formed by the Ichilo-Chapare watershed in central Bolivia. The genus *Grundulus* is present only in Colombia and Ecuador, and *Chaetostoma* from Colombia to Peru. The genus *Trichomycterus* stands out for its diversification throughout the tropical Andes and because it is the only genus distributed along the entire elevational gradient.

In Colombia, 70% of the recorded species are known from the Magdalena-Cauca watershed and 37% are endemic to the country. Species richness is highest between 500 and 1100 m, where 94% of all species occur, and it decreases drastically above 2000 m. Only one species of *Trichomycterus* is found above 3300 m (Tables 20.5, 20.6). Ninety-eight percent of all species are found in rivers, and only 2 % occur in lakes and high-Andean wetlands (data by Maldonado, unpublished).

In Ecuador, 45% of the 92 species recorded are endemic to the country (Table 20.7). Highest diversity is found in the Upper Amazon watershed (Napo, Pastaza, Morona rivers), whereas watersheds that drain to the Pacific (Esmeraldas, Guayas) have lower species richness but higher levels of endemism, with > 50 % of their species being endemic to Ecuador (J. F. Rivadeneira and J. Valdiviezo pers. comm., Román-Valencia et al. 2005, Velez-Espino 2004). Species richness is greatest below 1100 m and decreases markedly with increasing elevation. Between 2200 and 3300 m, only *Astroblepus* catfishes have been recorded, and above 3300 m only one species of *Grundulus* is known (Table 20.5).

Table 20.5. Composition of fish families and genera in the high-Andean and mid-montane zone in the four tropical Andean countries (number of species in parentheses).

COLOMBIA	**2200-3300**		**> 3300**	
	Characidae	*Grundulus* (2)	Trichomycteridae	*Trichomycterus* (1)
	Trichomycteridae	*Eremophilus* (1)		
		Rhizosomichthys (1)		
		Trichomycterus (1)		
ECUADOR	**2200-3300**		**> 3300**	
	Astroblepidae	(16)	Characidae	*Grundulus* (1)
PERU	**1500-3000**		**> 3500**	
	Characidae	*Acrobrycon (1)*	Trichomycteridae	*Trichomycterus* (2)
		Ceratobranchia (2)	Cyprinondontidae	*Orestias* (32)
		Creagrutus (2)	Astroblepidae	*Astroblepus* (3)
	Astroblepidae	*Astroblepus (5)*		
	Loricariidae	*Chaetostoma (4)*		
	Trichomycteridae	*Trichomycterus (3)*		
	Cyprinondontidae	*Orestias (6)*		
	Atherinopsidae	*Basilichthys (1)*		
BOLIVIA	**1500-3000**		**> 3000**	
	Characidae	*Hemibrycon* (1)	Trichomycteridae	*Trichomycterus* (6)
		Astyanax (1)	Cyprinondontidae	*Orestias* (24)
		Knodus (1)		
		Oligosarcus (2)		
	Astroblepidae	*Astroblepus* (1)		
	Loricariidae	*Ancistrus* (1)		
		Hypostomus (2)		
	Trichomycteridae	*Trichomycterus* (16)		
	Heptapteridae	*Cetopsorhamdia* 1)		
		Rhamdia (1)		
	Callichthyidae	*Callichthys* (1)		
	Cyprinondontidae	*Orestias* (1)		
	Prochilodontidae	*Prochilodus* (1)		

Peruvian lakes are characterized by low fish diversity, and some lakes do not hold any species at all, the exception being Lake Titiaca with high species richness and endemism (95 %) due to the genus *Orestias* (Tables 20.5, 20.8). Among Peruvian rivers, greatest diversity is found in the Upper Amazon watershed (Upper Marañon and Upper Ucayali), and about 30 % of its species are endemic to Peru. Elevational diversity patterns are poorly known. According to Ortega (1992) and Ortega and Hidalgo (2008), > 80 species of Characidae, Trichomycteridae, Loricariidae, and Astroblepidae have been recorded above 1000 m.

Table 20.6. Number of fish species recorded in Colombia by elevational zone and watershed.

Elevation (m)	500 - 1100	1100-2200	2200-3300	>3300	Total	Endemics
COLOMBIA						
No. of species	208	59	5	1	220	82
No. of endemic species	71	21	5	1		
Watersheds	**Magdalena-Cauca**	**Atrato-Sinú**	**Northern Pacific**	**Catatumbo**	**Orinoco-Guaviare**	**Upper Amazon**
No. of species	155	45	47	12	32	24
No. of endemic species	66	4	2	0	3	7

Table 20.7. Number of fish species recorded in Ecuador by elevational zone and watershed.

Elevation (m)	500 - 1100	1100-2200	2200-3300	>3300
Northern Pacific	29	7	6	1
Endemic species	18	7	6	1
Southern Pacific	12	5	5	0
Endemic species	7	5	5	0
Guayas	18	5	5	0
Endemic species	10	5	5	0
Upper Amazon	49	8	4	0
Endemic species	19	8	4	0

Table 20.8. Number of fish species recorded in Peru by elevational zone and watershed. Sources: Ortega et al. 2007, Ortega and Hidalgo (2008). ? = no information available.

	Lakes		**Rivers**	
Elevation (m)	**600 - 3000**	**≥ 3500**	**600 - 3000**	**>3000**
Southern Pacific	?	?	?	?
Endemic species	?	?	?	?
Upper Amazon				
Upper Marañón	3	0	75	9
Endemic species	2	0	26	6
Upper Ucayali	3	0	95	10
Endemic species	2	0	30	8
Madera	0	0	60	8
Endemic species	0	0	12	6
Titicaca	*	39	*	?
Endemic species	*	37	*	?

With the exception of the Lake Titicaca basin (see above in the Peru section), high-Andean lakes and cushion bogs in Bolivia have very low fish diversity: only two species have been recorded (*Orestias agassi* and *Trichomycterus* aff. *rivulatus*). The fish fauna of lakes in the montane zone is very poorly known and appears to be low in number of species (Tables 20.5, 20.9). In Bolivian rivers, species richness is highest below 1500 m (111 species). Between 1500 and 3000 m 30 species have been recorded, whereas above 3000 m only nine species are known to occur. With respect to watersheds, species richness is highest in the Madera basin (Table 20.9). With the exception of Lake Titicaca, few fish species are endemic to Bolivia. Different sources also provide different numbers for total and endemic species based on whole watershed surveys (compare numbers for the Titicaca watershed in tables 20.8 and 20.9), possibly because they discount introduced commercial species.

Table 20.9. Number of fish species recorded in Bolivia by elevational zone and watershed. Sources: Pearson (1924), Fowler (1940), Durand (1968), Lauzanne et al. (1991), Sarmiento y Barrera (1997, 2004), Fernández y Miranda (2007), unpubl. data of F. Carvajal-Vallejos, M. Maldonado, M. Arraya, E. de la Barra y J. Zubieta. * = not recorded in the respective elevational zone or watershed; ? = no information available.

	Lakes			**Rivers**			**Bogs**	**Total**	**Endemics**
Elevation (m)	**500 - 1500**	**1500-3000**	**>3000**	**500 - 1500**	**1500-3000**	**>3000**	**>3000**		
Titicaca	*	*	25	*	*	3	2	28	23
Endemic species			23			?	0		
Southern Altiplano	*	*	2	*	*	3	2	3	1
Endemic species			1			1	0		
Madera								112	2
Beni	?	?	?	57	7	2	?	61	?
Endemic species	?	?	?	?	?	?	?		
Ichilo-Chapare	?	?	?	13	2	1	?	16	?
Endemic species	?	?	?	?	?	?	?		
Grande	?	4	1	41	16	2	?	46	2
Endemic species	?	1	1		2	?	?		
Pilcomayo	?	?	?	10	8	3	1	18	1
Endemic species	?	?	?	1	?	?	0		
Bermejo	?	?	*	28	8	*	*	29	0
Endemic species	?	?		0	0				

Diversity Patterns in Summary

The information presented above on aquatic diversity patterns in the tropical Andes allows for the following observations:

- It is generally accepted that in tropical montane systems, elevational patterns of diversity prevail over latitudinal ones, and they are more pronounced in some groups such as fishes

(Winemiller et al. 2008), but less evident in others such as invertebrates (Jacobsen 2008). However, although these patterns have been recognized, they are poorly known.

- The data summarized here corroborate the pattern of decreased diversity with increasing elevation for fishes. For algae and aquatic plants, diversity apparently is greatest in the high-Andean zone (> 3000 m), perhaps as a result of the great number lentic environments in this zone. For algae, however, this could be an artifact of the emphasis of studies on high-Andean lakes rather than montane rivers. For planktonic and benthic invertebrates no clear elevational patterns can be observed.
- The two main elevational zones recognized here can be differentiated based on their particular characteristics: the high-Andean zone (> 3000 m) with its extreme climatic conditions stands out as a lacustrine landscape, with a characteristic flora and fauna. The montane zone (500-3000 m) is a predominantly fluvial landscape characterized by a high diversity of fishes,algae and benthic macroinvertebrates.
- Although the definition of the number of endemic species or levels of endemism is problematic given the current regional knowledge gaps, high endemism is evident in fishes. As a preliminary estimate, between 35 and 40 % of Andean fishes may be endemic, including almost all high-Andean species. For algae, aquatic plants, and invertebrates, endemism is low at the generic level, but at the species level this assessment may change as more information becomes available.

Determinant Factors of Diversity Patterns

Biodiversity is the result of a complex blend of processes that interact at a variety of spatial and temporal scales. Habitat determines which species can live in a given location, but how many species can coexist depends on a wide range of additional factors (Gaston and Blackburn 2000). To facilitate an understanding of these factors in aquatic environments, we here use the concept of biological filters, which act on historical (zoogeographic filters) to regional (hydrogeographic filters) and local scales (abiotic and local biotic filters) (Pouilly et al. 2004).

In aquatic environments, causal factors of observed diversity patterns have largely been examined for fishes, but these studies have primarily focused on local scale factors and processes such as physical factors, habitat diversity, and biotic interactions. At a regional scale, species richness and community composition have been linked to factors that include, among others, watershed area, energy availability, evolutionary history, climate, and regional species richness (Jackson and Harvey 1989, Oberdorff et al. 1995, Oberdorff et al. 2001, Walters et al. 2003, Currie et al. 2004, Tales et al. 2004, Pont et al. 2005).

Although it is generally accepted that diversity is high in the tropics, the causes of this pattern remain largely unexplained for freshwater ecosystems. In addition to a scarcity of species lists, an interpretation of the available information is obscured by the confounding influence of different evolutionary histories on aquatic communities (Boulton et al. 2008).

In the tropical Andes few studies have focused on examining the role local factors play in determining species richness. Examples include studies on macroinvertebrates and aquatic plants in Ecuadorian streams (Jacobsen and Encalada 1998, Jacobsen and Terneus 2001) as well as on algae, zooplankton, and aquatic plants in Bolivia (Acosta et al. 2003, De La Barra 2003, Aguilera et al. 2007, Coronel et al. 2007). We know of no tropical Andean studies on regional factors.

Based on this evaluation, the following knowledge gaps and priorities for future studies can be identified:

- Inventories of fishes and macroinvertebrates in lakes and wetlands such as cushion bogs and *Sphagnum* peat bogs, of algae in rivers and wetlands, of aquatic plants in general.
- Species-level taxonomic studies and revisions of macroinvertebrates.
- Improve geographic coverage of research, as almost all watersheds are understudied. Those that drain to the Pacific are the least known. More information is available for the Magdalena-Cauca, Upper Amazon, and Madera than for other watersheds, but it is still insufficient.
- Determine endemism in algae, aquatic plants, and invertebrates, and in fishes in Bolivia.
- Determine causal explanations of diversity patterns at local and regional scales.
- Make information available online, much of the existing information is currently only available through specialists.

Andean Aquatic Diversity and Climate Change

Freshwater ecosystems are particularly vulnerable to climate change, as changes in hydrological processes will combine with other pressures such as population growth, land-use changes, increasing demands for water, and water pollution (Kundzewicz et al. 2008). Effects on aquatic ecosystems will be diverse, including changes in the spatial distribution of environments, river geomorphology, inputs from terrestrial ecosystems, riparian zones and floodplains, water turnover and chemical influx in lakes, and ecosystem metabolism (Carpenter et al. 1992). All of these aspects will affect the abundance and distribution of species. As shown recently, a small change in the number of species can have consequences for community structure and ecosystem processes (trophic interactions, productivity, nutrient recycling, energy transfer, etc.) (Emmerson et al. 2005).

The expected increase in temperatures could affect freshwater ecosystems at different levels, from the physiology and phenology of individual organisms to the geographic distribution of species and community composition. Substantial changes in temperature and hydrological regimes are expected to occur in aquatic ecosystems in particular, especially in arid and semi-arid regions, causing local species extinctions due to physiological stress or interactions with other species. Above all, shallow lakes appear to be particularly vulnerable to climate change (Meerhof 2006).

Even though such changes are foreseeable, very little is currently known about the specific effects that may occur in aquatic ecosystems. Some studies have explored possible responses to climate change scenarios. In Europe, for example, cold-water fishes (e.g., species of headwater streams) are predicted to decline due to the warming of water bodies, whereas cool- and warm-water species are expected to expand their distribution ranges (Buisson et al. 2008). This will affect the diversity of species and of biological traits as well as species composition, with upstream and midstream assemblages expected to become more modified than downstream assemblages (Buisson et al. 2008, Buisson and Grenouillet 2009). Similar predictions have been made for other groups such as phytoplankton, zooplankton, and macroinvertebrates. Vadadi-Fülop et al. (2008), for example, indicated that changes in abundance and annual life cycles could occur under scenarios of drastic temperature increases.

Although temperature is one of the key factors considered in climate change predictions, UV radiation is receiving increasing attention (Williamson and Rose 2009) due to its significant effects on aquatic organisms and because of the potential changes it can cause at all levels of ecological functioning. It affects the structure of phytoplankton communities, growth and development processes, and various physiological responses of organisms (Häder et al. 2007). Clear-water lakes could be especially sensitive to changes in UV radiation (Williamson and Rose 2009, Häder et al. 2007).

Despite the risks that freshwater environments are facing, they have been neglected in adaptation and mitigation plans for global change. Freshwater systems are critical for the sustainability of ecosystems and society, and they are strongly linked to climate and land use (Kundzewicz et al. 2008). Although the majority of research in aquatic ecology is relevant in this respect, few studies focus on the consequences of global change. Freshwater ecologists and climatologists must readjust their research to form a common agenda. The former must consolidate work at landscape and watershed scales and overcome the boundaries that divide hydrology from wetland and river ecology as well as limnology. For this approach the generation of mesoscale climate models will be indispensable (Carpenter et al. 1992).

High-Andean aquatic ecosystems are likely most vulnerable, and could serve as highly sensitive indicators of climate change. As elevational distribution patterns of species are changing, lower limits of organisms adapted to low water temperatures could be shifted upward by several hundred meters. Increases in temperature and changes in hydrological regime of rivers due to changes in precipitation and glacial retreat will affect key processes and habitat characteristics, life cycles, community assembly, organic matter processing, and primary productivity (Jacobsen 2008).

We consider that a basic strategy for developing the minimum knowledge necessary to cope with the effects of climate change on Andean aquatic ecosystems should include:

- Compilation and integrated analytical documentation of the existing information on aquatic flora and fauna, which should be centered on online reference data bases on the occurrence and distribution of species.
- Taxonomic revisions of groups that are important in terms of their species diversity, endemism, or indicator qualities.
- Research on local versus regional factors that control diversity.
- A risk assessment and vulnerability evaluation of Andean aquatic biodiversity in the face of climate change.
- A regional analysis of conservation priority areas that could be resilient to climate change.

Acknowledgments

We thank Santiago Duque, Marcela Nuñez, and Hernán Aristizabal in Colombia, Christian Martínez and Antonio Torres in Ecuador, Edgar Goitia, Mariana Arraya, Evans de la Barra, and José Zubieta in Bolivia.

Literature Cited

Abell, R., M. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N. Mandrak, S. Contreras, W. Bussing, M. Stiassny, P. Skelton, G. Allen, P. Unmak, A. Naseka, R. Sindorf, J. Robertson, E. Armijo, J. Higgins, T. Heibel, E. Wikramanayake, D. Olson, H. López, R. Ries, J. Lundberg, M. Sabaj Pérez, and P. Petra. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* 58:403-414.

Acosta, F., M. Cadima, and M. Maldonado. 2003. Patrones espaciales de la comunidad planctónica lacustre en un gradiente geofísico y bioclimático de Bolivia. *Revista Boliviana de Ecologia y Conservación Ambiental* 13:31-53.

Aguilera, X., S. Declerck, L. De Meester, M. Maldonado, and F. Ollevier. 2006. Tropical high-Andes lakes: a limnological survey and an assessment of exotic rainbow trout (*Oncorhynchus mykiss*). *Limnologica* 36:258-268.

Aguilera, X., S. Declerck, and L. De Meester. 2007. Zooplancton en lagunas tropicales de la cordillera de los Andes: diversidad taxonómica y relación con factores ambientales. Pp. 1053-1058 in *Memorias del Congreso Internacional sobre Desarrollo, Medio Ambiente y Recursos Naturales, Vol. II*, edited by J. Feyen, L. F. Aguirre, and M. Moraes. Cochabamba: Universidad Mayor de San Simón.

Arévalo, R. 2005. Perú. Pp. 33-40 in *Turberas altoandinas, espacios frágiles de vida y cultura*, edited by X. Izurieta. Quito: Global Peatland Iniciative, Netherlands Committee for IUCN, ECOPAR, and Grupo Páramo.

Aristizábal, H. 2002. *Los hemípteros de la película superficial del agua en Colombia. Parte 1. Familia Gerridae*. Bogotá: Academia Colombiana de Ciencias Exactas, Físicas y Naturales and Editora Guadalupe. 239 pp.

Boulton, A., L. Boyero, A. P. Covich, M. Dobson, S. Lake, and R. Pearson. 2008. Are tropical streams ecologically different from temperate streams? Pp. 257-284 in *Tropical stream ecology*, edited by D. Dudgeon. Amsterdam: Elsevier – Academic Press.

Buisson, L., W. Thuiller, S. Lek, P. Lim, and G. Grenouillet. 2008. Climate change hastens the turnover of fish stream assemblages. *Global Change Biology* 14:2232-2248.

Buisson, L., and G. Grenouillet. 2009. Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. *Diversity and Distributions* 15:613-626.

Cadima, M., E. Fernández, and L. López. 2005. *Algas de Bolivia con énfasis en el fitoplancton*. Santa Cruz de la Sierra: Editorial Centro de Ecología y Difusión Simón I. Patiño.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23:119-139.

Castro, M. 2007. Humedales de la puna del norte de Chile. Pp. 15-46 in *Gestión sostenible de humedales*, edited by M. Castro and L. Fernández. Santiago de Chile: Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo and Universidad de Chile.

Coronel, J., S. Declerck, and L. Brendonck. 2007. High-Andes peatland temporary pools house a high cladoceran and macroinvertebrate diversity. *Wetlands* 27:1166-1174.

Crespo, A., P. van Damme, and M. Zapata. 2008. Clasificación de cuencas de Bolivia según la metodología de Pfafstetter. *Revista Boliviana de Ecología y Conservación Ambiental* 22:69-76.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guégan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate based hypothesis of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121-1134.

De la Barra, N. 2003. Clasificación ecológica de la vegetación acuática en ambientes lacustres de Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 13:65-93.

De Oliveira, P., and M. Steinitz-Kannan. 1993. The diatom flora (Bacillariophyceae) of the Cuyabeno Faunistic Reserve, Ecuadorian Amazonia. *Nova-Hedwigia* 54:515-552.

Díaz, C., and C. Rivera-Rondón. 2004. Diatomeas de pequeños ríos andinos y su utilización como indicadoras de condiciones ambientales. *Caldasia* 26:381-394.

Donato, J. 2001. *Fitoplancton de los lagos andinos del norte de Sudamérica (Colombia). Composición física y factores de distribución*. Bogotá: Academia Colombiana de Ciencias Exactas, Físicas y Naturales and Editora Guadalupe. 232 p.

Donato, J. 2004. Consideraciones generales sobre el estado de los ambientes acuáticos de agua dulce en Colombia. Pp. in 226-236 in *Humedales de Iberoamérica*, edited by J. J. Neiff. La Habana: Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo.

Durand, J. 1968. Etude des poissons récoltés dans la grotte de Umajalanta (Bolivie), *Trichomycterus chaberti* sp. n. *Annales de Spéléologie* 23:343-353.

Emmerson, M., M. Bezemmer, M. D. Hunter, and T. H. Jones. 2005. Global change alters the stability of food webs. *Global Change Biology* 11:490-501.

Encalada, A. 1997. *Diversidad y abundancia de macroinvertebrados en relación a factores físico-químicos y de fuentes de alimento en dos tipos de ríos de los páramos del Ecuador*. Licenciatura thesis. Quito: Pontifica Universidad Católica del Ecuador.

Fernández, L., and G. Miranda. 2007. A catfish of the genus *Trichomycterus* from a thermal stream in southern South America (Teleostei: Siluriformes, Trichomycteridae) with comments on relationships within the genus. *Journal of Fish Biology* 71:1303-1316.

Flachier, A. 2005. Ecuador. Pp. 25-32 in *Turberas altoandinas, espacios frágiles de vida y cultura*, edited by X. Izurieta. Quito: Global Peatland Iniciative, Netherlands Committee for IUCN, ECOPAR, and Grupo Páramo.

Fowler, H. W. 1940. Zoological results of the second Bolivian expedition for the Academy of Natural Sciences of Philadelphia, 1936-1937. Part I. The fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 92:43-103.

Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and process in macroecology*. Oxford: Blackwell.

Gaviria, S., and N. Aranguren. 2007. Especies de vida libre de la subclase Copepoda (Arthropoda, Crustacea) en aguas continentales de Colombia. *Biota Colombiana* 8:53-68.

Gery, J. 1969. The freshwater fishes of South America. Pp. 828-848 in *Biogeography and ecology in South America, vol. 2*, edited by E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli. The Hague: Junk.

Goitia, E., M. Maldonado, F. Acosta, N. de la Barra, M. Cadima, J. Coronel, and A. Salvatierra. 2007. Tipificación de humedales altoandinos de Bolivia: biocenosis acuática de los bofedales. Pp. 1125-1129 in *Memorias del Congreso Internacional sobre Desarrollo, Medio Ambiente y Recursos Naturales, Vol. II*, edited by J. Feyen, L. F. Aguirre, and M. Moraes. Cochabamba: Universidad Mayor de San Simón.

Häder, D. P., H. D. Kumar, R. C. Smith, and R. C. Worrest. 2007. Effects on aquatic ecosystems. *Journal of Photochemistry and Photobiology* 46:53-68.

Hurlbert, S. H., G. Rodriguez, and N. Dies Dos Santos (eds). 1981. *Aquatic biota of tropical South America, part I, Arthropoda*. San Diego: San Diego State University.

Hurlbert, S. H., W. Loayza, and T. Moreno 1986. Fish-flamingo-plankton interactions in the Peruvian Andes. *Limnology and Oceanography* 31:457-468.

Iltis, A., J. P. Carmouze, and J. Lemoalle. 1991. Características físico-químicas del agua. Pp.107-113 in *El lago Titicaca: síntesis del conocimiento limnológico actual*, edited by C. Dejoux and A. Iltis. La Paz: ORSTOM-HISBOL.

Izurieta, X. 2007. Estrategia de humedales altoandinos. Pp. 173-183 in *Gestión sostenible de humedales*, edited by M. Castro y L. Fernández. Santiago de Chile: Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo and Universidad de Chile.

Jackson, D. A., and H. H. Harvey. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. *Ecology* 70:1472-1484.

Jacobsen, D., and A. Encalada. 1998. The macroinvertebrate fauna of Ecuadorian highland streams in the wet and dry season. *Archiv für Hydrobiologie* 142:53-70.

Jacobsen, D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* 49:1293-1305.

Jacobsen, D. 2008. Tropical high-altitude streams. Pp. 219-256 in *Tropical stream ecology*, edited by D. Dudgeon. Amsterdam: Elsevier – Academic Press.

Jacobsen, D., and E. Terneus. 2001. Aquatic macrophytes in cool aseasonal and seasonal streams: a comparison between Ecuadorian highland and Danish lowland streams. *Aquatic Botany* 71:281-295.

Jacobsen, D., C. Cressa, J. M. Mathooko, and D. Dudgeon. 2008. Macroinvertebrates: composition, life histories and production. Pp. 65-105 in *Tropical stream ecology*, edited by D. Dudgeon. Amsterdam: Elsevier – Academic Press.

Koste, W., and J. De Paggi. 1982. Rotifera of the superorder Monogonta recorded from Neotropis. *Gewässer und Abwasser* 68-69:71-102.

Kundzewicz, Z. W., L. J. Mata, N. W. Arnell, P. Döll, B. Jimenez, K. Miller, T. Oki, Z. Sen, and I. Shiklomanov. 2008. The implications of projected climate change for freshwater resources and their management. *Hydrological Sciences Journal* 53:3-10.

Lauzanne, L., G. Loubens, and B. Le Guennec. 1991. Liste commentée de poisons de l'Amazonie Bolivienne. *Revue d'Hydrobiologie Tropicale* 24:61-76.

Lewis, W. 2008. Physical and chemical features of tropical flowing waters. Pp. 1-22 in *Tropical stream ecology*, edited by D. Dudgeon. Amsterdam: Elsevier – Academic Press.

Maldonado, M., and E. Goitia. 2003. Las hidroecoregiones del Departamento de Cochabamba. *Revista Boliviana de Ecología y Conservación Ambiental* 13:117-141.

Maldonado, M., E. Goitia, and M. Bustamante. 2007. Patrones de composición y distribución de la fauna bentónica fluvial sobre un gradiente geofísico y bioclimático en Bolivia. Pp. 1143-1149 in *Memorias del Congreso Internacional sobre Desarrollo, Medio Ambiente y Recursos Naturales, Vol. II*, edited by J. Feyen, L. F. Aguirre, and M. Moraes. Cochabamba: Universidad Mayor de San Simón.

Maldonado-Ocampo, J., A. Ortega-Lara, J. S. Usma, G. Galvis, F. A. Villa-Navarro, L. Vásquez, S. Prada-Pedreros, and C. Ardila. 2005. *Peces de los Andes de Colombia*. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. 346 pp.

Meerhoff, M. 2006. *The structuring role of macrophytes on trophic dynamics in shallow lakes under a climate warming scenario*. PhD thesis. Århus: University of Århus. 154 pp.

Montes de Oca, I. 2004. *Enciclopedia geográfica de Bolivia*. La Paz: Editorial Atenea SRL.

Muñoz-Quesada, F. 2004. El orden Trichoptera (Insecta) en Colombia II. Inmaduros y adultos, consideraciones generales. Pp. 319-349 in *Insectos de Colombia, vol. 3*, edited by M. G.

F. Fernández, G. Andrade, and G. Amat García. Bogotá: Academia Colombiana de Ciencias Exactas, Físicas y Naturales.

Navarro, G., and M. Maldonado. 2002. *Geografía ecológica de Bolivia: vegetación y ambientes acuáticos*. Cochabamba: Editorial Centro de Ecología y Difusión Simón I. Patiño.

Navarro, G., and W. Ferreira. 2007. *Mapa de vegetación de Bolivia, escala 1:250 000.* CD-ROM. Santa Cruz de la Sierra: The Nature Conservancy.

Oberdorff, T., J.-F. Guégan, and B. Hugueny. 1995. Global scale patterns of fish species richness in rivers. *Ecography* 18:345-352.

Oberdorff, T., D. Pont, B. Hugueny, and D. Chessel. 2001. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. *Freshwater Biology* 46:399-415.

Ortega, H. 1992. Biogeografía de los peces neotropicales de aguas continentales del Perú, con especial referencia a especies registradas a altitudes superiores a los 1000 m. *Memorias del Museo de Historia Natural (Lima)* 21:39-45.

Ortega, H., H. Guerra R., and R. Ramírez. 2007. The introduction of non-native fishes into freshwater systems of Peru. Pp. 247-278 in *Ecological and genetic implications of aquaculture activities*, edited by T. Bert. Berlin: Springer.

Ortega, H., and M. Hidalgo. 2008. Freshwater fishes and aquatic habitats in Perú: current knowledge and conservation. *Aquatic Ecosystem Health and Management* 11:257-271.

Pearson, N. E. 1924. The fishes of the eastern slope of the Andes. I. The fishes of the Rio Beni basin, Bolivia, collected by the Mulford expedition. *Indiana University Studies* 11(64):1-38.

Pont, D., B. Hugueny, and T. Oberdorff. 2005. Modelling habitat requirement of European fishes: do species have similar responses to local and regional environmental constraints? *Canadian Journal of Fisheries and Aquatic Sciences* 62:163-173.

Pouilly, M., F. Lino, and T. Yunoki. 2004. Peces de las lagunas. Pp. 323-350 in *Diversidad biológica en la llanura de inundación del Río Mamoré*, edited by M. Pouilly, S. Beck, M. Moraes, and C. Ibañez. Santa Cruz: Centro de Ecología y Difusión Simón I. Patiño.

Richerson, P. J., P. J. Neale, R. Alfaro, X. Lazzaro, W. Vincent, and W. Wurtsbaugh. 1991. Producción planctónica primaria y biomasa algal. Pp. 211-227 in *El lago Titicaca: síntesis del conocimiento limnológico actual*, edited by C. Dejoux and A. Iltis. La Paz: ORSTOM-HISBOL.

Ringuelet, R. A. 1975. Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. *Ecosur* 2:1-122.

Roldán-Perez, G. R. 1988. Guía para el estudio de los macroinvertebrados acuáticos del departamento de Antioquia. Bogotá: Fondo FEN and Colciencias. 217 pp.

Román-Valencia, C., R. Ruiz, and R. Barriga. 2005. Una nueva especie ecuatoriana del género de peces andinos *Grundulus* (Characiformes: Chararacidae). *Revista de Biología Tropical* 53:537-544.

Rubio, F., C. Amezquita, and R. Franco. 2005. Colombia. Pp. 17-24 in *Turberas altoandinas, espacios frágiles de vida y cultura*, edited by X. Izurieta. Quito: Global Peatland Iniciative, Netherlands Committee for IUCN, ECOPAR, and Grupo Páramo.

Rumrich, U., H. Lange-Bertalot, and M. Rumrich. 2000. Diatoms of the Andes from Venezuela to Patagonia/Tierra del Fuego. *Iconographia Diatomologica* 9:1-649.

Sala, S., J. Ramírez, and Y. Plata. 2008. Diatoms from lentic and lotic systems in Antioquia, Chocó, and Santander departments in Colombia. *Revista de Biología Tropical* 56:1159-1178.

Sarmiento, J., and S. Barrera. 1997. Observaciones preliminares sobre la ictiofauna de la vertiente oriental de los Andes. *Revista Boliviana de Ecología y Conservación Ambiental* 2:77-99.

Sarmiento, J., and S. Barrera. 2004. List of fish present in Bolivia. Pp. 573-582 in *Biodiversity: the richness of Bolivia*, edited by P. L. Ibisch and G. Merida. Santa Cruz de la Sierra: Editorial FAN.

Steinitz-Kannan, M. 1997. The lakes in Andean national parks and other protected areas in Ecuador. *The George Wright Forum* 14(3):33-43.

Steinitz-Kannan, M. 2000. *Las diatomeas del Ecuador*. Quito: Museo Ecuatoriano de Ciencias Naturales.

Tales, E., P. Keith, and T. Oberdorff. 2004. Density-range size relationships in French riverine fishes. *Oecologia* 139:360-370.

Vadadi-Fülop, C., L. Huenagel, C. Sipkay, and C. Veraszto. 2008. Evaluation of climate change scenarios based on aquatic food web modeling. *Applied Ecology and Environmental Research* 6:1-28.

Velez-Espino, L. A. 2004. Threatened fishes of the world: *Astroblepus ubidiai* (Pellegrin 1931) (Astroblepidae). *Environmental Biology of Fishes* 71:296.

Walters, D. M., D. S. Leigh, M. C. Freeman, B. J. Freeman, and C. M. Pringle. 2003. Geomorphology and fish assemblages in a piedmont river basin, USA. *Freshwater Biology* 48:1950-1970.

Williamson, C. E., and K. C. Rose. 2009. Ultraviolet insights: attempting to resolve enigmatic patterns in pelagic freshwaters – the historical context and a view to the future. *International Review of Hydrobiol*ogy 94:129-142.

Winemiller, K. O., A. Agostinho, and E. Pellegrini. 2008. Fish ecology in tropical streams. Pp. 107-146 in *Tropical stream ecology*, edited by D. Dudgeon. Amsterdam: Elsevier – Academic Press.

Zúñiga, M. del C., C. Molineri, and E. Domínguez. 2004. El orden Ephemeroptera (Insecta) en Colombia. Pp. 17-42 in *Insectos de Colombia, vol. 3*, edited by M. G. F. Fernández, G. Andrade, and G. Amat García. Bogotá: Academia Colombiana de Ciencias Exactas, Físicas y Naturales.

21

Species Distribution Modeling and the Challenge of Predicting Future Distributions

Catherine H. Graham, Bette A. Loiselle, Jorge Velásquez-Tibatá, and Francisco Cuesta C.

Climate change has caused reduction and expansion in the ranges of a variety of animals, and has altered community composition and dynamics (e.g., Parmesan 2006, La Sorte and Thompson 2007, Moritz et al. 2008). Scientists are now challenged to predict how species will respond to continued climate change. This challenge is particularly pressing since conservation practitioners are increasingly interested in adapting proactive management strategies to mitigate biodiversity loss with climate changes (Pressey et al. 2007, Hannah 2008, Thuiller et al. 2008). For instance, knowledge about how species distributions may change is necessary to determine if the protection conferred by national parks will persist (Araújo et al. 2004, Velasquez et al. unpublished, Hole et al. 2009) or how ecosystem services might be influenced by warming temperatures (Delucia et al. 2008, Vos et al. 2008).

One common approach to predict how climate changes will influence species ranges is species distribution modeling (SDM), a method that uses the relationships between species occurrence and climate for prediction (e.g., Peterson et al. 2002, Thomas, et al. 2004, Anciães and Peterson 2006). While it is difficult to assess the accuracy of forecasts for future biodiversity patterns, SDM has been successful in modeling historic distributions of species accurately over both long (Peterson et al. 2004, Hugall et al. 2002, Carnaval and Moritz 2008, Pearman et al. 2008, Peterson and Nyari 2008) and relatively short (i.e., Araújo et al. 2005, Mitikka et al. 2008) time scales.

While SDM is an important tool for predicting how species will respond to climate change it has a series of limitations and assumptions that must be considered. First, SDM must provide a reasonable estimate of a species' niche, which implies that it will capture meaningful relationships between species occurrence and the environment (Austin 1998, 2002, Holt and Keitt 2005, Elith and Graham 2009). Assuming this is possible, SDM can only estimate the realized niche because it is based on where a species currently exists and has no information about the complete range of climate conditions where it could exit. In addition, SDM does not consider how population dynamics vary under different environmental conditions (this requires an integration of ecophysiological models with population dynamics (e.g., see Crozier and Dwyer 2006, Buckley 2008). In particular, SDMs that do not include absence data will tend to give the potential distribution because information on species interactions or other factors limiting the species range are not taken into account. Absence data sometimes provides this additional information (Jimenez-Valverde et al. 2008). Further, for SDM to be useful in predicting changes in distribution it must consider a species' dispersal abilities at the leading edge of the range and genetic changes and population persistence at the trailing edge of its range (Malcolm et al. 2002, Pearson and Dawson 2005, Iverson et al. 2004, Hampe and Petit 2005, Thuiller et al. 2008). Finally, SDM will be challenged when predicting to future climates that have no current analogue; such models should consider a species' abilities to adapt to novel environments, including new climate conditions and biotic interactions (Parmesan 2006, Araújo and Luoto 2007, Thuiller et al. 2008). All of these aspects, among others, elucidate the inherent uncertainty and challenges associated with forecasting the effects of climate change on biodiversity. To this end, we summarize current best practices for modeling across time, highlight limitations in using SDM for forecasting, and describe how SDM can be used in conjunction with other types of models or empirical data. We conclude with suggestions for future research.

A Guide to Using SDM for Prediction of Future Species Distributions

Using SDM to explore how climate change will influence species distributions requires making a series of decisions relating to the specific objective of the study, the type and quality of data available and the skills of the modeler (Table 21.1). As the field is rapidly advancing, Table 21.1 emphasizes the types of issues, rather than specific guidelines that should be considered when using SDM to predict future species distributions.

Environmental Predictor Variables -- One important consideration when using SDM to predict future distributions is choice of environmental parameters. First, it is critical that the association between the species' occurrence and the environmental variables have a biological basis (often referred to as direct variables) and, if possible, that species-environment response curves conform to what is known about a given species. It is better to use variables, such as temperature, that are hypothesized to have a direct mechanistic influence on a species distribution through their effects on bioenergetics and, consequently, population parameters (Guisan and Thuiller 2005). A somewhat limited set of relatively uncorrelated variables should be used to predict distributions so that models are not over-parameterized (Araújo and Rahbek 2006, Hijmans and Graham 2006, Thuiller et al. 2008). To date, there is no simple guideline as to how many variables to use for a modeling exercise, though a larger number of occurrences (assuming they are relatively well distributed across the range of the species) likely affords a greater number of predictor variables. Finally, habitat alteration and land-use change also influence species distributions and may act synergistically with climate as species are forced into novel landscapes (Walther 2007, Pearson et al. 2004, Jump and Peñuelas 2005, Jetz et al. 2007). As a result, land-use may be an important predictor variable in modeling future species distributions, although land-use has yet to be extensively used in forecasting with SDM (but see Higgins 2007, Van Vuuren et al. 2006, Jetz et al. 2007).

Predictor variables are derived from a wide variety of sources including interpolated climate surfaces such as the Worldclim database (http://*www.worldclim.org/*, Hijmans et al. 2005) and land-use and remote-sensing data (reviewed by Kerr and Ostrovsky 2003, Turner et al. 2003; see also Hole et al., Chapter 2, this volume). Predictor variables for future climate change

Table 21.1: Questions that should be considered when modeling distributions under both current and future climate conditions.

Broad category	Comment	Example questions
About me	For this category the user needs to identify the relevant questions, then find answers through a series of "road tests" or reviews that honestly appraise both the data and candidate techniques by their ability to deliver the required features.	Why do I want to make a model or series of models? · to understand main correlates of distribution? · to plan a monitoring program to document and study changes in species ranges? · to look at mapped distributions currently and in the future? To evaluate effectiveness of protected areas for current and future conservation of a suite of species? What are the required outputs of the model? · fitted functions? · uncertainty estimates? · predictions as binary maps? · predictions as ranks, relative likelihoods or probabilities? What is the relative importance of features? · speed? · accuracy? · availability of evaluation statistics? What modeling and GIS skills do I have? How soon do I need a result?
About the species	This links knowledge about the ecology of the species to properties of the model and the data	What do I know about the species response to its environment in my region of interest? How should this affect how I prepare and present my predictor variables? Am I interested in the potential (i.e., without the influence of humans) or real distribution (i.e., with human influence) distribution of species? What are the types of environmental data that I should consider? What is known about other species that might interact with the species being modeled and thus limit its range (i.e., host, disease or competitor)? How much time has the species had to disperse and reach equilibrium with its environment (i.e., how likely is it that I can capture most of the environmental conditions where a species is capable of living)? What is known about the ability of this species to disperse? What are the life-history characteristics of the species in terms of generation time, reproductive rate, etc.? Is there any indication that a species might be able to evolve to occupy new environments (i.e., are traits associated with a given environmental parameter of interest highly conserved across a phylogenetic hypothesis)?

About my data		What sort of data do I have? (a) Species data • presence, presence-absence or counts? • number? • how well do the records cover the region of interest? • are there sampling biases? – e.g. geographic biases, or clumping of records so that records are not independent? (b) Predictors: • do I have the relevant environmental data? • what data are available for different time periods or regions? What climate emissions scenarios or general circulation models should I use? • do I also require data describing disturbances or current land use?
About the modeling algorithm: assumptions, limitations and features	This explores the method and provides answers that would inform typical buyers questions – the questions could refer to a broad method or a particular implementation of it.	What are the limitations of the method, and will these become a liability? What are the assumptions of the method? Are they consistent with the species' ecology and the data quality? What is the quality of the publications about the method? • are they convincing scientifically? • are the tests sensible and relevant? • is the basis for the conclusion clear and unambiguous? What is known about its performance across a range of conditions? • is the information anecdotal? • has it been broadly tested - many trials and many independent authors? • how consistent are the assessments? How does the method work, and what implications does this have for the output? What particular features does the method have in general or in this version of it? – e.g.: • uncertainty estimates, • ability to model both continuous and categorical data, • ability to handle missing data, • variable selection methods.
About the modeling algorithm: implementation	These match the difficulty of implementation to the users skills	Does good performance depend on expert implementation? • how dependent is performance on optimal use? • how hard is it to learn to use the method competently? Is the software reliable? – is it coded well, and doing what it should be? Is there sound scientific documentation? • is it clear how it works? • is there a community of users that can offer help? • are there informative published articles?

are derived from two sources: an emissions scenario, and a global climate model (GCM, also referred to as general circulation models; for review aimed at ecologists see Beaumont et al. 2008). Emission predictions are determined by a variety of interacting factors including demographics, socio-economic development and technological changes and can vary from those that assume rapid economic growth to those with more sustainable human behaviors (http://www.ipcc.ch/). There are also numerous types of GCMs that make different assumptions about the physical processes that drive global climates. While GCMs make consistent predictions about changes in temperature, variation in precipitation changes is greater than 300% across models. For instance, in the Ecuadorian Andes predicted changes in rainfall (based on 19 IPCC scenarios) range from a 3000 mm/year decrease in precipitation to a 5000 mm/year increase (Buytaert et al. 2009). Further, GCM models are generally run at a scale (i.e., 1 degree pixel) which is too large for most ecological studies. Therefore the output is usually downscaled either through statistical interpolation using GIS or dynamic downscaling where a regional climate model (RCM) is run within the GCM (Beaumont et al. 2008).

Species Occurrence Data -- Perhaps, the most time-consuming and challenging aspect of SDM is obtaining occurrence data. International (i.e., Global Biodiversity Information Facility; http://www.gbif.org/) and national (i.e., BIOMAP, http://www.biomap.net/English/news.htm) bioinformatic initiatives promise to provide new data for SDM (Graham et al. 2004) and georeferencing tools and guides aid in this process (see Hijmans et al. 2000, Wieczorek et al. 2004, Guralnick et al. 2006). Nonetheless, there are still limited data for most taxa in the Neotropics and enhancing existing electronic data-bases, including conducting new inventories are priorities.

Here we highlight recent research results that provide guidance for modeling with limited occurrences. First, research on rare species indicates that a limited amount of occurrence data (i.e., 10-20 localities) can be used to create distribution models if these occurrences are relatively unbiased (Hernandez et al. 2006, Pearson et al. 2007). Research done on plants in the Andes suggests that spatial distribution of voucher specimens are often biased but some bias may be permissible if sample sizes are reasonably large (Loiselle et al. 2008). Further, how background data are generated can have important implications on model performance, especially for spatially biased data. For example, Phillips et al. (2009) showed that when background (pseudo-absence) occurrences were generated based on the occurrences of a suite of species (i.e., other species occurrences used as background in a model), model performance improved substantially. In a related study, Vanderwal et al. (2009) demonstrated that there was an optimal, intermediate distance from which background data should be generated. Occurrence data also needs to come from across the range of environments that the species may inhabit to provide more complete information on the environmental conditions where a species can exist (Thuiller et al. 2004b).

Modeling Method and Evaluation -- Debate continues on which modeling method is best for a given question, though methods that use background data, fit non-linear relationships, integrate interactions among predictor variables, and have some mechanism to reduce over-fitting perform better than those that do not, at least when modeling current species distributions (Elith et al. 2006). However, there is concern that certain types of models might be prone to over-fit because either too many predictor variables are used or an overly complex relationship between occurrences and predictor variables is generated (Araújo and Rahbek 2006, Randin et al. 2006; see also Thuiller et al. 2008). Such models might perform relatively well in current climates but may be overly restrictive when projected onto the future. Indeed, when different models are projected onto future climates very different predictions can result (Thuiller et al.

2004b). For this reason, some researchers advocate ensemble modeling where a series of methods are run and the final model is a composite of all results (Araújo and New 2007). While this approach seems promising it assumes that the methods in the ensemble are appropriate and well-parameterized.

Of particular importance for future climate change modeling is using models that can fit biologically meaningful species-environment relationships. To begin to evaluate if models can perform this task, Elith and Graham (2009) created a simulated species based on known species-environment response curves and showed that some modeling methods can recreate these response curves and identify which variable(s) were most important in defining the distribution. They advocate further in-depth research to explore how well models fit biologically reasonable response curves (also see Austin et al. 2006, Hirzel and Le Lay 2008).

Clearly, it is difficult to determine how well a model predicts future species distributions. Hence, an important step of all modeling is evaluating performance using a series of approaches (see Fielding and Bell 1997, Hernandez et al. 2006, Elith and Graham 2009). Perhaps the most common evaluation measure is area under the receiver operating curve (AUC), which measures model performance across all possible thresholds. Note that this measure is sensitive to the extent from which absence data are taken and should be used with care (Lobo et al. 2008). Some evaluation measures, as well as applications, require binary predictions of species presence-absence. To create binary predictions, models must be thresholded (see Liu et al. 2005 for a review of methods). However, choosing the most appropriate threshold will depend to some extent on the question at hand (Loiselle et al. 2003).

At all steps in SDM there is uncertainty. Conceptual frameworks are beginning to emerge to guide quantification of this uncertainty (e.g., Heikkinen et al. 2006, Beaumont et al. 2007). Nonetheless, there still remains little guidance as to how to actually quantify the various types of uncertainty inherent in SDM and most studies have only evaluated one or more types of uncertainty in model performance (e.g., Graham et al. 2008). This is an area where future research is needed.

Research Needs and Integration

Increasing biological realism of SDM -- There are several other issues particular to forecasting biological diversity with SDM that merit further discussion. First, when faced with climate change, species will either track or adapt to changing climates. To date, most studies assume that species will be able to perfectly track their climate niches through time (unlimited dispersal) or that they will be completely unable to move (no dispersal). This is clearly over-simplified as species have different dispersal abilities and vary in how well they can move through human-modified landscapes or across biogeographic barriers. To address this issue Phillips et al (2008), building on work by Williams et al. (2005), used network flow analyses to measure and optimize connectivity of suitable habitat through time and predict if species with a given dispersal ability will be able to track suitable habitat. Critical to such modeling is an estimate of species' dispersal abilities and behavior in novel landscapes, such as those modified by anthropogenic activity. In plants, selection for traits that promote long-distance dispersal is thought to be strongest in environments that are spatially or temporally heterogeneous (Muller-Landau and Hardesty 2005, Nathan 2006). Information from the field of behavioral landscape ecology could inform models on species' movement behavior in human-modified landscapes

(Knowlton and Graham in press, Hughes et al. 2007). Likewise, species at leading range edges have been shown to often disperse over greater distances in order to move through degraded habitats and track climate changes (Hughes et al. 2007). Successful migration into new areas, however, is not only a function of dispersal abilities, but is influenced by local population dynamics at the leading edge of the range, and recruitment and population growth in new areas (Thuiller et al. 2008). As a result species that have similar dispersal abilities may still differ in the likelihood of expanding their range with climate change because of differences in population dynamics. At a broader scale, and in some cases when limited information is available on animal dispersal behavior, researchers have assumed that physical barriers may limit dispersal. For instance, in the Andes species restricted to one slope of the Andes are predicted to exist on the other slope where they in fact are absent (both currently and in the future).

Species may not track climate changes but instead may persist in a given region because they are phenotypically plastic and can exist in a broader range of climate conditions than is evident based on their current distribution (e.g., Kramer 1995, Ghalambor et al. 2007, Brommer et al. 2008). Species may also adapt to new climate conditions (e.g., Balanya et al. 2006, Byars et al. 2007, Jump et al. 2008, Smith and Bernatchez 2008). However, a number of studies suggest that evolutionary response to climate change is likely too slow or even, non-existent (e.g. Etterson 2004; see review by Jump and Peñuelas 2005). Gienapp et al. (2008) caution that few researchers have evaluated the relative influence of these two mechanisms, plasticity and evolutionary change, on species' persistence in the face of climate change. If these mechanisms are not considered in SDM, predictions may be overly pessimistic and predict extinction when species may actually be able to adapt (e.g., Skelly et al. 2007).

A second challenge in SDM and, more broadly, all forecasting attempts, is to incorporate species interactions into the predictions (Araújo and Luoto 2007, Brooks and Hoberg 2007, Preston et al. 2008, Tylianakis et al. 2008). For example, few attempts have been made to model competition in an SDM framework under current environment conditions (but see Anderson et al. 2002, Cadena and Loiselle 2007, Heikkinen et al. 2007) let alone future climates. In an extensive review of how global change might impact biotic interactions (e.g., pollination, herbivory, disease), Tylianakis et al. (2008) found some generalizations, but many more uncertainties. Uncertainties arise because variably complex networks of interactions occur among species, and different drivers of global change (e.g., climate, land use, biotic invasions) may impact biotic interactions in non-additive ways (Bascompte et al. 2006). Nonetheless, the charge for SDM is to use insights from local scale experimental and observation studies of species interactions to predict how changes in biotic interactions will influence species distributions and patterns of biodiversity.

Finally, certain life-history and niche characteristics might influence the likelihood that species will decline in the face of climate change. For instance, habitat specialists, especially those that exist in limited environmental space (Thuiller et al. 2004a, Broennimann et al. 2006), such as at the tops of isolated mountains, are particularly susceptible to climate change (Williams et al. 2003, Velasquez et al. unpublished). In the Andes, many neo-endemic species may have low ecological plasticity because they evolved under particular conditions and as a result have a specialized niche, low genetic variability and low population numbers (Arctander and Fjeldså 1994; Roy et al. 1997). In plants, C3 species are predicted to be more negatively affected by climate changes than C4 species, partly because the former have highly specialized physiological adaptations to extreme climate conditions (Buytaert et al. in press). Species that are unable to disperse through human-modified landscapes may require relocation, often referred to as assisted migration (Hoegh-Gulberg et al. 2008).

Use of SDM in combination with other types of data or modeling approaches represents a relatively unexplored but potentially very informative research agenda (Betts et al. 2008, Keith et al. 2008, McRae et al. 2008, Monahan and Hijmans 2008). For example, Keith et al. (2008) combined SDM to predict suitable habitat for a series of different future time slices and stochastic population models (in a meta-population framework which included dispersal) to predict plant species persistence in the Fynbos of South Africa. Additionally, correlative models can be combined with empirically based physiological measurements to map a species' environmental limits (Kearney and Porter 2004, Hijmans and Graham 2006, Buckley 2008, Monahan and Hijmans 2008). Physiological models have some advantages over correlative environmental modeling in that they are more likely to model a species fundamental niche (Buckley 2008, Morin et al. 2008). Nonetheless, physiological and demographic data are currently not available for most species in the Neotropics, though these techniques hold promise for the future.

SDMs, climate change, and conservation in South America— One of the most important uses of SDM in South America is to predict what species or regions are most likely to be threatened by climate change. While there has been limited research on this topic, two recent studies highlight the potential of SDM to address conservation-oriented problems. Cuesta-Camacho et al. (unpublished) used a maximum entropy method (MAXENT, Phillips et al. 2006) to model the current and future distribution of 125 bird species and 102 vascular plants in the Northern Andes. They found that many of these species would suffer range reductions with climate changes and the number of species listed as critically endangered would increase depending on the emissions scenario employed. Species restricted to certain habitats, including paramos and dry valleys, were predicted to suffer the greatest declines. Further, granivorous birds were predicted to expand their ranges while ranges were predicted to shrink for most species in other trophic groups. In a related study, Velásquez et al. (in review) modeled the distribution of 169 threatened and range-restricted species in Colombia to predict how the ranges of these species would change under a variety of emission and dispersal scenarios. They found that 86-89% of species would present a decline in range size, and that most species extinctions are predicted to occur at mid-elevations (1000-3000m) and on isolated mountains such as the Sierra Nevada de Santa Marta and the Darien Highlands, whereas inter-Andean valleys (>1000m) and paramos would have small increases in species richness (Figure 21.1). Further, they determined how well protected areas would conserve future biological diversity – in essence they asked if the parks of today will confer the same protection tomorrow. They showed that currently only 64% of species evaluated are adequately represented in protected areas and that under climate change, current levels of protection would be adequate for only 21-43% of species.

These two papers focused on montane species, which are often considered especially susceptible to climate change because with warming and an increase in precipitation seasonality the environmental conditions where they live may disappear. They emphasize that SDMs provide only a qualitative prediction of what species or regions will be most susceptible to climate changes. Nonetheless, these qualitative predictions identify regions and species of special conservation concern and can be followed with more in-depth study and monitoring. As such SDM provide an invaluable tool to begin to explore how climate change might influence species distributions and biological diversity in South America. SDM studies across different taxonomic groups and in additional regions may provide further insight into what types of regions or species are particularly susceptible to climate change. Further, SDM studies can guide research initiatives aimed at studying and mitigating the effects of both climate change and land cover land use change (LUCC) dynamics on biological diversity.

Conclusions— While a valuable tool, SDM studies alone will not provide a complete picture of how climate change will affect factors such as population persistence, community composition, and ecosystem services. Increasingly though, SDM is combined with physiological, behavioral, demographic, and genetic information and such approaches are likely to better predict the impacts of climate and land-use change on biological diversity. While it is clearly impossible to study all species in detail, carefully selected taxa or study regions should be identified as potential model species or regions for more detailed studies. SDM, combined with biological information about different taxa, can be used to identify which species or regions are particularly susceptible to climate change. Research initiatives can then target these species or regions. This combined approach of using SDM to obtain a broad-scale prediction of how species distributions may change and conducting detailed studies on specific taxa or regions should provide an effective way forward to predict how species and regions will respond to continued climate change.

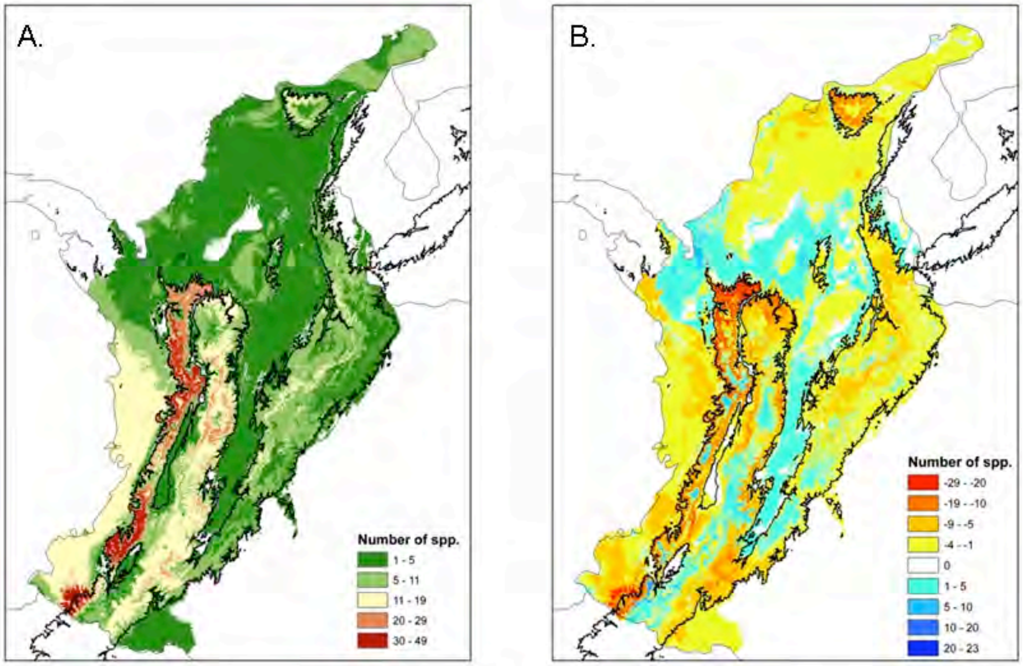

Figure 21.1. A: Current predicted species richness for 214 threatened, near-threatened and range restricted birds occurring in western Colombia, and B. change in richness (current predicted richness – future predicted richness) as a result of climate change, where red colors (negative values) indicate a predicted decrease in species richness and blue colors an increase in species richness.

Literature Cited

Anciaes, M., and A.T. Peterson. 2006. Climate change effects on neotropical manakin diversity based on ecological niche modeling. Condor 108:778-791.

Anderson, R. P., A. T. Peterson and Gomez-Laverde, M. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in south american pocket mice. Oikos 98:3-16.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743-753.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42-47.

Araújo, M. B., and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313:1396-1397.

Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species-climate impact models under climate change. Global Change Biology 11:1504-1513.

Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10:1618-1626.

Arctander, P., and J. Fjeldså. 1994. Avian tissue collections for DNA analyses. Ibis 136: 359-360.

Austin, M. P. 1998. An ecological perspective on biodiversity investigations: examples from Australian eucalypt forests. Annals of the Missouri Botanical Garden 85:2-17.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157:101-118.

Austin, M. P., L. Belbin, J. A. Meyers, M. D. Doherty, and M. Luoto. 2006. Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. Ecological Modelling 199:197-216.

Balanya, J., J. M. Oller, R. B. Huey, G. W. Gilchrist, and L. Serra. 2006. Global genetic change tracks global climate warming in Drosophila subobscura. Science 313:1773-1775

Bascompte, J., P. Jordano, and J. M. Olesen 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431-433.

Beaumont, L. J., L. Hughes, and A. J. Pitman 2008. Why is the choice of future climate scenarios for species distribution modelling important? Ecology Letters 11:1135-1146.

Beaumont, L. J., A. J. Pitman, M. Poulsen, and L. Hughes. 2007. Where will species go? Incorporating new advances in climate modelling into projections of species distributions. Global Change Biology 13:1368-1385.

Betts, M. G., N. L. Rodenhouse, T. S. Sillett, P. J. Doran, and R. T. Holmes 2008. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. Ecography 31:592-600.

Broennimann, O., W. Thuiller, G. Hughes, G. F. Midgley, J. M. R. Alkemade, and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Global Change Biology 12:1079-1093

Brommer, J. E., K. Rattiste, and A. J. Wilson. 2008. Exploring plasticity in the wild: laying date-temperature reaction norms in the common gull Larus canus. Proceedings of the Royal Society of London B, Biological Sciences 275:687-693.

Brooks, D. R., and E. P. Hoberg 2007. How will global climate change affect parasite-host assemblages? Trends in Parasitology 23:571-574.

Buckley, L. B. 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. American Naturalist 171:E1-E19.

Buyaert, W., F. Cuesta-Camacho, and C. Tobon. In press. Potential impacts of climate change on the environmental services of humid tropical alpine regions. Global Ecology and Biogeography.

Buytaert, W., R. Celleri, and L. Timbe 2009. Predicting climate change impacts on water resources in the tropical Andes: effects of GCM uncertainty. Geophysical Research Letters 36:L07406.

Byars, S. G., W. Papst, and A. A. Hoffmann. 2007. Local adaptation and cogradient selection in the alpine plant, Poa hiemata, along a narrow altitudinal gradient. Evolution 61:2925-2941.

Cadena, C. D., and B. A. Loiselle 2007. Limits to elevational distributions in two species of emberizine finches: disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. Ecography 30:491-504.

Carnaval, A. C., and C. Moritz 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography 35:1187-1201.

Crozier, L., and G. Dwyer 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. American Naturalist 167:853-866.

Delucia, E. H., C. L. Casteel, P. D. Nabity, and B. F. O'Neill. 2008. Insects take a bigger bite out of plants in a warmer, higher carbon dioxide world. Proceedings of the National Academy of Sciences of the United States of America 105:1781-1782.

Elith, J., and C. H. Graham 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. Ecography 32:66-77.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Etterson, J. R. 2004. Evolutionary potential of Chamaecrista fasciculata in relation to climate change. II. Genetic architecture of three populations reciprocally planted along an environmental gradient in the Great Plains. Evolution 58:1459-1471.

Fielding, A. H., and J. F. Bell 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38-49.

Ghalambor, C. K., J. K. Mckay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394-407.

Gienapp, P., C. Teplitsky, J. S. Alho, J.A. Mills, and J. Merila. 2008. Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17:167-178.

Graham, C. H., J. Elith, R. J. Hijmans, A. Guisan, A. T. Peterson, and B. A. Loiselle. 2008. The influence of spatial errors in species occurrence data used in distribution models. Journal of Applied Ecology 45:239-247.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution 19:497-503.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Guralnick, R. P., J. Wieczorek, R. Beaman, and R. J. Hijmans. 2006. Biogeomancer: automated georeferencing to map the world's biodiversity data. PLoS Biology 4:1908-1909.

Hampe, A., and R. J. Petit 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461-467.

Hannah, L. 2008. Protected areas and climate change. Annals of the New York Academy of Sciences 1134:201-212.

Heikkinen, R. K., M. Luoto, M. B. Araújo, R. Virkkala, W. Thuiller, and M.T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30:751-777.

Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J. H. Korber 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography 16:754-763.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773-785.

Higgins, P. A. T. 2007. Biodiversity loss under existing land use and climate change: an illustration using northern South America. Global Ecology and Biogeography 16:197-204.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

Hijmans, R. J., K. A. Garrett, Z. Huaman, D. P. Zhang, M. Schreuder, and M. Bonierbale. 2000. Assessing the geographic representativeness of genebank collections: the case of Bolivian wild potatoes. Conservation Biology 14:1755-1765.

Hijmans, R. J., and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12:2272-2281.

Hirzel, A. H., and G. Le Lay. 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology 45:1372-1381.

Hoegh-Guldberg, O., L. Hughes, S. Mcintyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. Science 321:345-346.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. Ecology Letters 12:420-431.

Holt, R. D., and T. H. Keitt. 2005. Species' borders: a unifying theme in ecology. Oikos 108:3-6.

Hugall, A., C. Moritz, A. Moussalli, and J. Stanisic. 2002. Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail Gnarosophia bellendenkerensis (Brazier 1875). Proceedings of the National Academy of Sciences of the United States of America 99:6112-6117.

Hughes, C. L., C. Dytham, and J. K. Hill. 2007. Modelling and analysing evolution of dispersal in populations at expanding range boundaries. Ecological Entomology 32:437-445.

Iverson, L. R., M. W. Schwartz, and A. M. Prasad 2004. Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern us species. Landscape Ecology 19:787-799.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology 5:1211-1219.

Jiménez-Valverde, A., J. M. Lobo, and J. Hortal. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. Diversity and Distributions 14:885-890.

Jump, A. S., and J. Peñuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8:1010-1020.

Jump, A. S., J. Penuelas, L. Rico, E. Ramallo, M. Estiarte, J.A. Martinez-Izquierdo, and F. Lloret. 2008. Simulated climate change provokes rapid genetic change in the Mediterranean shrub Fumana thymifolia. Global Change Biology 14:637-643.

Kearney, M., and W. P. Porter 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. Ecology 85:3119-3131.

Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araújo, and T. G. Rebelo 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4:560-563.

Kerr, J. T., and M. Ostrovsky 2003. From space to species: ecological applications for remote sensing. Trends in Ecology and Evolution 18:299-305.

Knowlton, J. L., and C. H. Graham. In press. Use of experiments to predict species' responses to land-use and climate change. Biological Conservation.

Kramer, K. 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. Plant Cell and Environment 18:93-104.

La Sorte, F. A., and F. R. Thompson 2007. Poleward shifts in winter ranges of North American birds. Ecology 88:1803-1812.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385-393.

Lobo, J. M., A. Jiménez-Valverde, and R. Real 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17:145-151.

Loiselle, B. A., C. A. Howell, C. H. Graham, J. M. Goerck, T. Brooks, K. G. Smith, and P. H. Williams 2003. Avoiding pitfalls of using species distribution models in conservation planning. Conservation Biology 17:1591-1600.

Loiselle, B. A., P. M. Jørgensen, T. Consiglio, I. Jimenez, J. G. Blake, L. G. Lohmann, and O. M. Montiel. 2008. Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? Journal of Biogeography 35:105-116.

Malcolm, J. R., A. Markham, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29:835-849.

McRae, B. H., N. H. Schumaker, R. B. McKane, R. T. Busing, A. M. Solomon, and C. A. Burdick. 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. Ecological Modelling 219:77-91.

Mitikka, V., R. K. Heikkinen, M. Luoto, M.B. Araújo, K. Saarinen, J. Poyry, and S. Fronzek. 2008. Predicting range expansion of the map butterfly in northern Europe using bioclimatic models. Biodiversity and Conservation 17:623-641.

Monahan, W. B., and R. J. Hijmans. 2008. Ecophysiological constraints shape autumn migratory response to climate change in the North American field sparrow. Biology Letters 4:595-598.

Morin, X., D. Viner, and I. Chuine. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. Journal of Ecology 96:784-794.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261-264.

Muller-Landau, H. C., and B. D. Hardesty 2005. Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. Pp. 267-309 in Biotic interactions in the tropics, edited by D. Burslem, M. Pinard and S. Hartley. Cambridge: Cambridge University Press.

Nathan, R. 2006. Long-distance dispersal of plants. Science 313:786-788.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637-669.

Pearman, P. B., C. F. Randin, O. Broennimann, P. Vittoz, W. O. Van Der Knaap, R. Engler, G. Le Lay, N. E. Zimmermann, and A. Guisan. 2008. Prediction of plant species distributions across six millennia. Ecology Letters 11:357-369.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102-117.

Pearson, R. G., T. P. Dawson, and C. Liu. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27:285-298.

Pearson, R. G., and T. P. Dawson 2005. Long-distance plant dispersal and habitat fragmentation: Identifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123:389-401.

Peterson, A. T., E. Martinez-Meyer, and C. Gonzalez-Salazar. 2004. Reconstructing the Pleistocene geography of the Aphelocoma jays (Corvidae). Diversity and Distributions 10:237-246.

Peterson, A. T., and A. S. Nyari 2008. Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, Schiffornis sp., in the Neotropics. Evolution 62:173-183.

Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier, and D. R. B. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416:626-629.

Phillips, S. J., M. Dudik, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19:181-197.

Phillips, S. J., P. Williams, G. Midgley, and A. Archer 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. Ecological Applications 18:1200-1211.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231-259.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A.Wilson. 2007. Conservation planning in a changing world. Trends in Ecology and Evolution 22:583-592.

Preston, K., J. T. Rotenberry, R. A. Redak, and M. F. Allen. 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. Global Change Biology 14:2501-2515.

Randin, C. F., T. Dirnbock, S. Dullinger, N. E. Zimmermann, M. Zappa, and A. Guisan. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33:1689-1703.

Roy, M. S., J. M. Cardosa da Sliva, P. Arctander, J. Garcia-Moreno, and J. Fjelsdå. 1997. The speciation of South American and African birds in montane regions. Pp. 325-344 in Avian molecular evolution and systematics, edited by D. Mindell. San Diego: Academic Press.

Skelly, D. K., L. N. Joseph, H. P. Possingham, L. K. Freidenburg, T. J. Farrugia, M.T. Kinnison, and A. P. Hendry 2007. Evolutionary responses to climate change. Conservation Biology 21:1353-1355.

Smith, T. B., and L. Bernatchez 2008. Evolutionary change in human-altered environments. Molecular Ecology 17:1-8.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E.Williams, 2004. Extinction risk from climate change. Nature 427:145-148.

Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgely, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: future challenges. Perspectives in Plant Ecology Evolution and Systematics 9:137-152

Thuiller, W., M. B. Araújo, R. G. Pearson, R. J. Whittaker, L. Brotons, and S. Lavorel. 2004a. Biodiversity conservation: uncertainty in predictions of extinction risk. Nature 430:145-148.

Thuiller, W., L. Brotons, M. B. Araújo, and S. Lavorel. 2004b. Effects of restricting environmental range of data to project current and future species distributions. Ecography 27:165-172.

Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote sensing for biodiversity science and conservation. Trends in Ecology and Evolution 18:306-314.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351-1363.

Vanderwal, J., L. P. Shoo, C. H. Graham, and S. E. Williams. 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecological Modeling 220:589-594.

Van Vuuren, D. P., O. E. Sala, and H. M. Pereira 2006. The future of vascular plant diversity under four global scenarios. Ecology and Society 11:25.

Vos, C. C., P. Berry, P. Opdam, H. Baveco, B. Nijhof, J. O'Hanley, C. Bell, and H. Kuipers. 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. Journal of Applied Ecology 45:1722-1731.

Walther, G. R. 2007. Tackling ecological complexity in climate impact research. Science 315:606-607.

Wieczorek, J., Q. G. Guo, and R. J. Hijmans 2004. The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. International Journal of Geographical Information Science 18:745-767.

Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araújo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the cape proteaceae. Conservation Biology 19:1063-1074.

Williams, S. E., E. E. Bolitho, and S. Fox 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. Proceedings of the Royal Society of London B, Biological Sciences 270:1887-1892.

22

Climate Change and Protected Areas in the Tropical Andes

Dirk Hoffmann, Imke Oetting, Carlos Alberto Arnillas,
and Roberto Ulloa

Climate change and global warming constitute a reality in the Andes region, and their impacts can be felt ever more strongly (Vuille et al. 2003; IPCC 2007b; Marengo et al. Chapter 7, this volume). Changes in temperature and humidity are reflected especially in the retreat of glaciers, changes in precipitation patterns, and a greater frequency and severity of extreme events such as droughts and inundations. The El Niño Southern Oscillation (ENSO) controls a number of these extreme events, and it has exhibited a greater recurrence and severity since the 1970s (Francou et al. 2005).

Despite the amount of evidence for climate change reported to date, future climatic conditions are uncertain, which is reflected in the variation in predictions between different global climate models (Stainforth et al. 2007, Buytaert et al. 2009, Marengo et al., Chapter 7, this volume). This uncertainty is particularly high for changes in precipitation and for mountainous regions. For example, temperature changes have been shown to increase with increasing elevation (Bradley et al. 2006, Hohmann et al. 2007). However, only a handful of studies exist on the impacts of climate change on tropical Andean biodiversity and, more specifically, on the region's protected areas.

Protected areas constitute one of the main tools for biodiversity conservation given that they contribute to the conservation of species and the preservation of key ecosystem processes crucial for the survival of all living beings, including humans and their productive systems (Convention on Biological Diversity - CBD, Seventh Conference of the Parties, Decision VII.28, 2004; Sandwith 2008, Lee and Jetz 2008). Many protected areas in the tropical Andes of Bolivia, Colombia, Ecuador, and Peru have existed for several decades (Figure 22.1), but only in the last 10-15 years have national governments been consolidating their protected area systems (see Chávez et al. 2005, Ribera and Liberman 2006, SERNAP 2007, Ulloa et al. 2007) following the Earth Summit in Rio de Janeiro in 1992. Almost 15% of the area of the four countries is currently included in national-level protected areas, compared to 12% globally (General Secreteriat of the Andean Community et al. 2007, Sandwith 2008). In addition, thanks to the contributions of the Protected Areas Program of the CBD, most tropical Andean countries are effecting changes in their protected area systems, such as the integration of complementary conservation mechanisms in the form of regional, municipal, private, community, indigenous, and Afro-American conservation areas (MAE 2007, GTZ – Grupo Biodiversidad 2008, PROMETA 2008).

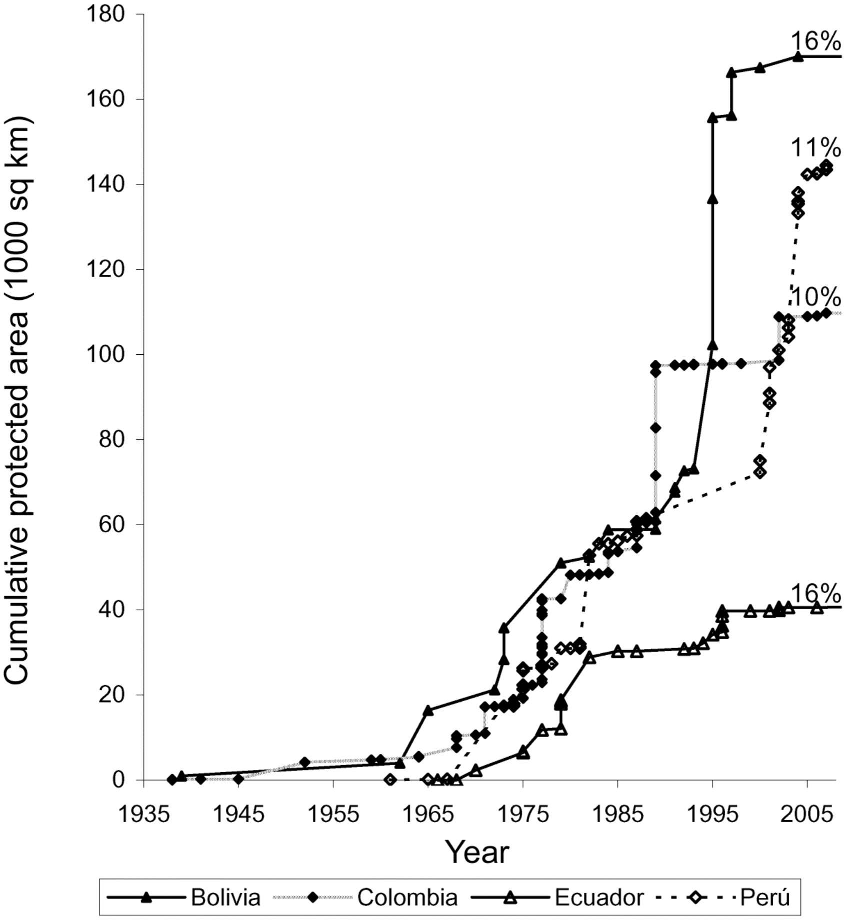

Figure 22.1. Increase over time in the area included in national-level protected areas in the tropical Andes countries of Bolivia, Colombia, Ecuador, and Peru. Each data point represents the creation of a new protected area. Values indicate current proportion of national area included in protected areas. Source: Andean Development Corporation and Conservation International, Geographic Information System Condor.

We are not aware of any reliable, detailed studies on the representativeness of the biodiversity protected by the different protected area systems in the region, and estimated values of the number of species included vary considerably. On the western versant of the Andes there are hardly any protected areas that cover wide elevational gradients. This is especially the case in Peru and for the western highlands of Bolivia, where coastal desert (in the case of Peru), puna, and other high-Andean ecosystems have received little interest and attention by the conservation world because they are considered poor in species (Chávez et al. 2005). In Ecuador and Colombia some more extensive protected areas are found on the Pacific slope, but not as many as on the Amazonian versant, resulting in a low representation of elevationally continuous samples.

In light of this situation, here we address the following questions: (1) What are the impacts of climate change on the biodiversity harbored by the protected areas of the region? (2) Are protected areas situated in the most suitable places to guarantee the continued survival of its species and ecosystem services under the possible impacts of climate change? (3) What are the (possible) reactions of protected area managers to deal with the threats of climate change? The chapter finishes with recommendations for the design and management of national protected area systems and directions for future research on the impacts of climate change on protected areas in the region.

This chapter is the first regional attempt to compile existing information and available literature and to synthesize the international discussion on the topic. In order to retrieve specific information from the four countries (Bolivia, Colombia, Ecuador, Peru) we especially included information from technical reports and documents from protected area offices and personal communications with a variety of experts. The GLORIA project (Global Research Initiative in Alpine Environments, www.gloria.ac.at) is a global research initiative that integrates climate change and biodiversity in high mountain systems, and maintains seven research sites (Pauli et al. 2003) in the tropical Andes.

The Impacts of Climate Change on Biodiversity

Climate change represents a new, complex reality which carries much uncertainty with respect to the magnitude and nature of its impacts on biodiversity (Schliep et al. 2008). Many studies raise concern about the consequences of fast climatic changes, especially shifts in the geographic distribution of species and ecosystems (Midgley et al. 2002, Dudley 2003, Hansen et al. 2003, Ibisch 2003, IPCC 2007b, Hannah et al. 2007, Higgins 2007). The resilience of many ecosystems to disturbance will probably be exceeded during this century as a result of the unprecedented combination of climate change, its associated disturbances (floods, droughts, fire, invasion of exotic species), and other factors such as land-use changes, contamination, and overexploitation of resources (IPCC 2007a, Stolton et al. 2008).

Information on the impacts of climate change on tropical Andean biodiversity is still very scarce (Larsen et al. Chapter 3; Aguirre et al. Chapter 4; and Anderson et al. Chapter 1, this volume; see also Gallardo et al. 2008 for a review of the Peruvian literature on climate change). In general, elevational and latitudinal shifts in the distributions of species and ecosystems are expected as a result of changes in temperature (Colwell et al. 2008), although not enough information exists to predict the extent of this phenomenon for the tropical Andes (see Larsen et al. Chapter 3, this volume). Glacier retreat entails changes in the seasonality of water availability to ecosystems (Francou 2000, 2005; Van der Hammen et al. 2002; Hoffmann 2008; Anderson et al. Chapter 1, this volume). Changes in the phenology of plants and animals (see Aguirre et al. Chapter 4, this volume) and in biogeochemical cycles are expected to occur, as well as an increase in evapotranspiration due to rising mean temperatures. In the tropical Andes, the impacts of climate change are superimposed on complex distribution patterns of biodiversity along elevational, latitudinal, and humidity gradients. As a consequence, the region's protected areas alone will not be sufficient as a tool for the conservation and management of biodiversity.

Relationships between Climate Change and other Factors that have an Impact on Biodiversity in Protected Areas

Various elements have an impact on Andean biodiversity, the primary factors being land-use change or inappropriate land use, which can lead to desertification (Hewson et al. 2008, Peredo-Videa 2008). The tropical Andes have been inhabited by humans for thousands of years, with extensive use of many areas (see Young, Chapter 8, this volume), and many ecosystems are not in a 'natural state' in the strict sense. Protected areas have often been created in regions with previously established human settlements or land-use activities, and not always with the consent of local populations. Therefore, it seems appropriate to refer to 'natural dynamics' interwoven with political, economic, and cultural dynamics.

People are already perceiving climatic changes, and this has brought about changes in local land-use patterns such as upslope movements of cultivated areas. Furthermore, temperature increases in high-Andean puna grassland could lead to increased ecosystem productivity, which in turn could result in greater livestock grazing pressure. A possible increase in evapotranspiration, on the other hand, could lead to reduced water availability in lower parts of watersheds. In conservation planning, analyses of land-use changes will be necessary for a comprehensive understanding of climate change impacts on biodiversity (Higgins 2007). The impacts of land-use changes may even be more relevant in the short and medium term than climate change itself (Jetz et al. 2007). Greater impacts are expected where land-use change and climate change act in synergy (Ibisch 2004; IPCC 2007a; Stolton et al. 2008; Suárez et al. Chapter 9, this volume). The use of ecological principles and models that do not incorporate human land use probably will not provide realistic results (Halpin 1997, Hannah et al. 2002).

Protected Areas as 'Victims' of Climate Change

Given that biodiversity and land use are being affected by climate change, and because land-use changes impact biodiversity directly, it is clear that protected areas are also 'victims' of climate change. It is therefore necessary to review conservation strategies so that they will be effective in a future characterized by a different climate (Hannah et al. 2002).

Already in the 1990s, Halpin (1997) pointed out that the possibility of rapid climatic change caused by greenhouse gas emissions represents a serious challenge to protected areas and other natural landscapes. During the past 10 years the conservation community has become increasingly aware of the potential impacts of climate change on protected area systems and their management (Hannah et al. 2002; Araújo et al. 2004; Ibisch 2004; Badeck et al. 2007; Hannah et al. 2007; Coenen et al. 2008; Hannah 2008; Hewson et al. 2008; Lee and Jetz 2008, Sandwith 2008; Welch 2008, Hole et al. 2009).

More recently, conservation organizations in the tropical Andes have begun to include the impact of climate change on protected areas in their agendas using scientific methods to guide conservation planning and practice. For example, a gap analysis of the Bolivian protected area system was one of the first exercises that took possible impacts of climate change into account in conservation planning (Consorcio FAN et al. 2005). In this analysis, elevational and riverine corridors are identified as a priority to ensure ecosystem connectivity and to mitigate the effects of climate change. Further, an increased risk of droughts was anticipated for humid tropical forests (Consorcio FAN et al. 2005).

In this strategy review, the conservation community has begun to discuss complementary options under current strategies such as biological latitudinal and elevational corridors (e.g., Bennett 1998), but the validity of the classic concept of protected areas is also being debated. There is increasing international agreement that geographically ‘fixed’ protected areas, which are ever more isolated due to the destruction of habitats in surrounding areas, will be incapable of responding to species range shifts under climate change (Coenen et al. 2008; Hannah et al. 2007).

Reactions of Protected Area Managers to Climate Change

At national levels protected areas are still the principal conservation tool. Thus, the principal climate change adaptation mechanism is also still the identification and designation of priority areas for conservation. Consequently, the identification of criteria and methods for the delimitation of priority areas and for the evaluation and corresponding up-date of management plans produced for each area is a key issue.

Important progress has been made in all tropical Andean countries with regard to the identification of priority zones for the creation of protected areas. In the case of Peru, for example, the earliest proposals set out to create national parks to ensure representation of three natural regions, the coast, the Andes, and Amazonia (Vílchez 1968), and the proposed areas did not guarantee the continuity of ecological processes. Subsequently, significant improvements in the mapping of ecosystems and species distributions were incorporated into conservation planning in the region, and in recent years more formal methods for the selection of priority sites have been employed (MDSP 2001, Ibisch and Mérida 2003, Consorcio FAN et al. 2005, MAE 2007, Carillo et al. 2007, SERNAP 2007, SERNANP 2009). However, none of the prioritization processes by national authorities have considered possible impacts of climate change due in part to the lack of baseline information and methodologies. Protected areas are mentioned in national climate change strategies, but conceptual tools especially for prioritizing research and developing adaptation and mitigation strategies are still lacking.

Some protected area management plans, on the other hand, have begun to incorporate the topic. In Bolivia, for example, possible impacts of climate change were considered in the management plans for protected areas Madidi (SERNAP and WCS 2005), Pilón Lajas (SERNAP and CRTM 2009), Apolobamba (SERNAP and CG ANMIN Apolobamba 2006), and San Matías (SERNAP and CG ANMI San Matías 2008). The impact of climate change was identified merely as a ‘threat’ in Madidi, and further research programs were solicited for Pilón Lajas and Apolobamba. A climate change projection was included only for San Matías, where gradual decreases in precipitation are expected. Yet, these management plans share a weakness in their capacity for climate change analysis, monitoring, adaptation and mitigation. The situation is similar in the other tropical Andean countries. Throughout the region the issue of climate change has not yet been given the importance it requires in the planning and management of national systems, nor in the management of individual protected areas.

This situation is partly explained by the fact that more urgent needs than planning for climate change exist from the point of view of protected area managers, including the expansion of the agricultural frontier and human settlements, infrastructure projects, exploitation of oil, gas, and minerals, coca production and others (Fjeldså et al. 2005, Greenwood 2005, Schliep et al. 2008). The scarcity of scientific information in the tropical Andes also hampers decision making with respect to climate change. Taking into account recent studies (Ibisch and Nowicki 2004, Ibisch et al. 2007) and initiatives (Global Research Initiative in Alpine Environments, www.gloria.ac.at; see also Pauli et al. 2003) there is an urgent need for the design and implementation of more effective conservation strategies both in and outside of protected areas. This includes the necessity to consolidate planning processes that include analyses of climate change and that strengthen the governance of protected areas, mechanisms for land-use planning, and natural resource management in general.

Protected Areas: Key Elements of Mitigation and Adaptation

Protected area networks still constitute the most important tool for biodiversity conservation at the global level (Hole et al. 2009). In addition, the role of protected areas in carbon sequestration and retention, and therefore in the mitigation of the impacts of climate change, is being recognized (Dudley 2008, Sandwith 2008). A series of project proposals are underway in the tropical Andean countries that seek to contribute to the prevention of deforestation and the degradation of forests in areas of influence of protected areas (REDD) and inside protected areas (REDD+). However, the viability and relevance of such initiatives are still being discussed as part of the debate about a post-Kyoto agreement. This uncertainty has not stopped the implementation of several projects in the region, although countries follow dissimilar approaches. Different initiatives are revising methods for the estimation of biomass, historical deforestation rates, and the modeling of future deforestation. To strengthen proposals it will be essential to encourage both research on the role of ecosystems in the emission and sequestration of greenhouse gases, and the reduction of deforestation rates as part of national policies (PNCC 2007; Gobierno del Perú, D.S. Nº 086-2003-PCM).

In addition to the mitigation of negative climate change impacts, there is evidence that protected area systems and well managed protected areas can offer opportunities for the design and implementation of adaptation strategies through the provision of key ecological services (Dudley and Stolton 2003, Sandwith 2008). Some studies linked to the Program on Climate Change Adaptation in Peru (Salzmann et al. 2009) have evaluated the best climate change adaptation strategies for the high-Andean zone, although most did not consider protected areas. For protected areas to fulfill a role in climate change adaptation, a paradigm shift in conservation strategies and actions is required to ensure that conservation targets remain within protected areas over time and that protected areas can continue to provide key environmental services. It is important in this context that national climate change strategies include strategic objectives directly linked to protected areas, strengthening mechanisms of adaptation to projected changes in nearby populations and preserving strategic ecosystems as protection against natural disasters resulting from climate change.

According to Stolton et al. (2008), the functions of protected areas in the mitigation and adaptation to climate change should receive greater recognition and be incorporated into the planning and effective management of protected areas and their funding strategies. The analysis of the interface between ecological and social systems is an innovative approach that contributes to strengthening the adaptation capacity of protected areas, and it is reflected in the ecosystem approach of the Convention on Biological Diversity, which leads to the resilience of socioeconomic systems, systems of social and institutional learning (F. Berkes pers. comm., Berkes 2002; Shepherd 2006; Buitrón personal communication). This interaction is evident through social participation in the management of protected areas, as for example in the management committees of protected areas in Bolivia, Ecuador, and Peru. Another example are mechanisms of shared management that involve local stakeholders to different degrees in the planning and management of protected areas, where capacity building for climate change adaptation should be included (F. Berkes pers. comm., Berkes 2002; Holling 1973; Carillo et al. 2007; Schliep et al. 2008).

An interesting approach is taken in Colombia, where current developments of climate change adaptation for the high Andes focus on designing adaptive "living" plans. These plans are built in a participatory fashion and enable the initiation of discussions on land use planning and adaptation to climate change with local communities and institutions. In addition, because this is a documented process, it allows for the compilation of lessons learned (M. M. Medina in litt.).

Climate Change and the Design of (National) Protected Area Systems

A decade ago Cowling et al. (1999) noted that the incorporation of climate change elements in the design of protected area systems was still in its early stages. The academic discussion on the topic has progressed (Araújo et al. 2004, Hannah et al. 2008), focusing on two principal lines of thinking: (1) Should conservation efforts concentrate exclusively on national or regional protected area systems, or also include landscapes outside protected areas? What measures should be taken outside formally protected areas? (2) Are protected areas an ideal and sufficient tool? Should the representation of species, habitats, and ecosystems still constitute the main conservation objectives, or should dynamic targets be adopted such as the maintenance of ecosystem functioning? How would national systems have to change to adapt to climate change? Based on a comparative study of Mexico, South Africa, and Europe, Hannah et al. (2007) concluded that current protected area systems would require substantial increases in surface area to guarantee the goal of species representation in the face of climate change, especially to provide adequate habitats within future distribution ranges of species (Hannah et al. 2002, Jetz et al. 2007).

In the Andean region there is a trend to incorporating new protected areas managed at local and regional levels into the national systems (Hoffmann 2007) which can also be seen in the “Planes Maestros” of Colombia, Ecuador, Bolivia and Peru. Such areas, which are generally managed by municipal governments, local communities, or indigenous peoples, can play a vital role in complementing national efforts of biodiversity conservation (MAE 2007, PROMETA 2008). Additionally, the establishment of several conservation corridors has been underway at international to regional levels (e.g., the Vilcabamba-Amboró corridor between Peru and Bolivia; the Abiseo-Condor Kutukú and Podocarpus-Tabaconas-El Tablón corridors between Peru and Ecudor; three elevational corridors on eastern versants in Colombia). This reflects the concern about the necessity of establishing vertical and horizontal protected area corridors, both to increase the probability of protecting conservation targets and to provide dispersal corridors for species (Hannah et al. 2002, Ibisch and Araújo 2003, Consorcio FAN et al. 2005, Ibisch et al.

2007). Even though these initiatives are important, they appear insufficient given the limited knowledge on the distribution and ecological requirements of species in the Andes. A first step towards climate change adaptation is the inclusion of uncertainty and surrogate analyses into strategic planning (Hannah et al. 2002).

However, this approach appears to have its limits. For example, in a modeling study on the African Important Bird Area (IBA) network Hole et al. (2009) determined that climate change will lead to both a loss of species as well as 'new arrivals' in the different IBAs. This is a prime example for the limitations of an approach based on species representation, concluding that the concept of establishing protected areas solely based on maintaining current species composition needs to be reevaluated (Ibisch et al. 2007, Hole et al. 2009). Similarly, Hansen and Biringer (2003) concluded that environmental threats such as climate change make it indispensable that conservation efforts are extended beyond the limits of protected areas given that the future distribution of ecosystems and biomes could differ from that of today.

These concerns are beginning to shape a new line of discussion. Ibisch et al. (2007) provide a description of a new paradigm: the persistence of biodiversity can be guaranteed only if ecological and evolutionary processes are maintained as they form the very basis of biodiversity. The application of this new paradigm is also expressed in the CBD's ecosystem approach (Shepherd 2006). Ecological and evolutionary processes as well as the identification of their spatial requirements must be effectively incorporated into conservation planning (Balmford et al. 1998, Ibisch et al. 2007). This implies a need for the definition of dynamic conservation objectives for protected areas – a shift from 'representation' to 'persistence' may be the most important paradigm shift in modern conservation (Cowling et al. 1999).

In an analysis of the Amboró-Madidi corridor, Ibisch et al. (2007) suggest some essential components for a successful paradigm shift towards functional conservation within the context of the ecosystem approach: conservation efforts should not focus exclusively on species and/or current biodiversity patterns, but rather include larger and more complex temporal and spatial dimensions, aiming for the conservation of ecosystem functioning with all of its processes, including spatial shifts of biodiversity (see also Bennett 1998). It can be concluded that effective global biodiversity conservation in the face of climate change will depend on well defined protected area networks, integrating functional connectivity at regional and continental scales (Hannah 2008, Hole et al. 2009). Future requirements for the design of protected area systems should also include conservation and management strategies for cultural landscapes outside protected areas taking into account the CBD's ecosystem approach (Recharte 2001; Shepherd 2006; Buitrón personal communication). This approach is critical given the current tendency of restricting protected area management to areas confined within reserve limits without much consideration for adjacent buffer zones. Therefore, a proposal is needed so that protected areas provide tools for institutional agreements at local and subregional levels for the participation of civil society.

The incorporation of environmental services that improve living conditions of people inhabiting the vicinity of protected areas also needs to be consolidated in conservation planning. Protected area categories whose explicit purpose is the provisioning of services such as water supply already exist. However, it is necessary to create mechanisms that will facilitate the inclusion of such criteria in the identification of priority areas, considering local populations as direct beneficiaries rather than a source of resistance.

Finally, it is necessary to consolidate regional strategies that facilitate the identification of trans-boundary protected areas. Regional initiatives such as the tropical Andean ecosystem atlas

(Josse et al. 2009; see also Josse et al. Chapter 10, this volume) represent an important step in this direction to guarantee ecosystem connectivity. Means of communication between civil society and national governments also need to be promoted so that initiatives and priorities identified by populations in border areas can be incorporated into national agendas. In this context, the experience of the Madre de Dios-Acre-Pando region is of particular interest due to its successful establishment of communication channels between NGOs, universities, local governments, local civil society committees, regional, and even national governments.

Conclusions and Recommendations

Protected areas have experienced major developments as a conservation strategy in the region during the past 30 years. Their maturation has been slow and is still in the process of legal and institutional consolidation and social legitimization. Important progress has been made on the premise that protected areas must guarantee representativeness of present-day ecosystems and species. However, climate change is imposing new challenges and restrictions.

In order to evaluate if current conservation efforts are adequate and to attain a better understanding of climate change impacts on biodiversity in protected areas both small-scale regional climate models and the initiation of long-term biodiversity monitoring are essential. For a proactive strategy on climate change in protected areas and their networks, the evaluation of projected impacts on species turnover and survival over time is indispensable (Hole et al. 2009).

Given that in the face of climate change representativeness alone should no longer be the criterion for conservation planning, new planning processes should take into account data requirements, modeling approaches, and institutional needs. Through adaptive management (see Hole et al. Chapter 2, this volume) this would allow for adjustments in methodologies as changes in ecosystems and species composition become more evident through time. Such new proposals should consider aspects of climate change and environmental services in relation to the conservation and use of biodiversity. It is also fundamental that gap analyses incorporate climate change in a more integral manner (Ibisch 2004, Ervin 2008).

Although protected areas are likely ‘victims’ of climate change it is important to emphasize that they are also affected negatively by other phenomena. This implies that conservation strategies must confront the impacts of both climate change and of the synergistic relationship between climate and land-use changes. In addition, it is important to recover the role of protected areas as key elements in the mitigation of climate change impacts mainly through environmental services, especially the regulation of water cycles and carbon sequestration.

A greater involvement of protected area managers in education, research, and monitoring activities is fundamental (Halpin 1997, Schliep et al. 2008), realizing that only an alliance based on the concept of adaptive management, where *in situ* administration contributes progressively to the testing and refinement of new ideas, can effectively confront the uncertainties of climate change impacts on biodiversity (Hannah et al. 2002, Barnard and Thuiller 2008, Coenen et al. 2008). Flexible and dynamic management approaches are needed to cope with demands of constantly changing future conditions (Halpin 1997), which in turn requires creative and incentivizing regulations for an appropriate governance of protected area systems. Although such efforts have recently been initiated at different levels in Colombia, Ecuador, Peru, and Bolivia, the lack of human and financial resources are a permanent concern. In light of the existing gaps in information and in north-south communication, we therefore support Barnard and Thuiller’s

(2008) call for research collaboration between northern and southern hemisphere teams and within the tropical Andes region.

The recognition of the role of protected areas in the generation of information that supports decision making in relation to climate change and associated local environmental changes is fundamental. The establishment of systems for monitoring key biodiversity aspects and environmental services to generate information for the quantification of climate change impacts within and outside of protected areas would thus be advantageous.

Finally, it is important to reconsider the role of protected areas in their interaction with other land-use forms that are necessary for society. The development of local conservation strategies, landscape reserves, multiple use areas, environmental services payments, and similar approaches can contribute to society perceiving protected areas as a key component of its own survival in the medium- to long-term. Therefore, the Colombian proposal of incorporating two approaches, the ecosystem approach and ecosystem-based adaptation, into conservation planning and management (M. M. Medina in litt.) represents considerable progress. In this combination approach a wide range of strategies for the management, conservation, and restoration of ecosystems is identified and implemented to ensure that ecosystems increase their resistance and reduce their vulnerability and thereby continue to provide the services that permit people to adapt to the impacts of climate change (M. M. Medina in litt.).

Biodiversity conservation in the face of climate change requires both adaptation – better conservation strategies – and mitigation – stabilization of greenhouse gas concentrations in the atmosphere – to be effective, especially during the second half of this century (Hannah et al. 2007, Hewson et al. 2008).

Acknowledgments

We would like to express our sincere gratitude to E. Müller, S. Sanchez, and an anonymous reviewer for comments on the manuscript, and to Pedro Vásquez and María Mercedes Medina for their valuable contributions.

Literature Cited

Araújo, M. B., M. Cabezas, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* 10:1618-1626.

Badeck, F.-W., K. Böhning-Gaese, W. Cramer, P. L. Ibisch, S. Klotz, S. Kreft, I. Kühn, K. Vohland, and U. Zander. 2007. Schutzgebiete Deutschlands im Klimawandel – Risiken und Handlungsoptionen. *Naturschutz und biologische Vielfalt* 46:151-167.

Balmford, A., G. M. Mace, and J. R. Ginsberg. 1998. The challenges to conservation in a changing world: putting processes on the map. Pp. 1-28 in *Conservation in a changing world*, edited by G. M. Mace, A. Balmford, and J.R. Ginsberg. Cambridge: Cambridge University Press.

Barnard, P., and W. Thuiller. 2008. Global change and biodiversity: future challenges. *Biology Letters* 4:553-555.

Bennett, A. F. 1998. *Linkages in the landscape: the role of corridors and connectivity in wildlife conservation*. Gland and Cambridge: International Union for the Conservation of Nature.

Berkes, F. 2002. Cross-scale institutional linkages: perspectives from the bottom up. Pp. 293-321 in *The drama of the commons*, edited by E. Ostrom, T. Dietz, N. Dolsak, P. C. Stern, S. Stonich, and E. U. Weber. Washington, DC: National Academy Press.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Climate change: threats to water supplies in the tropical Andes. *Science* 312:1755-1756.

Buytaert, W., R. Celleri, and L. Timbe. 2009. Predicting climate change impacts on water resources in the tropical Andes: the effects of GCM uncertainty. *Geophysical Research Letters* 36:L07406.

Carrillo, J., A. Castillo Ordinola, P. Fernández-Dávila, C. F. Ponce del Prado, I. Prem, and S. Sánchez Huamán. 2007. *Informe Nacional - Perú, 2007, del sistema nacional de áreas naturales protegidas por el Estado Peruano (SINANPE)*. Lima: Instituto Nacional de Recursos Naturales, UICN, and Programa Desarrollo Rural Sostenible de la GTZ. Available at: http://www.iabin.info/RANPA_SP/Alianzas/Informe%20Nacional%202007.pdf.

Chávez, J., S. Sánchez, C. Ponce, and L. Alfaro (eds.). 2005. *Las áreas naturales protegidas del Perú: informe nacional 2005*. Lima: INRENA, UICN, WCPA, KfW, Conservación Internacional, and BIOFOR. 179 pp.

Coenen, D., I. Porzecanski, and T. L. Crisman. 2008. Future directions in conservation and development: incorporating the reality of climate change. *Biodiversity* 9(3-4):106-113.

Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261.

Consorcio Fundación Amigos de la Naturaleza (FAN) – Tropico – CEP – NORDECO. 2005. *Análisis de vacíos de representatividad del sistema nacional de áreas protegidas*. Unpublished report. Santa Cruz de la Sierra: Fundación Amigos de la Naturaleza.

Convention on Biological Diversity (CBD). 2004. Seventh Conference of the Parties, Decision VII/28. Protected areas. Available at: http://www.cbd.int/doc/decisions/cop-07/cop-07-dec-28-en.pdf.

Cowling, R. M., R. L. Pressey, A. T. Lombard, P. G. Desmet, and A. G. Ellis. 1999. Diversity, stability and conservation of Mediterranean-type ecosystems in a changing world. *Diversity and Distributions* 5:51-71.

Dudley, N. 2003. *No place to hide: effects of climate change on protected areas*. Berlin: WWF. 12 pp.

Dudley, N. 2008. The use of protected areas as tools to apply REDD carbon offset schemes. *Policy Matters* 16:99-107.

Dudley, N., and S. Stolton. 2003. Ecological and socio-economic benefits of protected areas in dealing with climate change. Pp. 217-233 in *Buying time: a user's manual for building resistance and resilience to climate change in natural systems*, edited by L. J. Hansen, J. L. Biringer, and J. R. Hoffman. Berlin: WWF. 246 pp.

Ervin, J. 2008. Integrating climate change into the ecological gap assessment process. *Policy Matters* 16:116-118.

Fjeldså, J., M. D. Álvarez, J. M. Lazcano, and B. León. 2005. Illicit crops and armed conflict as constraints on biodiversity conservation in the Andes region. *Ambio* 34:205-211.

Francou, B., E. Ramírez, B. Cáceres, and J. Mendoza. 2000. Glacier evolution in the tropical Andes during the last decades of the 20th century: Chacaltaya, Bolivia, and Antizana, Ecuador. *Ambio* 29:416-422.

Francou, B., P. Ribstein, P. Wagnon, E. Ramírez, and B. Pouyaud. 2005. Glaciers of the tropical Andes. Indicators of global climate variability. Pp. 197-204 in *Global change in mountain regions*, edited by U. M. Huber, H. K. M. Bugman, and M. Reasoner. Springer.

Gallardo, M., A. Gómez, J. Torres, and A. Walter (eds.). 2008. Directorio nacional. Cambio climatic en el Perú. Lima: Soluciones Prácticas-ITDG. 130 pp. Available at: http://www.itdg.org.pe/publicaciones/pdf/CAMBIO%20CLIMATICO%20PERU.pdf.

General Secretariat of the Andean Community, United Nations Environmental Program, and Spanish International Cooperation Agency. 2007. *Where do we start? The Andean Community´s top climate change priorities*. Lima: General Secretariat of the Andean Community, United Nations Environmental Program, and Spanish International Cooperation Agency.

Gobierno del Perú. 2003. *Decreto supremo 086-2003-PCM. Estrategia nacional sobre cambio climático*. (Norma actualizada al 25 de mayo de 2009). Lima: Gobierno del Perú.

Greenwood, G. B. 2005. What are the important global change themes and issues in mountain biosphere reserves? Pp. 179-194 in *Projecting global change impact and sustainable land use and natural resources management in mountain biosphere reserves*. Paris: UNESCO.

GTZ – Grupo Biodiversidad. 2008. *Áreas de conservación municipal. Una oportunidad para la conservación de la biodiversidad y el desarrollo local. Reflexiones desde América Latina y el Caribe*. Available at: http://www.pdrs.org.pe/img_upload_pdrs/36c22b17acbae902af95f805cbae1ec5/Informativo_ACM.pdf.

Halpin, P. N. 1997. Global climate change and natural-area protection: management responses and research directions. *Ecological Applications* 7:828-843.

Hannah, L., G. Midgley, D. Millar. 2002. Climate change-integrated conservation strategies. *Global Ecology and Biogeography* 11:485-495.

Hannah, L., G. Midgley, S. Andelman, M. B. Araújo, G. Hughes, E. Martinez-Meyer, R. G. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5:131-138.

Hannah, L. 2008. Protected areas and climate change. *Annals of the New York Academy of Sciences* 1134:201-212.

Hannah, L., R. Dave, P. P. Lowry II, S. Andelman, M. Andrianarisata, L. Andriamaro, A. Cameron, R. Hijmans, C. Kremen, J. MacKinnon, H. Hanitriniaina Randrianasolo, S. Andriambololonera, A. Razafimpahanana, H. Randriamahazo, J. Randrianarisoa, P. Razafinjatovo, C. Raxworthy, G. E. Schatz, M. Tadross & L. Wilmé. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters* 4:590-594.

Hansen, L. J., and J. L. Biringer. 2003. Building resistance and resilience to climate change. Pp. 9-14 in *Buying time: a user's manual for building resistance and resilience to climate change in natural systems*, edited by L. J. Hansen, J. L. Biringer, and J. R. Hoffman. Berlin: WWF. 246 pp.

Hansen, L. J., J. L. Biringer, and J. R. Hoffman (eds.). 2003. *Buying time: a user's manual for building resistance and resilience to climate change in natural systems*. Berlin: WWF. 246 pp.

Hewson, J., E. Ashkenazi, S. Andelman, and M. Steininger. 2008. Projected impacts of climate change on protected areas. *Biodiversity* 9(3-4):100-105.

Higgins, P. A. T. 2007. Biodiversity loss under existing land use and climate change: an illustration using northern South America. *Gobal Ecology and Biogeography* 16:197-204.

Hoffmann, D. 2007. *El rol de las áreas protegidas municipales en el Sistema Nacional de Áreas Protegidas (SNAP) de Bolivia*. La Paz: Servicio Nacional de Áreas Protegidas de Bolivia.

Hoffmann, D. 2008. Consecuencias del retroceso glaciar en la cordillera boliviana. *Pirineos* 163:77-84.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continentwide protected area network. *Ecology Letters* 12:420-431.

Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecologogy and Systematics* 4:1-23.

Ibisch, P. L. 2003. Actores que tienen impactos sobre la biodiversidad sin aprovecharla. Pp. 204-212 in *Biodiversidad: la riqueza de Bolivia*, edited by P. L. Ibisch and G. Mérida. Santa Cruz de la Sierra: Editorial FAN.

Ibisch, P. L., and N. Araújo 2003. Conservación regional y corredores biológicos. Pp. 417-427 in *Biodiversidad: la riqueza de Bolivia*, edited by P. L. Ibisch and G. Mérida. Santa Cruz de la Sierra: Editorial FAN.

Ibisch, P. L., and G. Mérida (eds). 2003. *Biodiversidad: la riqueza de Bolivia.* Santa Cruz de la Sierra: Editorial FAN.

Ibisch, P. L., and C. Nowicki 2004. Biodiversity patterns, conservation planning, and science: general reflections and examples from the tropical developing country Bolivia. Pp. 181-197 in *Results of worldwide ecological studies*, edited by S. W. Breckle, B. Schweizer, and A. Fangmeier. Stuttgart, Germany: Verlag Günter Heimbach.

Ibisch, P. L. 2004. In situ biodiversity conservation: notes concerning gaps in protection in Bolivia. Pp. 382-406 in *Biodiversity: the richness of Bolivia*, edited by P. L. Ibisch and G. Mérida. Santa Cruz de la Sierra: Editorial FAN.

Ibisch, P. L., N. Araújo, and C. Nowicki (eds.). 2007. *Visión de conservación de la biodiversidad del corredor Amboró – Madidi*. Santa Cruz de la Sierra: Editorial FAN.

IPCC. 2007a. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Soloman, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. Cambridge: Cambridge University Press.

IPCC. 2007b. *Climate change 2007: synthesis* report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by R. K. Pachauri and A. Reisinger. Geneva: IPCC.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211-1219.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009. *Mapa de ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela*. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

Lee, T. M., and W. Jetz. 2008. Future battlegrounds for conservation under global change. *Proceedings of the Royal Society of London B, Biological Sciences* 275:1261-1270.

Ministerio del Ambiente del Ecuador. 2007. *Políticas y plan estratégico del sistema nacional de áreas protegidas del Ecuador 2007-2016*. Quito: Ministerio del Ambiente. 36 pp.

Ministerio de Desarrollo Sostenible y Planificación. 2001. *Estrategia nacional para la conservación de la biodiversidad de Bolivia (ENCB)*. La Paz: Ministerio de Desarrollo Sostenible y Planificación.

Midgley, G. F., L. Hannah, D. Millar, M. C. Rutherford, and L. W. Powrie. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* 11:445-451.

Hohmann, R., E. Thalmann, G. Müller-Ferch, U. Neu, C. Ritz, and C. Kull (eds.). 2007. *Klimaänderung und die Schweiz 2050. Erwartete Auswirkungen auf Umwelt, Gesellschaft und Wirtschaft*. Bern: Organe consultatif sur les changements climatiques and ProClim-Forum for Climate and Global Change.

Pauli, H., M. Gottfried, D. Hohenwallner, K. Reiter, and G. Grabherr (eds.). 2003. *Manual para el trabajo de campo del proyecto GLORIA. Aproximación al estudio de las cimas*. Available at: www.gloria.ac.at/downloads/GLORIA_MS4_Web_espanol.pdf.

Peredo-Videa, B. 2008. Climate change, biodiversity conservation, deforestation and its policy responses in Bolivia under the current political context: what scope for synergies and interactions? Pp. 295-324 in *Climate change and biodiversity in the Americas*, edited by A. Fenech, D. MacIver, and F. Dallmeier. Toronto: Environment Canada.

Programa Nacional de Cambios Climáticos (PNCC). 2007. *Vulnerabilidad y adaptación al cambio climático en las regiones del lago Titicaca y los valles cruceños de Bolivia*. La Paz: PNCC and Ministerio de Planificación y Desarrollo.

Protección del Medio Ambiente Tarija (PROMETA). 2008. Áreas protegidas municipales y departamentales facilitan las acciones contra el cambio climático. *Revista Hábitat* 74:4. Available at: http://www.lidema.org.bo/portal/index.php?option=com_content&view=article&id=205&Itemid=331.

Recharte, J. 2001. La categoría de reserva paisajística como estrategia de conservación en el contexto de los Andes: naturaleza y cultura en la Cordillera de Huayhuash, Perú. Pp. 137-148 in *Paisajes culturales en los Andes: memoria narrativa, casos de estudio, conclusiones y recomendaciones de la reunión de expertos*, edited by E. Mujica Barreda. Lima: Centro del Patrimonio Mundial de la UNESCO. Available at: http://www.condesan.org/unesco/paisajes_culturales_andes.htm.

Ribera, M. O., and M. Liberman. 2006. *El uso de la tierra y los recursos de la biodiversidad en las áreas protegidas de Bolivia. Un análisis crítico con propuestas para su conservación y manejo sostenible*. La Paz: Servicio Nacional de Areas Protegidas. 520 pp.

Salzmann, N., C. Huggel, P. Calanca, A. Díaz, T. Jonas, C. Jurt, T. Konzelmann, P. Lagos, M. Rohrer, W. Silverio, and M. Zappa. 2009. Integrated assessment and adaptation to climate change impacts in the Peruvian Andes. *Advances in Geosciences* 22:35-39.

Sandwith, T. 2008. Protected areas and climate turnaround strategy (PACT) – an insurance policy for the world's greatest risk. *Policy Matters* 16:119-126.

Schliep, R., M. Bertzky, M. Hirschnitz, and S. Stoll-Kleemann. 2008. Changing climate in protected areas? Risk perception of climate change by biosphere reserve managers. *GAIA* 17:116-124.

Servicio Nacional de Áreas Naturales Protegidas (SERNANP). 2009. *Plan director de las áreas naturales protegidas (estrategia nacional)*. Lima: Servicio Nacional de Áreas Naturales Protegidas.

Servicio Nacional de Áreas Protegidas (SERNAP). 2007. *Informe sobre el sistema nacional de áreas protegidas*. La Paz: Servicio Nacional de Áreas Protegidas.

Servicio Nacional de Áreas Protegidas (SERNAP) and Wildlife Conservation Society (WCS). 2005. *Plan de manejo del PN – ANMI Madidi*. Unpublished report. La Paz: Servicio Nacional de Áreas Protegidas and Wildlife Conservation Society.

Servicio Nacional de Áreas Protegidas (SERNAP) and Comité de Gestión (CG) ANMIN Apolobamba. 2006. *Plan de manejo del ANMIN Apolobamba*. Unpublished report. La Paz: Servicio Nacional de Áreas Protegidas and Comité de Gestión ANMIN Apolobamba.

Servicio Nacional de Áreas Protegidas (SERNAP) and Consejo Regional T'simane Mosetene (CRTM). 2009. *Plan de manejo y plan de vida de la Reserva de la Biosfera y Tierra Comunitaria de Origen Pilón Lajas 2007-2017*. La Paz and Rurrenabaque: Servicio Nacional de Áreas Protegidas and Consejo Regional T'simane Mosetene. 249 pp.

Servicio Nacional de Áreas Protegidas (SERNAP) and Comité de Gestió (CG) ANMI San Matías. 2008. *Plan de manejo del ANMI San Matías*. Unpublished report. La Paz: Servicio Nacional de Áreas Protegidas and Comité de Gestión ANMI San Matías.

Shepherd, G. 2006. El enfoque ecosistémico: cinco pasos para su implementación. Gland and Cambridge: UICN. 30 pp.

Stainforth, D. A., T. E. Downing, R. Washington, A. Lopez, and N. New. 2007. Issues in the interpretation of climate model ensembles to inform decisions. *Philosophical Transactions of the Royal Society of London A* 365:2163-2177.

Stolton, S., J. Randall, and N. Dudley. 2008. Protected areas, climate change, and disaster mitigation. *Policy Matters* 16:82-91.

Ulloa, R., M. Aguirre, J. Camacho, M. Cracco, A. Dahik, M. Factos, I. Gutiérrez, S. Kigman, M.D. Quishpe, F. Moreno, M. Ribadeneira, J. Rivas, A. Rodríguez, J. Samaniego, L. Suárez, M. Tobar, X. Viteri, and E. Von Horstman. 2007. *Situación Actual del Sistema Nacional de Áreas Protegidas del Ecuador. Informe Nacional Ecuador* 2007. Quito: Ministerio del Ambiente del Ecuador, Comité Ecuatoriano de la Union Internacional para la Conservacion de la Naturaleza, and Fundacion Natura. 152 pp.

Van der Hammen, T., J. D. Pabón Caicedo, H. Gutiérrez, and J. C. Alarcón. 2002. *El cambio global y los ecosistemas de alta montaña de Colombia*. Pp. 163-209 in Páramos y ecosistemas alto-andinos de Colombia en condición hotspot y Gglobal climatic tensor, edited by C. Castaño Uribe. Bogotá: Ministerio del Medio Ambiente, Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia.

Vílchez, S. 1968. *Parques nacionales del Perú*. Lima: Editorial Cajamarca. 128 pp.

Vuille, M., R. S. Bradley, M. Werner, and F. Keimig. 2003. 20th century climate change in the tropical Andes: observations and model Results. *Climatic Change* 59:75-99.

Welch, D. 2008. What should protected area managers do to preserve biodiversity in the face of climate change? *Biodiversity* 9(3-4):84-88.

23

Environmental Flows: a Concept for Addressing Effects of River Alterations and Climate Change in the Andes

Elizabeth P. Anderson, Andrea C. Encalada,
Javier A. Maldonado-Ocampo, Michael E. McClain, Hernan
Ortega, and Bradford P. Wilcox

Rivers are dynamic systems and many facets of a river's flow regime—magnitude, timing, frequency, duration, and rate of change—influence the structure and function of aquatic and riparian ecosystems (Poff et al. 1997). Flow shapes physical habitat and biotic composition in rivers; life history strategies of aquatic species have evolved in response to natural flow variability (Bunn and Arthington 2002). On a global scale, flow alterations present a serious and extensive threat to the integrity of aquatic ecosystems and the persistence of freshwater species. Over half of the world's major river systems are presently affected by flow regulation (Nilsson et al. 2005), and climate change is predicted to further modify historical flow patterns in many rivers. The impacts of river alterations manifest themselves in the imperilment of aquatic biota, particularly migratory species (Pringle et al. 2000; Bunn and Arthington 2002; Xenopoulos et al. 2005), and in the reduced ability of rivers to provide valued ecosystem services—sources of water and food, recreation, waste assimilation, flood control (see Anderson et al. Chapter 1, this volume)—upon which humans depend (Postel and Richter 2003; Millennium Ecosystem Assessment 2005).

A response to extensive river alteration in many countries has been an evolving movement to recognize flow needs of ecosystems and allocate freshwater accordingly through determination of environmental flows (Naiman et al. 2002; Tharme 2003; Poff et al. 2010). An environmental flow is a management concept that aims to establish the flow regime needed to sustain ecosystems and the amount of water available for off-channel human uses or storage in reservoirs at different times of the year. To date, the concept has been primarily applied to temperate rivers (e.g., the U.S., South Africa, Australia, Europe), or in tropical countries where water laws and policies recognize the necessity of maintaining specific flow regimes to sustain ecosystems (Tharme 2003). New water laws and policies in some tropical regions (e.g., East Africa) make explicit mention of preserving flows to sustain ecosystems.

Until recently, tropical Andean countries have not applied the concept of environmental flow in management, even though Andean rivers harbor important reserves of freshwater biodiversity and are increasingly subject to flow alterations. Water withdrawals for agriculture and urban populations already substantially affect flow, and hydropower projects impound many Andean rivers (Harden 2006; Buytaert et al. 2006). To address future demands for water and energy of expanding human populations, networks of new dams and water withdrawal projects have been proposed for construction in the next decades (Consejo Nacional de Electricidad del Ecuador pers. comm; Pelaez-Samaniego et al. 2007). Climate change projections for the Andes also predict substantial flow alterations, with implications for both water supply and freshwater ecosystem integrity (Bradley et al. 2006; Vuille et al. 2008).

A considerable challenge facing Andean countries is finding a way to satisfy growing human demands for water and energy without compromising the biodiversity and ecological function of riverine ecosystems. Given the current pace and intensity of river alterations, there is an urgent need to develop environmental flow management standards that sustain ecosystems, can be effectively applied within a regional context, and that can be adapted to future climate change scenarios. This chapter reviews the concept of environmental flows, discusses regional trends in river alteration and their ecological implications, and outlines research needs for flow management in four Andean countries: Colombia, Ecuador, Perú, and Bolivia.

Environmental Flows: Balancing Water Needs of Humans and Ecosystems

The term environmental flow refers to the quantity, quality, and timing of water flow needed to sustain ecosystems and the services they provide to humans (Dyson et al. 2003; Poff et al. 2010). A distinction should be made between the natural flow regime of a river that would maintain ecosystems in a pristine state and an environmental flow. An environmental flow has the goal of allocating sufficient water to ecosystems to maintain a certain level of ecological integrity based on an appropriate management vision. Environmental flow standards can be restrictive management thresholds—designed to limit water withdrawals—or active management thresholds—designed to control flow releases downstream from dams (Poff et al. 2010).

Since the concept emerged in the mid-20th century, more than 200 methods for estimating environmental flows have been developed globally. These methods can be classified into four approaches (Table 23.1; Tharme 2003). *Hydrology-based methodologies* use historical discharge records to make environmental flow recommendations, usually expressed as a fixed proportion of flow intended to sustain river health (e.g., 10% of average annual discharge). *Hydraulic-rating methodologies* rely on basic hydraulic parameters (e.g., depth, wetted perimeter) that relate to habitat for aquatic biota; environmental flow recommendations are made by plotting acceptable levels of reduction in these parameters against discharge. Hydraulic-rating methodologies preceded more sophisticated *habitat simulation methodologies*, that employ hydrological,

Table 23.1. Examples of common methodologies used to determine environmental flows worldwide (excerpted from Tharme 2003).

Category	**Methodology**	**Brief description**
Hydrology-based	Tennant (Montana) Method (Tennant 1976)	Provides guidelines for flow management based on the percentage of average flow that would maintain biological attributes of a river as optimum (>60%), outstanding (40%), excellent (30%), good (20%), fair, poor, minimum, or degrading (10%).
Habitat simulation	Instream Flow Incremental Methodology (IFIM; Stalnaker et al. 1995)	Uses a model (PHABSIM) to simulate physical habitat and model habitat changes with changing flow, quantifies habitat preferences for selected biota (usually fish) based on hydraulic variables, and then identifies flows at which acceptable habitat is available for target species.
Holistic	Building Block Methodology (BBM; King and Louw 1998; King et al. 2000)	Uses the natural flow regime as a guideline and involves a team of interdisciplinary scientists to examine flow needs for ecological processes. The environmental flow recommendation is presented as a set of flow targets during different months that aim to achieve management goals.
	Downstream Response to Imposed Flow Transformation (DRIFT; King et al. 2003)	Combines data and knowledge from various disciplines to produce flow-related scenarios that can be considered in determining environmental flows. Aims to manage all aspects of flows, including temporal and spatial variability.
	Benchmarking (Arthington 1998; Arthington et al. 2006)	Aims to identify the level of flow alteration at which important ecological and geomorphological changes would begin to be detected through extensive measurements of stream conditions.

hydraulic, and biological response data to quantify suitable instream physical habitat available to target species, usually fish, under different flow regimes. Habitat-discharge curves depicting the range of habitat for biota as a function of flow are then used to determine environmental flow recommendations.

Contemporary advances in scientific understanding have shown that rivers are dynamic ecosystems and that a naturally variable flow regime is required to sustain them (Richter et al. 1997; Poff et al. 1997). *Holistic methodologies* aim to approximate the natural flow regime, and often employ some of the tools of hydrology-based, hydraulic-rating, and habitat-simulation approaches. Environmental flow recommendations can be expressed as a constructed, modified flow regime that varies intra-annually, or defined as acceptable levels of change from natural or reference flow conditions (Tharme 2003). Increased recognition of the services provided by intact freshwater ecosystems has led to the development of holistic methodologies that involve society in setting goals for flow management (King et al. 2000, Arthington et al. 2006). Environmental flow recommendations are designed to help achieve these goals (Table 23.2).

Perspectives on Water Use and River Alteration in the Andes

Human populations in the Andes and adjacent lowlands have long relied on rivers to meet needs for water and energy (Buytaert et al. 2006; Harden 2006). Historically, human impact on Andean landscapes has been most intense at high elevations (>2500 m), but

Table 23.2. An example classification system of management goals for rivers, which are used to guide the environmental flow assessment process. Based on applications of environmental flow methodologies in South Africa (King et al. 2000).

Ecological category	**Description**
A	Unmodified, natural
B	Largely natural with few modifications. Small changes in natural habitats and biological assemblages. Ecosystem functions are essentially unchanged.
C	Moderately modified. Some loss and change of natural habitat and biological assemblages. Basic ecosystem functions are still intact.
D	Largely modified. Major loss of natural habitat, biological assemblages, and basic ecosystem functions.
E	Seriously modified. Extensive loss of natural habitat, biological assemblages, and basic ecosystem functions.
F	Critical / extremely modified. River alterations have resulted in almost complete loss of natural habitat and biological assemblages. Basic ecosystem functions are destroyed and changes may be irreversible.

*Categories E and F are only used to describe the present state of a river. Management classes are A-D.

increasing colonization at mid and lower elevations (500 – 2500 m) has extended human influence on water resources (Mena et al. 2006; Buytaert et al. 2006). Existing dams and water diversions already have resulted in substantial flow alterations to many Andean rivers. The extent and magnitude of flow alterations are expected to increase in the next decade as a function of human population growth, increasing demands for water and energy, and climate change. Because of limited data, the number of existing and future dams and diversions is difficult to quantify and information availability varies by country. Some general trends are discussed below.

In terms of domestic water usage, several of the region's largest cities depend on Andean páramo streams as their principal source of water supply (Bradley et al. 2006; Vuille et al. 2008). For example, in Quito, Ecuador, approximately 85% of water supply is derived from streams draining Andean páramos (Buytaert et al. 2006). The average water demand of Bogotá, Colombia, is met almost entirely by diverting water from Andean páramo streams (Buytaert et al. 2006; P. Tellez pers. comm.). Lima and other arid coastal cities in Perú obtain water through a highly engineered system of dams and diversions extending to the headwaters of Andean rivers. Moreover, a growing proportion of coastal cities' water is transferred across the continental divide from Amazon bound rivers (La Touche 1997). La Paz, Cochabamba, and Potosí in Bolivia also rely predominantly on high Andean rivers as a source of water (M. Maldonado, pers. comm.).

Water for irrigated agriculture is the single largest consumptive use of fresh water in Ecuador, Peru, and Bolivia (>80% of surface water withdrawals), and accounts for ~40% of water withdrawals in Colombia (FAO 2003; J. Jurado pers. comm.). In the Ecuadorian Andes, many rivers are subject to water withdrawals by multiple irrigation projects along their courses, resulting in substantially reduced flows or even zero flows during dry periods (Buytaert et al. 2006). Irrigation efficiency is a concern for water resource use and management. The irrigation potential for Andean countries greatly exceeds the current irrigated area (FAO 2000), thus water withdrawals for agriculture are expected to increase in the future.

Climate and topography have created considerable hydropower potential for Andean rivers. Relatively constant base flow in glacier-fed, high-elevation streams, and annual rainfall in excess of 2 meters at middle and lower elevations guarantees sufficient water for electricity generation across the region; high relief increases the amount of power that can be produced from available water. Regionally, hydropower dams generate ~54% of electricity, although reliance on hydropower varies by country. These trends mirror those reported for neighboring Central America, where hydropower also generates more than half of regional electricity (Anderson et al. 2006). Colombia leads the Andean region in hydropower development, where approximately 50 large (>15 m high) and many smaller dams generate ~80% of electricity (World Commission on Dams 2000; Diez and Burbano 2006; P. Petry, pers. comm.). In Ecuador, ~45% of electricity comes from hydropower, largely generated by a single 1075 MW plant on the Paute River (Consejo Nacional de Electricidad del Ecuador pers. comm.). Other important dams in the Ecuadorian Andes include the Pucara (68 MW), Agoyan (156 MW) and San Francisco (230 MW) plants in the Pastaza River basin (Consejo Nacional de Electricidad del Ecuador pers. comm.). In Perú ~70% of electricity is generated by hydropower dams, including the Santiago Antúnez de Mayolo Dam, one of the country's largest projects (798 MW), and numerous small projects, many <1 MW (Ministerio de Energía y Minas, Peru 2010). In Bolivia's hydropower accounts for ~40% of electricity (US EIA 2009).

Much of the tropical Andean region's hydropower potential remains untapped. Ecuador provides an example: as of 2007, Ecuador had exploited only 15% of its estimated hydropower potential (Pelaez-Samaniego 2007). Regionally, many more dams are proposed and will result in increased fragmentation and flow alteration of rivers. Future hydropower development is motivated by the region's untapped potential but also by other interrelated factors. First, to meet current and future demands for electricity, installed generation capacity in many Andean countries will be increased. In Ecuador, for example, demand for electricity is expected to grow at a rate of 4-6% annually between 2006-2015, and new hydropower dams are viewed as a solution to meet demands (Consejo Nacional de Electricidad del Ecuador pers. comm.; Pelaez-Samaniego 2007). A plan presented by the Consejo Nacional de Electricidad (CONELEC) in 2007 proposed 23 new hydropower projects >100 MW, 76 projects between 10-100 MW, 45 projects between 1-10 MW, and 82 <1 MW (Consejo Nacional de Electricidad del Ecuador pers. comm.). Many of these dams could be located along gradient breaks between 500 – 2000 m elevation in the Napo, Pastaza, and Santiago River Basins. In Bolivia, the hydropower potential of each watershed is being evaluated, and several projects are currently proposed for Andean-Amazon rivers (M. Pouilly, IRD, pers. comm.). A second noteworthy point is the role of the Clean Development Mechanism in promoting new hydropower development in the region. In Peru, many new hydropower dams are being proposed under this framework (T. Zamora pers. comm.). Finally, the influence of neighboring countries, particularly Brazil, on hydropower development in Andean countries should not be overlooked. Brazil has pursued new hydropower developments on rivers in both Peru and Bolivia. Electricity generated by these projects is largely intended for export to Brazil.

In addition to direct human modifications like dams and water withdrawals, climate change has the potential to substantially alter historical flow patterns of Andean rivers. Current projections suggest temperatures in the Andes may increase by 4.5–5 ºC in the 21st century (Vuille et al. 2008). This warming would cause extensive melt of mountain glaciers and result in an initial increase in runoff followed by abrupt changes in flow regimes of glacier-fed Andean rivers. Glaciers are melting in other tropical regions (e.g., East Africa), but the Andean case is of special concern as there is such heavy reliance on glacier-fed water supplies to meet human demands for water and energy (Bradley et al. 2006; Vuille et al. 2008).

Linking Flows and Aquatic Biodiversity in Andean Rivers

Tropical Andean rivers are extremely diverse, varying from slow-moving, high-elevation streams to fast-flowing, mountain torrents in areas of high relief, and ranging from aseasonal equatorial systems to rivers with marked wet and dry seasons. This natural spatial and temporal heterogeneity in flow has helped shape biological communities and ecological and evolutionary processes. The general ecology of Andean rivers remains understudied (Allan et al. 2006), and even less is known about the specific consequences of flow alterations for Andean freshwater biodiversity. Nevertheless, some predictions can be made based on past research in Andean streams.

Macroinvertebrates (e.g., insects, crustaceans, mollusks, oligochaetes) are a key component of riverine fauna, and the structure and composition of macroinvertebrate assemblages vary widely within and between rivers as a function of flow conditions, geomorphology, and elevation (Jacobsen et al. 1997; Jacobsen 2003; 2004). Flow disturbances (e.g., floods and droughts) and seasonality have been shown to strongly influence the density and diversity of macroinvertebrates present at different times of the year (Flecker and Feifarek 1994; Ríos 2008). Changes in seasonality or changes to timing and magnitude of high and low flow events caused by river alterations could have profound effects on macroinvertebrate distribution and abundance. Flow alterations could affect life history strategies of macroinvertebrates, particularly where periodic water releases from a dam disrupt natural cues for downstream movement (drift), typically linked to high flows (Turcotte and Harper 1982; Ríos 2008). Altered flows could also influence timing of other life history events such as frequency of breeding, time of emergence, and time of reproduction (Jacobsen et al. 2008). In some cases, flow modifications associated with dams and water withdrawals alter a river's thermal regime, which controls many vital processes (Sweeney et al. 1991; Poff et al. 1992; Atkinson 1994; Olden and Naiman 2010).

The tropical Andes are a global center of fish species richness in high-elevation tropical streams, characterized by a highly endemic (estimated at 40% of species), yet poorly studied, fish fauna. Siluriformes (44%) and Characiformes (40%) are the dominant orders, followed by Gymnotiformes, Perciformes, Cyprinodontiformes, and Synbranchiformes. Maldonado-Ocampo et al. (2005) classify Andean fishes into three groups: torrent species that can adhere to hard surfaces and withstand strong currents; fusiform species that inhabit fast-flowing areas and exhibit a hydrodynamic body form; and species found in more still-water environments. Many Siluriformes (catfish) species widely distributed along elevational gradients are considered torrent species and potentially highly susceptible to flow alterations and subsequent changes in habitat (e.g., Astroblepidae, Trichomycteridae, and Loricariidae). Several migratory species of importance to regional fisheries (e.g. *Prochilodus magdalenae*, *P. reticulatus*, *P. nigricans*, *Salminus affinis, Brycon sp., Pseudoplatystoma sp.*) also inhabit Andean rivers (Ortega and Hidalgo 2008). Hydrologic alterations and physical barriers presented by dams impede these species' vital migrations, especially when modifications occur on mainstem rivers (Pringle et al. 2000; Galvis and Mojica 2007). Flow alterations could also affect resource availability and reproduction of Andean fishes in general. Macroinvertebrates are a primary component of the diet of many species and any changes in these communities as a consequence of flow alterations could affect fishes. Evidence suggests that some tropical Andean fishes reproduce during dry periods (Torres-Mejia and Ramírez-Pinilla 2008), thus changes in seasonal flow patterns could thus affect reproductive strategies of these species.

Flow alterations of Andean rivers, as a consequence of dams and water diversions or from climate change, have the potential to affect ecosystems thousands of kilometers downstream. The tropical Andes encompass the headwaters of two of the world's largest and most biologically diverse river basins, the Amazon and the Orinoco, and strongly influence many fundamental characteristics of the geomorphology, biogeochemistry, and ecology of these mainstem rivers (McClain and Naiman 2008). Andean rivers provide an important source of sediments, organic matter, and nutrients, and diverse organisms, particularly fishes, have adapted to the seasonal delivery of water and materials from the Andes to downstream ecosystems (Edmund et al. 1996; Allan et al. 2006; Jepsen and Winemiller 2007; McClain and Naiman 2008). Downstream ecosystems in both the Amazon and the Orinoco depend on unobstructed riverine connectivity between the Andes and the lowlands. By trapping sediments and altering flows, dams on Andean rivers could result in changes to the geomorphology of downstream reaches, affecting aquatic and riparian habitats, and impede movement of the many fish species that migrate along mountain-lowland river corridors (McClain and Naiman 2008).

Sustainable Flow Management in the Andes

In light of existing and future flow alterations of Andean rivers and their potential for wide-ranging consequences, there is a strong need for proactive flow management to sustain freshwater ecosystems and the ecosystem services they provide. The social and ecological value of environmental flows should be recognized, as addressing flow needs of ecosystems typically generates societal benefits (Dyson et al. 2003). Environmental flow assessment remains relatively new in Andean countries and present legal backing and institutional capacity for determining and implementing environmental flows vary by country (Table 23.3).

Scientific research can help guide Andean countries as they move forward in defining policies that support environmental flows. We have identified several research priorities to facilitate more sustainable flow management of Andean rivers:

1. *Maintenance, rehabilitation, and expansion of the network of stream gauges*. Hydrologic records are either incomplete or non-existent for many tropical Andean rivers. Without freely available, scientifically sound gauge data, environmental flows are very difficult to assess.

2. *Investigation of flow-ecology relationships of aquatic and riparian biota and migration patterns of migratory species*. Understanding the flow dependence of freshwater and riparian biota is essential to determination of flows that sustain conditions necessary for their survival. Much aquatic research in the tropical Andes is focused on species distribution. Collection and analysis of quantitative habitat data alongside species surveys would help provide critical information on flow preferences.

3. *Identification of societal goals for river management and acceptable levels of river alteration*. Tropical Andean rivers are more than just a source of water and energy. Loss or replacement of other services (e.g., scenic beauty, recreation, waste assimilation, food) compromised by flow alterations would be costly (Costanza et al. 1997). It is in society's interest to consider the range of benefits that rivers provide when making flow management decisions.

4. *Greater understanding of cumulative effects of multiple water withdrawals and dams on individual river systems, and possible interactions with climate change.* Under present and future scenarios, individual basins in the tropical Andes are subject to multiple dams and water diversions. Many of these are also glacier-fed systems. Understanding which unregulated rivers should be maintained to sustain biota and ecosystem services is crucial to flow management.

5. *Development of new approaches or adaptation of existing environmental flow methodologies to be applicable on a regional scale and adaptive in nature*. The pace of river alteration in the Andes greatly exceeds the time and ability to conduct environmental flow assessments on a river-by-river basis. Methodologies that are regionally appropriate and flow management strategies that can be adapted to deal with changing flow patterns are needed to safeguard rivers amidst existing and future alteration.

Table 23.3. Overview of environmental flow assessments and implementation in the four Andean countries. Sources for this information include: Instituto de Hidrología, Meteorología y Estudos Ambientales 2000; Diez and Burbano 2006; Diez and Ruiz 2007; Marc Pouilly and Mabel Maldonado (Bolivia) pers. comm. 2009; Lucia Ruiz (Perú) pers. comm. 2009.

Country	**Legislative frameworks for environmental flows**	**Institutional frameworks for environmental flows**	**Examples of environmental flow related research to date**
Colombia	Article 21 of the proposed new Ley de Aguas defines the concept of environmental flow (Ministerio de Ambiente 2006); Ley Ambiental 99/1993 (and modifications), requires an 'environmental license' for hydropower projects.	The Instituto de Hidrología, Meteorología y Estudos Ambientales (IDEAM) is one of the responsible government authorities for determining and implementing environmental flows.	Environmental flow estimation for the Palacé River downstream from a water diversion using habitat simulation and application of the Instream Flow Incremental Methodology (Diez and Ruiz 2007). Pilot project to determine environmental flows for the Chuza River, downstream from reservoir for water supply for Bogotá using holistic methodology similar to Richter et al. 2006 (P. Tellez pers. comm..). Development of preliminary methodology for estimating environmental flows at water projects that require licenses (Ministerio de Ambiente, Vivienda y Desarrollo Territorial and Facultad de Ingeneria, Universidad Nacional de Colombia, Workshop, October 2008)
Ecuador	The Acuerdo Ministerial No. 155 (Ministerio del Ambiente, 14 March 2007) mentions environmental flows but doesn't provide specific rules for calculation; a new proposed water law also mentions environmental flows. The new Constitution (2008) contains several Articles relevant to water resources management and specifically mentions environmental flows.	The Secretaria Nacional de Agua (SENAGUA) and its basin-level administrative units, the Water Agencies, coordinates with other government authorities to determine and implement environmental flows.	Definition of environmental flows for rivers in the Papallacta system, downstream from water supply reservoirs for the city of Quito using habitat simulation models AndeSim and PHABSIM (D. Rosero et al. pers. comm..). Determination of environmental flows for rivers of the Pastaza Basin, subject to multiple water diversions and flow alterations, using hydrology-based methods (C. Moreno and C. Galárraga pers. comm..; Moreno 2008) and holistic approaches Estimation of environmental flows downstream from a hydropower project on the Topo River using hydrology-based methodologies as part of an environmental impact assessment (ENTRIX unpublished report)
Peru	The current water law, which dates back to 1969, does not make reference to environmental flows.	The Autoridad Nacional del Agua (ANA), based out of the Ministerio de Agricultura, was recently created and will have a role in determining and implementing environmental flows.	
Bolivia	The current water law does not make reference to environmental flows, but the new constitution indicates the need to avoid damage to freshwater ecosystems.	The Ministerio del Medio Ambiente y Agua (MMyA) will have a role in determining and implementing environmental flows.	Research project on application of PHABSIM to study environmental flow requirements for the Beni River and two other systems (C. Ibañéz pers. comm..)

Acknowledgments

We thank M. Maldonado, R. Naiman, M. Pouilly, J. Schedlbauer, and all participants at the May 2009 workshop for information and suggestions that helped improve this chapter. J. A. Maldonado-Ocampo acknowledges the TWAS-CNPq Postgraduate Fellowships program for support.

Literature Cited

Allan, J. D., A. S. Flecker, S. Segnini, D. C. Taphorn, E. Sokol, and G. W. Kling. 2006. Limnology of Andean piedmont rivers of Venezuela. *Journal of the North American Benthological Society* 25:66-81.

Anderson, E. P., C. M. Pringle, and M. Rojas. 2006. Transforming tropical rivers: an environmental perspective on hydropower development in Costa Rica. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16:679-693.

Arthington, A. H. 1998. *Comparative evaluation of environmental flow assessment techniques: review of holistic methodologies. Occasional Paper No. 26/98.* Canberra: Land and Water Resources Research and Development Corporation.

Arthington, A. H., S. E. Bunn, N. L. Poff, and R. J. Naiman. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications* 16:1311-1318.

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* 25:1-58.

Bradley, R. S., M.Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. *Science* 312:1755-56.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492-507.

Buytaert, W., R. Celleri, B. DeBievre, F. Cisneros, G. Wyseure, J. Deckers, and R. Hofstede. 2006. Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews* 29:53-72.

Costanza, R., R. d'Arge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253-260.

Diez H., J. M., and L. Burbano B. 2006. Técnicas avanzadas para la evaluación de caudales ecológicos en el ordenamiento sostenible de cuencas hidrográficas. *Revista Ingeniería e Investigación* 26:58-68.

Diez H., J. M., and D. H. Ruiz C. 2007. Determinación de caudales ambientales confiables en Colombia: el ejemplo del río Palacé (Cauca). *Gestión y Ambiente* 10(4):153-166.

Dyson, M., M. Bergkamp, and J. Scanlon. 2003. *Flow: the essentials of environmental flows*. Gland and Cambridge: International Union for the Conservation of Nature.

Edmond, J. M., M. R. Palmer, C. I. Measures, E. T. Brown, and Y. Huh. 1996. Fluvial geochemistry of the eastern slope of the northeastern Andeas and its foredeep in the drainage of the Orinoco in Colombia and Venezuela. *Geochimica et Cosmochimica Acta* 60:2949-2976.

FAO. 2000. Irrigation in Latin America and the Caribbean in figures. *FAO Technical Papers, Water Reports 20*. Rome: Food and Agriculture Organization.

FAO. 2003. *Review of world water resources by country. FAO Technical Papers, Water Reports 23*. Rome: Food and Agriculture Organization.

Flecker, A. S., and B. P. Feifarek. 1994. Disturbance and temporal variability of insect assemblages in two Andean streams. *Freshwater Biology* 31:131-142.

Galvis, G., and J. I. Mojica. 2007. The Magdalena River fresh water fishes and fisheries. *Aquatic Ecosystem Health and Management* 10:127-139.

Harden, C. P. 2006. Human impacts on headwater fluvial systems in the northern and central Andes. *Geomorphology* 79:249-263.

Instituto de Hidrología, Meteorología y Estudios Ambientales. 2000. *Estudio nacional del agua*. Bogotá: Instituto de Hidrología, Meteorología y Estudios Ambientales. 39 pp.

Jacobsen, D. 2003. Altitudinal changes in diversity of macroinvertebrates from small streams in the Ecuadorian Andes. *Archiv für Hydrobiologie* 158:145-167.

Jacobsen, D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* 49:1293-1305.

Jacobsen, D., R. Schultz, and A. Encalada. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* 38:247-261.

Jacobsen, D., C. Cressa, J. M. Mathooko, and D. Dudgeon. 2008. Macroinvertebrates: composition, life histories, and production. Pp. 65-105 in *Tropical stream ecology*, edited by D. Dudgeon. London: Elsevier Academic Press.

Jepsen, D. B., and K. O. Winemiller. 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four Neotropical rivers. *Ecology of Freshwater Fish* 16:267-281.

King, J. M., and D. Louw. 1998. Instream flow assessments for regulated rivers in South Africa using the building block methodology. *Aquatic Ecosystem Health and Management* 1:109-124.

King, J. M., R. E. Tharme, and M. S. de Villiers (eds.). 2000. *Environmental flow assessments for rivers: manual for the building block methodology. Water Research Commission Report TT 131/00*. Pretoria: South African Water Research Commission.

King, J., C. Brown, and H. Sabet. 2003. A scenario-based holistic approach to environmental flow assessments for rivers. *River Research and Applications* 19:619-639.

La Touche, M. C. D. 1997. The water resources of Lima, Peru. *Water and Environment Journal* 11:437-439.

Maldonado-Ocampo, J. A., A. Ortega-Lara, J. Usma, G. Galvis, F. Villa-Navarro, G. Vásquez, S. Prada-Pedreros, and C. Ardila. 2005. *Peces de los Andes de Colombia, guia de campo*. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

McClain, M. E., and R. J. Naiman. 2008. Andean influences on the biogeochemistry and ecology of the Amazon River. *BioScience* 58:325-338.

Mena, C. A., R. Bilsborrow, and M. E. McClain. 2006. Socioeconomic drivers of deforestation in the Napo River Basin of Ecuador. *Environmental Management* 37:802-815.

Millennium Ecosystem Assessment. 2005. *Millennium Ecosystem Assessment synthesis report*. Washington, DC: Island Press.

Ministerio de Energia y Minas, Peru. 2010. www.minem.gob.pe. Accessed in May 2010.

Moreno, C. 2008. *Metodología y determinación de caudales ambientales en la cuenca del río Pastaza*. Licenciatura thesis. Quito: Escuela Politécnica Nacional.

Naiman, R. J., S. E. Bunn, C. Nilsson, G. E. Petts, G. Pinay, and L. C. Thompson. 2002. Legitimizing fluvial ecosystems as users of water: an overview. *Environmental Management* 30:455-467.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308:405-408.

Olden, J., and R. J. Naiman. 2010. Incorporating thermal regimes in environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology* 55:86-107.

Ortega, H., and M. Hidalgo. 2008. Freshwater fishes and aquatic habitats in Peru: current knowledge and conservation. *Aquatic Ecosystem Health and Management.* 11:257-271.

Pelaez-Samaniego, M. R., M. Garcia-Perez, L. A. B. Cortez, J. Oscullo, and G. Olmedo. 2007. Energy sector in Ecuador: current status. *Energy Policy* 35:4177-4189.

Poff, N. L., S. Tokar, and P. Johnson. 1992. Stream hydrological and ecological responses to climate change assessed with an artificial neural network. *Limnology and Oceanography* 41:857-863.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769-784.

Poff, N. L., B. D. Richter, A. H. Arthington, S. E. Bunn, R. J. Naiman, E. Kendy, M. Acreman, C. Apse, B. P. Bledsoe, M. C. Freeman, J. Henriksen, R. B. Jacobson, J. G. Kennen, D. M. Merritt, J. H. O'Keeffe, J. D. Olden, K. Rodgers, R. E. Tharme, and A. Warner. 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology* 55:147-170.

Postel, S., and B. D. Richter. 2003. *Rivers for life: managing water for people and nature*. Washington, DC: Island Press.

Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical-temperate comparisons. *BioScience* 50:807-823.

Richter, B. D., J. V. Baumgartner, R. Wigington, and D. P. Braun. 1997. How much water does a river need? *Freshwater Biology* 37:231-249.

Richter, B. D., A. T. Warner, J. L. Meyer, and K. Lutz. 2006. A collaborative and adaptive process for developing environmental flow recommendations. *River Research and Applications* 22:297-318.

Ríos, B. 2008. *Comunidades de macroinvertebrados en un río altoandino: importancia de microhabitat, dinamica de la deriva, paperl de la material orgánica, y relevancia de la oviposición*. Doctoral thesis. Barcelona: Universidad de Barcelona.

Stalnaker, C. B., B. L. Lamb, J. Henriksen, K. D. Bovee, and J. Bartholow. 1995. *The instream flow incremental methodology: a primer for IFIM. Biological Report 29*. Washington, DC: National Biological Service, United States Department of the Interior. 45 pp.

Sweeney, B. W., J. K. Jackson, J. D. Newbold, and D. H. Funk. 1991. Climate change and the life histories and biogeography of aquatic insects in eastern North America. Pp. 143-176 in *Global climate change and freshwater ecosystems*, edited by P. Firth and S. G. Fisher. New York: Springer.

Tennant, D. L. 1976. Instream flow regimes for fish, wildlife, recreation and related environmental resources. *Fisheries* 1(4):6-10.

Tharme, R. E. 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications* 19:397-441.

Torres-Mejia, M., and M. P. Ramírez-Pinilla. 2008. Dry-season breeding of a characin in a Neotropical mountain river. *Copeia* 1:99-104.

Turcotte, P., and P. P. Harper. 1982. Drift patterns in a high Andean stream. *Hydrobiologia* 89:141-151.

U.S. Energy Information Administration. 2009. *Bolivia energy profile*. Available at: www.eia.doe.gov. Accessed May 2009.

Vuille, M., B. Francou, P. Wagnon, I. Juen, G. Kaser, B. G. Mark, and R. S. Bradley. 2008. Climate change and tropical Andean glaciers: past, present and future. *Earth-Science Reviews* 89:79-96.

World Commission on Dams. 2000. *Dams and development*. Available at: www.dams.org.

Xenopoulos, M. A., D. M. Lodge, J. Alcamo, M. Marker, K. Schulze, and D. P. Van Vuurens. 2005. Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology* 11:1557-1564.

List of Contributors

Luis Marcelo Achite
Inter-American Institute for Global Change Research (IAI)
Av. dos Astronautas, 1758, 12227-010
São José dos Campos, SP
Brazil

Francisca Acosta
Universidad Mayor de San Simón (UMSS)
Unidad de Limnología y Recursos Acuáticos
Campus Universitario, Calle Sucre y Parque La Torre s/n, Cochabamba
Bolivia

Luis Fernando Aguirre Urioste
Universidad Mayor de San Simón (UMSS)
Centro de Biodiversidad y Genética
Campus Universitario, Calle Sucre s/n., frente Parque La Torre, Cochabamba
Bolivia

Elizabeth P. Anderson
Florida International University
Department of Earth & Environment
Global Water for Sustainability Program
Miami, FL 33199
USA

Angela Andrade
Integrated National Adaptation Plan (INAP)
Cr. 13 # 71-41, Bogotá
Colombia

Marcos Andrade
Universidad Mayor de San Andrés (UMSA)
Av. Villazón 1995 Monoblock Central, La Paz Bolivia

Jaime Argollo Bautista
Universidad Mayor de San Andrés (UMSA)
Calle 27 s/n, Cota Cota, La Paz
Bolivia

Inge Armbrecht
Universidad del Valle
Facultad de Ciencias Naturales y Exactas
Dept. Biología
Calle 13 # 100-00 Ed. 320. Of. 3025, Cali
Colombia

Carlos Alberto Arnillas
Universidad Nacional Agraria de La Molina
Facultad de Ciencia Forestales
Centro de Datos para la Conservación
Apartado 12-056
Peru

María del Pilar Arroyave Maya
Escuela de Ingeniería de Antioquia
Programa en Ingeniería Ambiental
Grupo de Investigación Gestión del Ambiente para el Bienestar Social (GABiS)
km 2 + 200 Via al Aeropuerto Jose Maria Cordova, Envigado, Antioquia
Colombia

Jacinto Arroyo Aliaga
Instituto Geofísico del Perú (IGP)
Calle Badajoz # 169
Mayorazgo IV Etapa, Ate Vitarte
Peru

Jesús Eduardo Arroyo Valencia
Corporación Autónoma Regional del Valle del Cauca (CVC)
Carrera 56 # 11 - 36, Cali
Colombia

Grinia Ávalos
Servicio Nacional de Meteorologia e Hidrologia (SENAMHI)
Jr. Cahuide 785, Lima
Peru

Diana K. Avilés Betancourt
Pontificia Universidad Católica del Ecuador (PUCE)
Av. 12 de Octubre 1076 y Roca, Quito
Ecuador

Victor Barrena
Universidad Agraria La Molina
Laboratorio de Teledetección Aplicada
Dept. Manejo Forestal
Casilla Postal 456, Lima
Peru

María Teresa Becerra
Secretaría General de la Comunidad Andina (CAN)
Av. Paseo de la República 3895, San Isidro, Lima
Peru

Stephan G. Beck
Universidad Mayor de San Andrés
Herbario Nacional de Bolivia
Apartado Postal 10077, La Paz
Bolivia

Rodrigo Bernal
Universidad Nacional de Colombia
Instituto de Ciencias Naturales
Apartado 7495, Bogotá
Colombia

Luis A. Blacutt Benavides
Universidad Mayor de San Andrés (UMSA)
Av. Villazón, 1995, Monoblock Central, La Paz
Bolivia

Gunnar Brehm
Institute of Special Zoology
Erbertstrasse 1, 07743 Jena
Germany

Edersson Cabrera
Instituto de Investigacion de Recursos Biologicos Alexander von Humboldt
Universidad Distrital Francisco José de Caldas
Carrera 7 No. 40 - 53 Bogotá
Colombia

Vanderlei Perez Canhos
Centro de Referência em Informação Ambiental (CRIA)
Av Romeu Tórtima, 388, 13084-791
Campinas, SP
Brazil

Juan Pablo Carrera
Texas Tech University
Department of Biological Sciences and the Museum
Lubbock, TX 79409
USA

Fernando M. Carvajal-Vallejos
Universidad Mayor de San Simón (UMSS)
Unidad de Limnología y Recursos
Acuáticos
Campus Universitario, Calle Sucre y
Parque La Torre s/n
Cochabamba
Bolivia

Asociación Faunagua
Final Av. Max Fernández,
Zona Arocagua, Cochabamba
Bolivia

Eulogio Chacón-Moreno
Universidad de los Andes
Facultad de Ciencias,3er Piso,
Núcleo La Hechicera, Mérida 5101
Venezuela

Marcela Celis
Universidad Nacional de Colombia
Instituto de Ciencias Naturales
Apartado 7495, Bogotá
Colombia

Steven P. Churchill
Missouri Botanical Garden
PO Box 299, St. Louis, MO 63166-0299
USA

Doris Cordero Camacho
International Union for the Conservation of
Nature (IUCN)/Regional Office for South
America
Calle Quiteño Libre E15-12 y La Cumbre,
Sector Bellavista, Casilla Postal 17-17-626,
Quito
Ecuador

Álvaro Crespo
Asociación FAUNAGUA
Asociación Faunagua
Final Av. Max Fernández,
Zona Arocagua, Cochabamba
Bolivia

Mónica Cuellar Buraglia
Instituto de Hidrología, Meteorología y
Estudios Ambientales (IDEAM)
Av. Carrera 45 No. 128 D-92, apto 406,
Bogotá
Colombia

Francisco Cuesta Camacho
Consorcio para el Desarrollo Sostenible de
la Ecorregión Andina (CONDESAN)
Proyecto Páramo Andino
Diego De Brieda E17-169, Quito
Ecuador

Amelia Díaz
Servicio Nacional de Meteorologia e
Hidrologia (SENAMHI)
Jr. Cahuide 785, Lima
Peru

Andrea C. Encalada
Universidad San Francisco de Quito
Colegio de Ciencias Biológicas y
Ambientales
Diego de Robles y Vía Interoceánica, Quito
Ecuador

University of Coimbra
Institute of Marine Research (IMAR)
Department of Zoology, 3000 Coimbra
Portugal

Federico Escobar Sarria
Instituto de Ecología, A.C.
Carretera antigua a Coatepec 351, Colonia
El Haya, CP 91070, Xalapa, Veracruz
Mexico

Juan Carlos Espinosa
World Wide Fund for Nature (WWF)
Colombia
Carrera 35 No.4A-25, Cali
Colombia

Susan Greenwood Etienne
Scientific Committee on Problems of the Environment (SCOPE)
c/o UNESCO
Bât. VII, Room 316
1, rue Miollis
75015 Paris
France

Christian F. Euscategui Collazos
Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM)
Carrera 10 No 20-30, Bogotá
Colombia

Wanderley Ferreira
RUMBOL S.R.L.
Avenida d'Orbigny 1608, Cochabamba
Bolivia

Padu Franco Creutzberg
Wildlife Conservation Society
Calle 3A no. 35A-57, Cali
Colombia

Fernando Gast
Car 7b # 134b - 11 Torre 1 Apto. 1105,
Bogotá Colombia

Luis Humberto Gómez Cerveró
Fundación Amigos de la Naturaleza
Km 7 1/2 Doble Vía a La Guardia
Santa Cruz de la Sierra
Bolivia

Carla C. Gómez Wichtendahl
University of Ottawa, Institute of the Environment
555 King Edward Avenue
Ottawa ON K1N 6N5 Canada

S. Robbert Gradstein
Muséum National d'Histoire Naturelle,
57 rue Cuvier, 75231 Paris Cedex 05
France

Catherine H. Graham
Stony Brook University
Department of Ecology and Evolution
650 Life Sciences Building
Stony Brook, NY 11789
USA

Héctor Ricardo Grau
Universidad Nacional de Tucumán
Casilla de Correo 34 (4107)
Yerba Buena, Tucumán
Argentina

John-Arvid Grytnes
University of Bergen
Department of Biology
Postbox 7803, N-5020, Bergen
Norway

María Elena Gutiérrez Lagoueyte
Escuela de Ingeniería de Antioquia
Programa en Ingeniería Ambiental
Grupo de Investigación Gestión del Ambiente para el Bienestar Social (GABiS)
km 2 + 200 Via al Aeropuerto Jose Maria Cordova, Envigado, Antioquia
Colombia

Stephan R. P. Halloy
The Nature Conservancy
Marchant Pereira 367, Of. 801
Providencia, Santiago
Chile

Sebastian K. Herzog
Asociación Armonía - BirdLife International
Av. Lomas de Arena 400
Casilla 3566, Santa Cruz de la Sierra
Bolivia

Dirk Hoffmann
Bolivian Mountain Insitute (BMI)
Casilla 3-12417, La Paz
Bolivia

David G. Hole
Conservation International
2011 Crystal Drive, Suite 500
Arlington, VA 22202
USA

Dean Jacobsen
University of Copenhagen
Freshwater Biological Section, Department of Biology
Helsingørsgade 51, DK-3400 Hillerød
Denmark

Ena M. Jaimes Espinoza
Servicio Nacional de Meteorologia e Hidrologia (SENAMHI)
Jr. Cahuide, 785 Jesus Maria, Lima
Peru

Peter Møller Jørgensen
Missouri Botanical Garden
P.O. Box 299, St. Louis, MO 63166-0299
USA

Carmen Josse Moncayo
Nature Serve
1101 Wilson Blvd., 15th floor
Arlington, VA 22209
USA

Mary T. Kalin de Arroyo
Universidad de Chile
Av. Libertador Bernardo O'Higgins 1058, Santiago
Chile

Gustavo H. Kattan
Depart. de Ciencias Naturales y Matemáticas
Universidad Javeriana Cali
Calle 18, No. 118-250, Cali, Colombia

Michael Kessler
University of Zurich
Institute of Systematic Botany
Zollikerstrasse 107, CH-8008 Zurich
Switzerland

Jürgen Kluge
University of Marburg
Faculty of Geography
Deutschhausstrasse 10
D-35032 Marburg
Germany

Thorsten Krömer
Universidad Veracruzana
Centro de Investigaciones Tropicales
Interior de la Ex-hacienda Lucas Martín, Privada de Araucarias s/n, Col. 21 de Marzo, C.P. 91019 Xalapa, Veracruz
Mexico

Daniel M. Larrea Alcázar
Fundación Amigos de la Naturaleza
Km 7 1/2 Doble Vía a La Guardia
Santa Cruz de la Sierra
Bolivia

Trond H. Larsen
Conservation International
Science and Knowledge Division
2011 Crystal Drive, Suite 500
Arlington, VA 22202
USA

Blanca León
University of Texas at Austin
Plant Resources Center &
Dept. of Geography and the Environment
1 University Station F0404
Austin, TX 78712-0471,
USA

Museo de Historia Natural
Universidad Nacional Mayor de San Marcos
Apartado 14-0434, Lima
Peru

Gloria León
Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM)
Carrera 10 No. 20-30, Bogotá
Colombia

Susana León-Yánez
Pontificia Universidad Católica del Ecuador (PUCE), Herbario QCA
Apartado 17-01-2184, Quito
Ecuador

Bette A. Loiselle
University of Florida
Center for Latin American Studies and Dept. of Wildlife Ecology and Conservation
343 Grinter Hall, Gainesville, FL 32611-5530
USA

Roseli Luz
Inter-American Institute for Global Change Research (IAI)
Av. dos Astronautas, 1758, 12227-010
São José dos Campos, SP
Brazil

Manuel J. Macía
Universidad Autónoma de Madrid
Departamento de Biología, Área de Botánica, Edificio de Ciencias Biológicas, Campus de Cantoblanco, Calle Darwin 2, E-28049 Madrid,
Spain

Mabel T. Maldonado Maldonado
Universidad Mayor de San Simón (UMSS)
Unidad de Limnología y Recursos Acuáticos
Campus Universitario, Calle Sucre y Parque La Torre s/n, Cochabamba
Bolivia

Javier A. Maldonado-Ocampo
Universidade Federal do Rio de Janeiro (UFRJ)
Departamento de Vertebrados, Setor Ictiologia, Museu Nacional, Quinta da Boa Vista, 20940-040 Rio de Janeiro, RJ
Brazil

José A. Marengo
Instituto Nacional de Pesquisas Espaciais (INPE)
Centro de Ciência do Sistema Terrestre
Av. dos Astronautas, 1758, 12227-010
São José dos Campos, SP
Brazil

Rodney Martínez Güingla
Centro Internacional para la Investigación del Fenómeno de El Niño (CIIFEN)
Escobedo 1204 y 9 de Octubre, Guayaquil
Ecuador

Michael E. McClain
UNESCO-IHE Institute for Water Education, Department of Water Engineering,
PO Box 3015
2601 DA Delft
The Netherlands

José Luis Mena Alvarez
Universidad Nacional Autónoma de Mexico (UNAM)
Instituto de Ecología, México, DF
Mexico

Edgard Montealegre
Universidad Nacional de Colombia
Carrera 45 No 26-85, Bogotá
Colombia

Mariano S. Morales
Instituto Argentino de Nivología,
Glaciología y Ciencias Ambientales
(IANIGLA)
CC 330, 5500 Mendoza
Argentina

Víctor R. Morales Mondoñedo
Universidad Ricardo Palma
Av. Benavides 4550, Apartado Postal 1801,
Las Gardenias, Surco, Lima
Peru

Douglas M. Muchoney
U.S. Geological Survey (USGS)
12201 Sunrise Valley Drive
Reston, VA 20192
USA

Luis Germán Naranjo
World Wide Fund for Nature (WWF)
Colombia
Cra. 35 # 4A-25, Cali
Colombia

Hugo G. Navarrete Zambrano
Pontificia Universidad Católica del
Ecuador (PUCE)
Av. 12 de Octubre 1076 y Roca, Quito
Ecuador

Gonzalo Navarro Sánchez
RUMBOL S.R.L.
Avenida d'Orbigny 1608, Cochabamba
Bolivia

Michael Nee
The New York Botanical Garden
Bronx, NY 10458-5126
USA

Imke Oetting
Fundación para el Desarrollo del Sistema
Nacional de Áreas Protegidas
Prolongación Cordero 127, Casilla 3667,
La Paz
Bolivia

Marcella Ohira
Inter-American Institute for Global Change
Research (IAI)
Av. dos Astronautas, 1758, 12227-010
São José dos Campos, SP
Brazil

Hernán Ortega
Universidad Nacional Mayor de San
Marcos
Dep. de Ictiologia, Museo de Historia
Natural
Avenida Arenales 1256, Jesús Maria
San Isidro, Lima
Peru

José Daniel Pabón Caicedo
Universidad Nacional de Colombia
Oficina 317, Edifico 212, Bogotá
Colombia

Manuel Peralvo
Consorcio para el Desarrollo Sostenible de
la Ecorregión Andina (CONDESAN)
Proyecto Páramo Andino
Diego De Brieda E17-169, Quito
Ecuador

Germán Poveda
Universidad Nacional de Colombia
Carrera 45 No 26-85
Edificio Uriel Gutiérrez, Bogotá
Colombia

María Paula Quiceno
Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH)
Calle 28A# 15-09, Bogotá
Colombia

Juan Quintana
Dirección Meteorológica
Av. Portales 3450, Estación Central
Casilla 140, Sucursal Matucana, Santiago
Chile

Edson E. Ramírez Rodríguez
Universidad Mayor de San Andrés (UMSA)
Calle 30 s/n, Cota Cota, La Paz
Bolivia

Juan Francisco Rivadeneira
Ministerio de Relaciones Exteriores, Comercio e Integración
Carrión E1-76 y Av. 10 de Agosto, Quito
Ecuador

Carlos A. Rivera-Rondón
Centre for Advanced Studies of Blanes (CEAB)
Spanish Council for Scientific Research (CSIC) Acces Cala St. Francesc 14,
Blanes 17300, Girona
Spain

Pontificia Universidad Javeriana
Unidad de Ecología y Sistemática,
Departamento de Biología, Cra 7 No. 40-82, Bogotá
Colombia

Maisa Rojas
Universidad de Chile
Departamento de Geofísica
Blanco Encalada 2002, Santiago
Chile

Gabriela Rosas
Servicio Nacional de Meteorología e Hidrología (SENAMHI)
Jr. Cahuide 785 Jesús María, Lima
Peru

Daniel Ruiz Carrascal
Programa en Ingenieria Ambiental, Escuela de Ingenieria de Antioquia
km 2 + 200 Via al Aeropuerto Jose Maria Cordova, Envigado, Antioquia
Colombia

International Research Institute for Climate and Society, Lamont-Doherty Earth Observatory
Columbia University in the City of New York
61 Route 9W - PO Box 1000
Palisades, NY 10964-8000
USA

Javier Sabogal
World Wide Fund for Nature (WWF) Colombia
Carrera 35 No.4A-25, Cali
Colombia

José Antonio Saito
Universidad Agraria La Molina
Centro de Datos para la Conservación (CDC)
Facultad de Ciencia Forestales
Apartado 12-056, Lima
Peru

Fernando Salazar Holguín
Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM)
Calle 152B No. 59 C - 17 C.5, Bogotá
Colombia

Pablo Sánchez
Pontificia Universidad Católica del Ecuador (PUCE)
Av. 12 de Octubre 1076 y Roca, Quito
Ecuador

Silvia R. Sánchez Huaman
Asociacion Perúana para la Conservación de la Naturaleza (APECO)
Parque Jose de Acosta 187, Lima
Peru

Klaus Schutze Páez
Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM)
Cra. 10 No. 20-30 P9, Bogotá
Colombia

Anton Seimon
Wildlife Conservation Society
2300 Southern Boulevard, Bronx, NY 10460
USA

Harrie J. M. Sipman
Free University of Berlin, Botanic Garden & Botanical Museum
Königin-Luise-Str. 6-8
D-14195, Berlin
Germany

Sergio Solari
Universidad de Antioquia
Instituto de Biología
Calle 67 53 - 108 / P.O. Box 1226, Medellín
Colombia

Silvina Solman
Universidad de Buenos Aires
Centro de Investigaciones del Mar y la Atmósfera (CIMA), Facultad de Ciencias Naturales
Pabellón II - Piso 2, Ciudad Universitaria
1428 Buenos Aires
Argentina

César Freddy Suárez
World Wide Fund for Nature (WWF) Colombia
Carrera 35 No.4A-25, Cali
Colombia

Holm Tiessen
Inter-American Institute for Global Change Research (IAI)
Av. dos Astronautas, 1758, 12227-010
São José dos Campos, SP
Brazil

Cecilia Toledo
Universidade de Taubaté
Av. Juscelino K Oliveira, 148, 12010-600
Taubaté, SP
Brazil

L. Antonio Tovar Narváez
Universidad Agraria La Molina
Centro de Datos para la Conservación (CDC)
Facultad de Ciencia Forestales
Apartado 12-056, Lima
Peru

Roberto Ulloa
Conservation Internacional (CI)
Ave. Coruña N29-44 y E. Noboa Caamaño, Quito
Ecuador

Carmen Ulloa Ulloa
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299
USA

Isabel Vega
Instituto Nacional de Pesquisas da
Amazônia (INPA)/The Large Scale
Biosphere-Atmosphere Experiment in
Amazonia (LBA)
Av. André Araújo, 2936, Aleixo
Manaus, AM 69060-001
Brazil

Jorge Velásquez-Tibatá
Stony Brook University
Department of Ecology and Evolution, 650
Life Sciences Building, Stony Brook, NY
11789
USA

Marcos Joshua Villacís Erazo
Escuela Politécnica Nacional
Ladrón de Guevara E11 – 253, Quito
Ecuador

Ricardo Villalba
Instituto Argentino de Nivología,
Glaciología y Ciencias Ambientales
(IANIGLA)
CC 330, 5500 Mendoza
Argentina

Bradford P. Wilcox
Texas A&M University
Department of Rangeland Ecology and
Management
College Station, TX 77843
USA

Bruce E. Young
NatureServe
Apdo. 358, Plaza Colonial, 1260, San José
Costa Rica

Kenneth R. Young
University of Texas at Austin
Department of Geography and the
Environment
1 University Station A3100
210 W. 24th, Austin, TX 78712
USA

Paula Andrea Zapata Jaramillo
Escuela de Ingeniería de Antioquia
Programa en Ingeniería Ambiental
Grupo de Investigación Gestión del
Ambiente para el Bienestar Social (GABiS)
km 2 + 200 Via al Aeropuerto Jose Maria
Cordova, Envigado, Antioquia
Colombia

James L. Zarucchi
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299
USA