Biogeography of the Indo-Australian Archipelago

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Abstract

The extraordinary species richness and endemism of the Indo-Australian
Archipelago (IAA) exists in one of the most geologically dynamic regions of
the planet. The provenance of its biota has been debated, particularly in the
area known as Wallacea. Application of molecular genetic approaches and a
better understanding of the region's complex geology have stimulated much
recent biogeographic work in the IAA. We review molecular phylogenetic
and phylogeographic studies in light of current geological evidence. Present
distribution patterns of species have been shaped largely by pre-Pleistocene
dispersal and vicariance events, whereas more recent changes in the connec-
tivity of islands within the Archipelago have influenced the partitioning of
intraspecific variation. Many genetic studies have uncovered cryptic species
with restricted distributions. We discuss the conservation significance of
the region and highlight the need for cross-taxon comparative studies us-
ing newly developed analytical approaches well suited to the challenges of
historical inference in this region.

INTRODUCTION

Vicariance:
division of a formerly continuously distributed population or species due to the formation of a barrier

Dispersal: movement of organisms across a barrier

IAA: Indo-Australian Archipelago

The Indo-Australian Archipelago (IAA), also known as Malesia or the Malay Archipelago, is the most geographically complex tropical region on Earth. It comprises more than 20,000 islands straddling the equator in Southeast Asia, and includes Brunei, East Timor, Indonesia, Malaysia, New Guinea, Philippines, Singapore, and peninsular Thailand (**Figure 1**). Over the past 50 My, the geography of this region has changed considerably (**Figure 2**), and ancient vicariance events have given rise to remarkable patterns in the distribution of higher taxa. More recently, rising and falling sea levels during the Pleistocene caused islands on the Sunda Shelf to repeatedly sunder and fuse with each other and/or the mainland as the sea floor was exposed and then submerged. Land area was considerably greater during periods of low sea levels, which facilitated terrestrial dispersal between islands that are currently separated. In contrast to the Holarctic, where current organismal distributions frequently reflect range expansions from Pleistocene refugia, distributions in the IAA
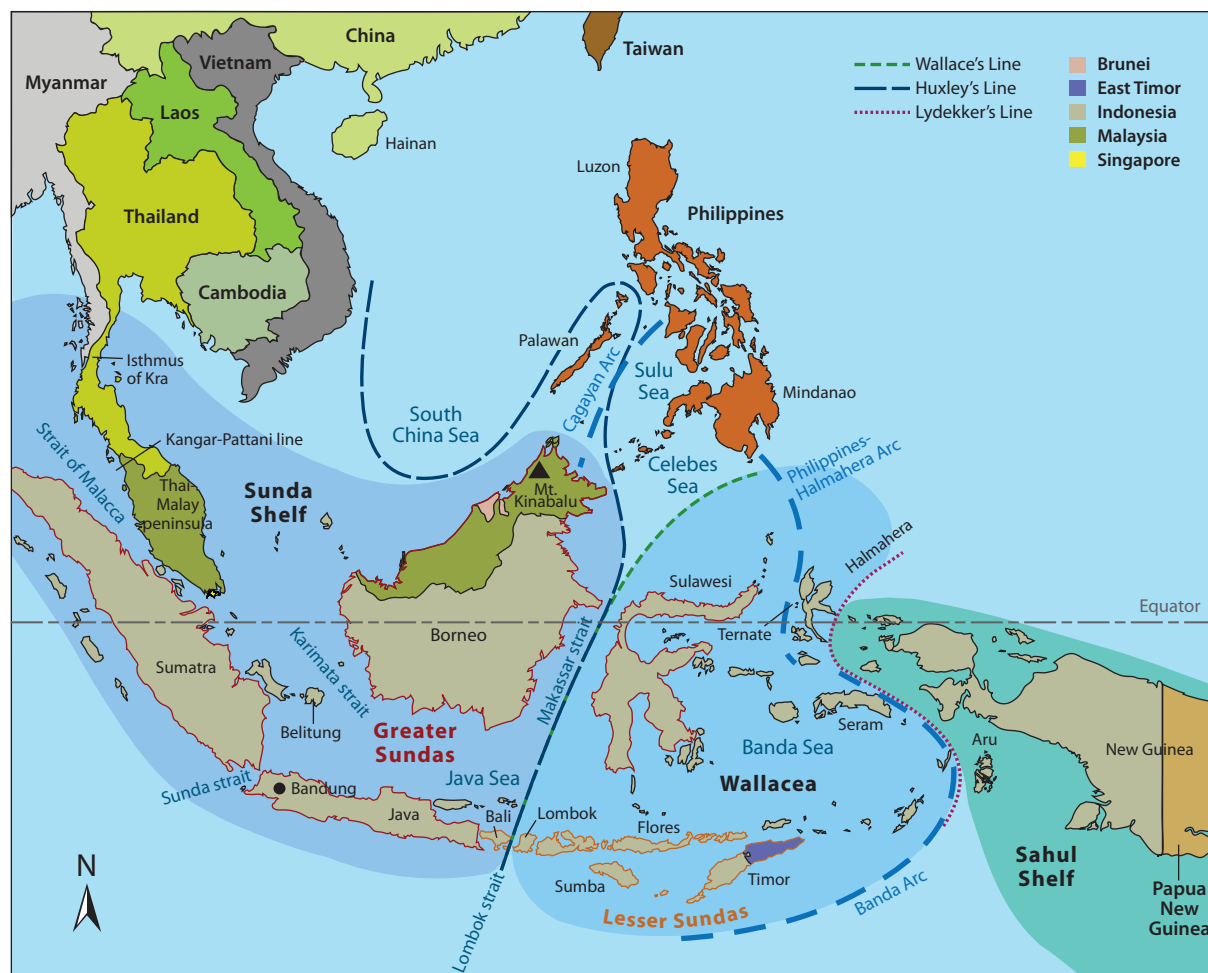

Figure 1
Map of the Indo-Australian Archipelago (IAA) indicating contemporary landmasses, straits, seas, arcs, and faunal lines. Major islands are labeled; different countries in the IAA are indicated by color. Red or orange borders around an island indicate membership in the Greater or Lesser Sundas, respectively.
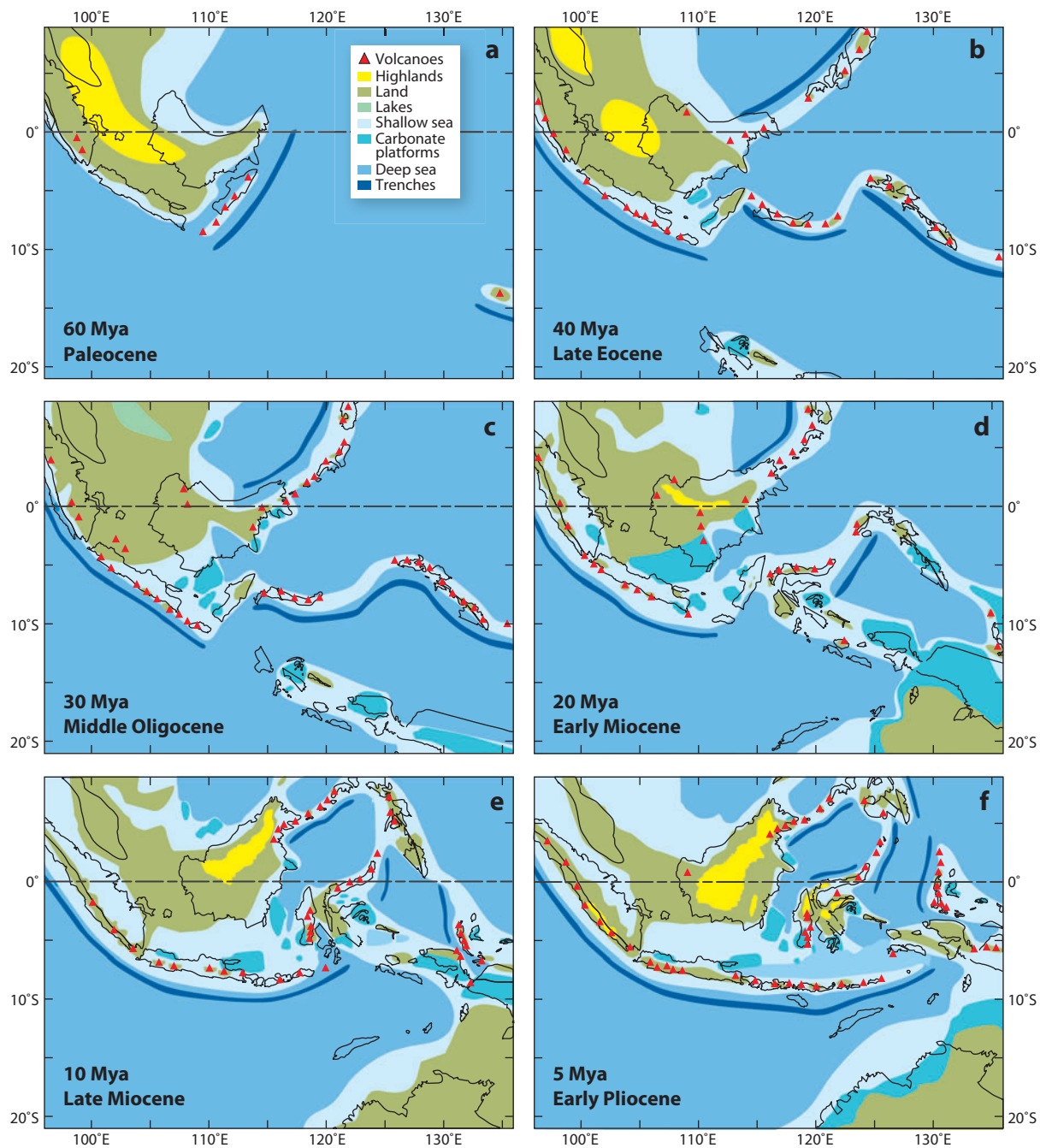
Figure 2

Six Cenozoic reconstructions of land and sea in the Indo-Australian Archipelago.

are currently refugial (Cannon et al. 2009). During the Pleistocene, the Sunda Shelf had half the coastline and twice the land area as today; this exposed shelf is known as "Sundaland" (Woodruff 2010). The complex history of the IAA has given rise to a diverse and highly endemic biota. Although it occupies just 4% of the planet's land area, the IAA is home to nearly one-quarter of all terrestrial species and the most species-rich coral reefs in the world (Corlett 2009). Four biodiversity hotspots are at least partly in the IAA: Indo-Burma, Philippines, Sundaland, and Wallacea (Myers et al. 2000), but this incredible diversity is under severe anthropogenic threat.

Islands and archipelagos have long been considered natural laboratories for the study of evolution. While the Galapagos Islands stimulated Charles Darwin's seminal work, the IAA was Alfred Russel Wallace's muse. He famously sent Darwin a manuscript from Ternate, in what is now Indonesia, in which he articulated his concept of evolution by natural selection (Darwin & Wallace 1858), stimulating Darwin to complete *On the Origin of Species* (Darwin 1859). Observations in the IAA also motivated Wallace to develop many of his ideas on the relationship between geological history and animal distributions, and the region should therefore be regarded as the birthplace of modern biogeography. Unlike the Azores and the Canary, Galapagos, and Hawaiian islands, where all islands are truly oceanic and arose from the ocean floor through volcanism, the islands of the IAA are of more varied origin, comprising pieces of continental crust (terranes), oceanic islands, and landmasses of composite origin, such as Sulawesi and New Guinea. These two islands attained their present configuration after separate terranes collided, potentially with any resident biota.

Recent work in geology, palynology, paleoclimatology, and molecular systematics has advanced historical reconstruction of the region's unique history. We summarize previous biogeographic study in the IAA; review recent empirical advances in geology, phylogenetics, and animal phylogeography; and suggest future directions for biodiversity research and conservation.

HISTORY OF BIOGEOGRAPHIC STUDY IN THE INDO-AUSTRALIAN ARCHIPELAGO

The Uniqueness of Wallace's Line

> "South America and Africa, separated by the Atlantic, do not differ so widely as Asia and Australia" (Wallace 1860, p. 174).

Wallace's Line demarcates the most abrupt faunal transition in the world. To a seasoned naturalist like Wallace, this unique juxtaposition of dramatically different faunas, first noted by Müller (1846), was obvious, was anomalous, and begged explanation; so it is perhaps no accident that biogeographic study effectively began in the IAA. The range limits of many terrestrial taxa are coincident with the eastern edge of the Sunda Shelf, and the taxonomic compositions of communities on either side are distinctly different. Wallace advocated geological explanations for these biological differences. He suggested, for example, that Bali and Lombok were formerly widely separated and had only recently moved to their present positions <40 km apart; he also noted that faunal discontinuities were associated with deep straits (Wallace 1860). Wallace first described the Line in an 1858 letter to H.W. Bates (Marchant 1916, p. 66) before he mapped the Line (Wallace 1863) that was later given his name by Huxley (1868) and expounded upon these observations in books on the IAA and biogeography in general (e.g., Wallace 1869). The veracity of Wallace's observations was debated because the existence of such a stark faunal divide seemed improbable, and this spurred intense study of distribution patterns in the region (e.g., Weber 1902).

One product of this debate was the designation by Dickerson (1928) of a faunal transition zone called Wallacea. Although the relevance of this area became controversial (Mayr 1944),

Sundaland: a terrestrial extension of mainland Southeast Asia formed during periods when low sea levels exposed seabeds between the Malay Peninsula, Java, Sumatra, and Borneo

Terrane: a fragment of crust bounded by faults with a distinctive stratigraphy and history

usage of the term has become entrenched to refer to the zone of islands between the Asian Sunda Shelf and Australian Sahul Shelf—continental shelves that are traced by Wallace's Line [with Huxley's modification (Huxley 1868)] in the west and Lydekker's Line (Lydekker 1896) in the east (**Figure 1**). Dickerson's original concept of Wallacea included the Philippines, but we concur with modern usage and consider these islands to be a separate entity.

Simpson's (1977) critical review of Wallace's and six other faunal lines questioned the importance of choosing a single faunal line rather than acknowledging that patterns of community diversity among different taxa are too varied to make one, universally applicable distinction. Nevertheless, Wallace's Line has remained a heuristic concept and is still widely cited because it highlights the striking faunal discontinuities observed in this region, even if those patterns are not universal.

In the early 1980s, advances in geology and the recognition of plate tectonic concepts allowed the formulation of plausible vicariant mechanisms to explain the distribution of taxa on multiple islands (Whitmore 1981). These geological advances complemented methodological refinements in phylogenetic systematics to support the novel hypothesis that some organisms dispersed within the region on mobile terranes (Michaux 1996). Much early research, including Wallace's own observations, focused on vertebrates, but insects featured prominently in this new fusion of plate tectonics and cladistics (Knight & Holloway 1990). In the late 1990s, biogeographic research in the IAA benefitted enormously from more reliable and detailed plate tectonic models (Hall 1996), which made an immediate impact on biogeographical interpretation (Hall & Holloway 1998). These models coincided with the explosive growth of molecular phylogenetics and phylogeography made possible by PCR and affordable DNA sequencing technology.

Vicariant Versus Dispersalist Schools of Biogeography

Since the latter half of the nineteenth century, biogeographers have debated whether vicariance or dispersal is the predominant force explaining distributions spanning more than one landmass (Lomolino et al. 2010). Wallace (1863) espoused a vicariant hypothesis invoking a former Pacific continent to explain his eponymous Line before adopting dispersalist scenarios in his later publications (e.g., Wallace 1876). Vicariant explanations were never completely abandoned in IAA biogeography, and Rensch (1936) invoked a number of hypothetical land bridges across deep water straits as late as 1936. Today, many of the Philippine and Wallacean islands are generally regarded as oceanic islands because they have had no terrestrial connection to any surrounding land since their emergence (van Oosterzee 1997). Consequently, their biota arose predominantly via dispersal and not vicariance. Sulawesi is a special case because the island was formed by the collision of different terranes and subsequent fragmentation beginning approximately 15 Mya (**Figure 2d,e**). Some of its current biota may therefore have vicariant origins from Sundaland in the west or New Guinea/Australia to the east (Wilson & Moss 1999, but see Hall 2001, 2011). However, there is now little doubt that the bulk of Sulawesi's fauna is of Asian origin, and dispersal has replaced land bridges as the favored explanation for the origins of the island's biota (van Oosterzee 1997).

GEOLOGICAL RECONSTRUCTIONS OF THE INDO-AUSTRALIAN ARCHIPELAGO

Cenozoic Geological Changes

The network of islands that forms the IAA comprises two continental shelves and numerous smaller terranes. These elements are in a state of continuous flux, and the geography of the IAA during the Cenozoic was markedly different from today (**Figure 2**; **Supplemental**

Emergent:
protruding above sea
level

Subduction: a
process in which one
tectonic plate moves
under another

Supplemental Material

Figure 1, follow the **Supplemental Material link** from the Annual Reviews home page at
http://www.annualreviews.org). The Philippine islands of Palawan and Luzon, for example,
were separated by at least 1,300 km during the early Eocene approximately 50 Mya (Hall 1996),
but today are separated by less than 300 km. As terranes were moving around what is now the
South China Sea, they did not necessarily remain above sea level (Hall 2001); submergence would
presumably have extinguished all terrestrial and freshwater life they may have hosted. Recon-
structing the geological history of the IAA is essential for understanding contemporary patterns of
diversity because the likelihood of dispersal or vicariance between particular landmasses differed
at different times in the past.

At the beginning of the Cenozoic approximately 65 Mya, Sundaland was a continental promon-
tory at the southern end of Eurasia (Hall 1996). It was an emergent terrestrial region that crossed
the equator, probably with a mountainous interior and rivers carrying sediments to the continental
margins. During the Paleocene–Early Eocene thermal maximum approximately 56 Mya, the cli-
mate was similar to or warmer and wetter than today, but from approximately 45 Mya during the
Middle Eocene onward was probably much more seasonal and possibly drier up to the Neogene
approximately 23 Mya (Heaney 1991, Morley 2000).

Major changes began in the Eocene (Hall 2002). India had moved rapidly north during the
Cretaceous to collide with Asia at some time in the Paleogene (Rowley 1996). During this time,
Australia had barely separated from Antarctica. It began to move rapidly northward from ap-
proximately 45 Mya (Hall 2002). Northward subduction of the Australian plate resumed beneath
Indonesia, causing widespread volcanism at the active margin and producing chains of islands
(arcs) similar to those of the West Pacific today. The Sunda Arc stretched from Sumatra, through
Java and the north arm of Sulawesi, and continued into the western Pacific to join the Philippines–
Halmahera Arc (**Figure 1**). One of the deepest and widest rifts, the Makassar Strait separating
Borneo from western Sulawesi (**Figure 1**), was created by stretching of the Sundaland margin,
thus forming the geological basis for Wallace's Line. Southward subduction of the proto-South
China Sea also began beneath Borneo. Sundaland was surrounded by subduction zones until the
Miocene (except for the border with western Sulawesi, which appears to have been a fault along
the boundary margin) and was probably mainly close to sea level, with elevated areas in western
Borneo and the Thai-Malay Peninsula.

In the Early Miocene approximately 23 Mya (**Figure 2d**), the Australian plate made contact
with the submerged Sundaland margin near Sulawesi, and the Sunda region began to rotate,
initially keeping pace with Australia's northward movement. From approximately 20 Mya, New
Guinea began to emerge from the sea, probably as small islands along the northern edge, but most
of the area that is now mountains was shallow sea. At about the same time, mountains rose from
central Borneo to Palawan. Rivers flowing from these mountains began to shed large amounts of
sediment into the onshore and offshore basins around Borneo. The collisions led to closure of
the deep ocean barrier between Sundaland and Australia, an increase in the area of shallow seas
throughout the region, and significant reduction in flow from the Pacific to the Indian Ocean.
The rise of mountains and changes in ocean circulation probably contributed to the change to a
generally wetter climate in Sundaland from the Miocene onward (Morley 2000). Despite uplift
in Borneo, there was a gradual increase in the area of shallow seas and reduction in land area on
Sundaland during the Neogene until the Pliocene approximately 5 Mya (**Figure 2f**). Collision
contributed to emergence of more land in Wallacea, including intermittently emergent islands,
extensive carbonate reefs, and shallow buildups between continental Australia and Sundaland, but
there was no permanent land connection.

During the Late Neogene, Australia continued to move north, and subduction-related defor-
mation led to the gradual emergence of Sumatra and Java as major land areas during the Pliocene.

From Borneo to New Guinea, several small oceanic basins subducted at different times, leading to a complex pattern of uplift and subsidence, contraction and extension, and the development of new deep oceanic basins and volcanic arcs. Over the past 7 million years, crustal melting in Borneo caused the rise of Mount Kinabalu to its present height of more than 4 km, and deep crustal processes contributed to widening the area of lower hills surrounding it. The Makassar Strait remained a deep but narrowing marine barrier east of Borneo as mountains rose rapidly in Sulawesi during the past five million years. At the same time, deep basins formed between the arms of Sulawesi (**Figure 2f**). In the Banda Arc region, subduction eliminated an old, deep oceanic embayment, but new deep basins formed, the Australian continental margin extended, and there was collision of a young volcanic arc with the Australian margin (Spakman & Hall 2010). As a result, the islands of the Banda Arc, notably Timor and Seram, emerged in the past two million years from depths of several kilometers to elevations of more than three kilometers. At the same time, even higher mountains rose to form the Central Ranges of New Guinea, and most of that island emerged from the ocean. New Guinea has never been closer to the Sunda Shelf than it is at present, but the two have always been separated by ocean.

Quaternary Geological Changes

Sea level change driven by polar ice volume changes modified land area over much of the IAA during the Quaternary (Hanebuth et al. 2009). It is possible to make realistic assessments of areas of land and shallow seas on the Sunda and Sahul shelves by using present-day bathymetry and estimates of historical changes in sea level. Such reconstructions infer major rivers draining from the Thai-Malay Peninsula, Sumatra, and northern Borneo toward the South China Sea and a major river system flowing east along the present Java Sea with a drainage divide at approximately 3°S near the present position of Belitung (Molengraaff & Weber 1921, Voris 2000). Rivers flowed toward Wallacea from the northern interior of Australia during periods of lowest sea level (Torgersen et al. 1985). Today, Sundaland has a humid, tropical climate with seasonal monsoons. During the Pleistocene glacial intervals, much of it may have been cooler and drier, but everwet conditions appear to have persisted in northern Sumatra, western and northern Borneo, and parts of the emergent Sunda Shelf (Bird et al. 2005, Morley 2000). During cooler intervals, only Mount Kinabalu and possibly small areas of north Sumatra were high enough to have been capped by ice, whereas New Guinea had extensive montane glaciers (Hope 2007).

It is not possible to estimate the Quaternary distribution of land and sea in Wallacea using the same approach because of very recent tectonic changes. This region is characterized by mountainous islands surrounded by narrow shelves and separated by basins much deeper than 120 m—the greatest sea level decrease thought to have occurred. Timor and Sumba, for example, have been rising at rates of 1–1.5 km My^{-1} since the mid-Pliocene (Roosmawati & Harris 2009), whereas Gorontalo Bay between the east and north arms of Sulawesi attained a depth of 1–2 km relatively recently (Hall 2011). Rapid vertical changes like this likely occurred in other Wallacean locales. Although the paleogeography of Wallacea is uncertain, it is clear that deep marine areas persisted between the Sahul and Sunda shelves and there was no land connection.

There are a number of large freshwater lakes, or former lakes, in land areas such as Java, Sulawesi, and Mindanao that emerged in the Plio-Pleistocene approximately 1.5 Mya, but few have been studied to determine their age. Detailed work near Bandung in Java shows that a large lake formed 135 kya and disappeared in the past few thousand years (van der Kaars & Dam 1995). Other large lakes are in tectonically or volcanically precarious areas (e.g., Matano, Poso and Towuti in Sulawesi, and Lanao in Mindanao) and, where dated, are younger than the Bandung Lake (e.g., Dam et al. 2001a). It is unlikely that any lakes have the ages of several million years

that are sometimes attributed to them (e.g., Tamuntuan et al. 2010). Until there is evidence to the contrary, all—including those lakes postulated on the submerged shelf areas (Sathiamurthy & Voris 2006)—should cautiously be considered as geologically ephemeral with lifetimes of hundreds of thousands of years at most. Recent seismic data on Sulawesi's Lake Towuti suggest an age of approximately 600 ky (J. Russell, personal communication).

PALEOCLIMATE RECONSTRUCTIONS

Climate: Miocene to Present

While the changing configuration of land and sea affected the likelihood of dispersal around the IAA, changes in climate affected the type and extent of different habitats. Inferred land connections between formerly isolated islands may not have been conducive to biotic interchange if intervening habitats were not suitable. Pollen records and paleoclimatic information are used to infer past habitats, and ancient climates are often reconstructed through marine sediment cores using Foraminifera and isotopes of oxygen and carbon (Zachos et al. 2001). More recent Pleistocene and Holocene climates are inferred by combining global predictions based on these data with regional data on pollen, diatom and sedimentary studies of lake and bog cores (Dam et al. 2001a), faunal distributions (Meijaard 2003), magnetic susceptibility of sediments (Tamuntuan et al. 2010), and landscape features (Hope 2007).

The northward movement of Australia in the Miocene approximately 15 Mya affected not only the geological but also the climatic setting, both regionally and globally, by changing patterns of ocean currents and the relative distribution of land and sea (Morley 2000). Warm, humid global climates peaked in the mid-Miocene 17–15 Mya (Zachos et al. 2001). Global and regional climates slowly became cooler and drier, but remained relatively warm and humid through to the Pliocene approximately 5 Mya (Morley 2000, Woodruff 2010).

The interplay between the movement of tectonic plates, oscillations in the Earth's orbit, and the variable amount of land and sea in the IAA due to sea level change led to consistent and periodic climate change during the Quaternary (Dam et al. 2001b), which had approximately 50 separate glacial cycles (Woodruff 2010). The repeated flooding and draining of the huge Sunda plain constantly altered the extent of dry land, thus changing the timing and moisture content of the monsoons (Hope 2007). The climate during most of the Quaternary was characterized by long glacial phases (with the Sunda plains exposed and a cool and dry climate), interspersed with short warm humid interglacial periods, such as the present day (Morley 2000, van der Kaars & Dam 1995).

The last glacial maximum approximately 18 Kya was among the most severe of these cycles (Morley 2000), with temperatures 6–9°C lower in the uplands, leading to expanding glaciers and lower tree lines in the New Guinea highlands and other high-elevation areas (Hope 2007). In contrast, the lowlands may have been only 1–2°C cooler (Pickett et al. 2004). Specific geographic features, such as higher-altitude islands (Meijaard 2003), would have affected local climates in some areas. By approximately 6 Kya, temperatures had warmed again, and the climate and geography across the region was broadly similar to the present day (Pickett et al. 2004), although dissimilar to most of the preceding two million years (Woodruff 2010).

Sundaland Habitat Reconstructions

It is uncertain whether vegetation covering the exposed Sunda Shelf during the last glacial maximum was dominated by savannah or by evergreen forest. Fossil distributions and paleoclimatic

reconstructions suggest that an area of low rainfall extended from the Thai-Malay Peninsula to eastern Java and was covered with seasonal forest or savannah (Heaney 1991). For rainforest taxa, these habitats would have been a significant barrier to dispersal between the west (Sumatra and the Thai-Malay Peninsula) and the east (Borneo), but would have enabled species adapted to open vegetation, such as *Homo erectus* ("Java Man"), to disperse easily to Java from mainland Asia (Bird et al. 2005, Morley 2000). Pollen records, subfossil evidence, and genetic data from vertebrates support this savannah corridor hypothesis (**Figure 3**) (Bird et al. 2005, Gorog et al. 2004, Lim et al. 2011). In contrast, distributional and molecular phylogeographic data of some rainforest-associated taxa suggest that evergreen rainforests were continuously distributed across the Sunda Shelf (Bird et al. 2005, Cannon & Manos 2003). Recently, a spatially explicit vegetation model of the Sunda Shelf incorporating geologic, geographic, and paleoclimatic evidence projected a corridor of seasonal forest separating Sumatra from Borneo. In some projections, however, an east-west band of evergreen forest connecting Sumatra and Borneo bisected this north-south corridor. The presence of this connecting corridor of evergreen forest depended on parameterization of the model (Cannon et al. 2009). Further phylogeographic work in this region will require the analysis of rapidly evolving markers and dense sampling of rainforest-dependent taxa throughout Borneo, Java, Sumatra, and the Thai-Malay Peninsula to determine whether a savannah corridor was a pervasive barrier to dispersal across the Sunda Shelf during the Pleistocene.

SYSTEMATIC AND PHYLOGEOGRAPHIC PATTERNS IN THE INDO-AUSTRALIAN ARCHIPELAGO

Wallace's (1859) earliest writings from Southeast Asia stress similarities between Java and Borneo and differences between Borneo and Sulawesi. Similarly, he drew attention to islands on either side of the Lombok Strait, where faunal limits are "most intimately connected." Wallace (1860) documented birds of five Sundaic genera on Bali but found none on Lombok, and located three avian genera on Lombok that were common in Sulawesi and Maluku but absent from Bali. While stressing that faunas on either side of the divide were dramatically different, he did note that the boundary was porous. Squirrels, for example, are common on the west, but a few species made it to the east (Wallace 1860). These exceptions to the rule were attributed to rare migrants between areas recently brought into proximity after higher taxa had evolved and diversified in relative isolation (Wallace 1859, 1860). These astute observations summarize the most salient taxonomic patterns in the region; a number of additional patterns have been documented subsequently.

The practices of taxonomy and systematics in the IAA have changed substantially in the years since Wallace. Improved infrastructure has made exploration of natural areas easier, which has aided the discovery of new habitats, and new collecting methods further aid biodiversity exploration (e.g., Mendoza et al. 2010). Molecular data gathered in the late twentieth century offer a number of refinements over morphology-based methods in biogeography because (*a*) DNA sequence data generally offers a larger number of characters that help determine relationships among taxa, (*b*) confidence in the strength of relationships can be assessed, (*c*) relationships among morphologically static taxa can be ascertained, (*d*) divergence times can be estimated, and (*e*) relative probabilities of different evolutionary hypotheses can be gauged (Avise 2000, Knowles 2009). These properties allow the evolutionary histories of co-distributed taxa to be compared spatially and temporally to assess general patterns, and they permit phylogenetic histories to be mapped on geological reconstructions, allowing calibration of divergence times with DNA sequence data.

Phylogenetic and phylogeographic research in the IAA, much like conservation biology studies in the region (Sodhi & Liow 2000), has lagged behind other parts of the world. The wealth of
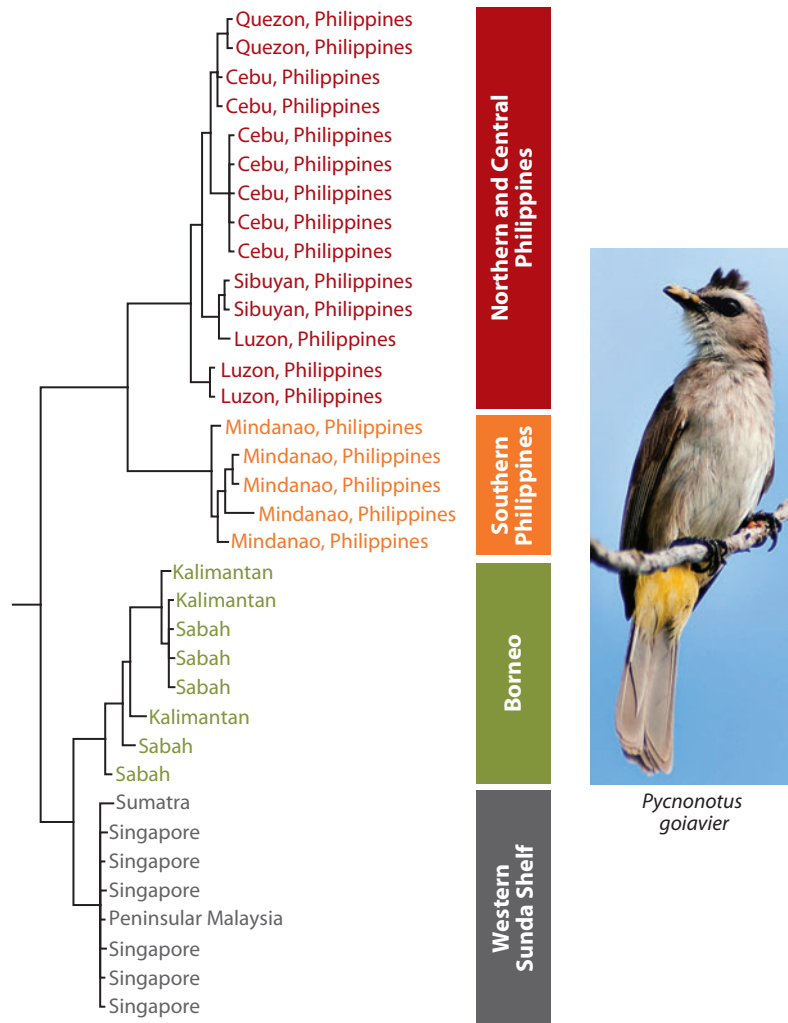
Figure 3

Phylogeographic history of the Yellow-vented Bulbul, *Pycnonotus goiavier*, demonstrating some common patterns observed in animals distributed across the Indo-Australian Archipelago (IAA). Reciprocal monophyly of Bornean and western Sunda Shelf populations suggests lack of gene flow between these areas despite terrestrial connectivity during the Pleistocene, consistent with the hypothesis of an ecologically impassable savannah corridor between the two regions. Similarly, monophyly of Mindanao relative to other Philippine populations implicates a role for this Pleistocene Aggregate Island Complex in Philippine biogeography. The Bayesian tree is based on approximately 1,875 bp of mitochondrial sequence data; posterior probabilities at every node between different regions are 1. Tree adapted from Lohman et al. (2010); photo copyright © Lim Kian Peng and used with permission.

geologic, paleoclimatic, and bathymetric data available for the IAA enables the interpretation of distributions and phylogeny in light of these extrinsic factors. Here, we highlight several recurrent themes in IAA biogeography illustrating patterns of dispersal and diversification illuminated by molecular phylogenetic and phylogeographic evidence. We summarize salient cross-taxon patterns emerging from these data.

Sea Level Minima During the Pleistocene Facilitated Dispersal Among the Asian Mainland and Islands of the Sunda Shelf

This pattern is common (Fuchs et al. 2008, Luo et al. 2004, Su et al. 2007, Vidya et al. 2009), but not universal (Esselstyn & Brown 2009, Gorog et al. 2004). Earlier Neogene diversification has been reported in a variety of plant and animal taxa, suggesting a possible vicariant history caused by isolation during the Pliocene (Gorog et al. 2004, Molengraaff & Weber 1921). Studies on fruit bats and rodents have identified a strong correlation between genetic distance among populations and sea-crossing distance at times of low sea level among paleo-island aggregates in parts of the Philippines and Lesser Sunda Islands (Hisheh et al. 1998, Schmitt et al. 1995).

Genetic Differentiation on the Asian Mainland Appears To Be Rare in Terrestrial Invertebrates but More Common in Vertebrates

Widespread terrestrial arthropods that are genetically differentiated in the IAA show little intraspecific genetic variation across mainland Southeast Asia north of the Isthmus of Kra (Azuma et al. 2006, Lohman et al. 2008, Su et al. 2007). In contrast, many studies on vertebrates have found genetically distinct lineages and/or cryptic species in this area, including palm civets (Patou et al. 2010), tigers (Luo et al. 2004), and birds (Fuchs et al. 2008). Differences in rates of cryptic species discovery may reflect differing research traditions between taxonomists of vertebrates and invertebrates.

The Thai-Malay Peninsula Is a Biogeographic Crossroads

The Thai-Malay Peninsula is an important transition zone between the Indo-Burmese and Sundaic faunal regions. Half of all Thai forest bird species have their distributional limits on the Thai-Malay Peninsula, and most of these limits occur around the Isthmus of Kra, the narrowest (<60 km) portion of the peninsula. In contrast, more than 500 plant genera reach their northern or southern limit at the Kangar-Pattani Line (van Steenis 1950), which occurs three latitudinal degrees to the south at the Thai-Malay border and marks the latitudinal transition from seasonal to evergreen forest (Woodruff & Turner 2009). Although ecological traits may limit the latitudinal distribution of rainforest trees (Baltzer et al. 2007), historical demographic factors have been implicated in shaping mammal distributions. Repeated Plio-Pleistocene sea-level changes drastically altered the land area of the peninsula. During sea level minima, the peninsula widened, but the peninsula became an archipelago when the sea rose higher than its present level. These changes are believed to have shrunk population ranges and sizes, thereby increasing extinction risk, particularly at narrow points of the peninsula where low species diversity is observed today (Woodruff & Turner 2009). Geographic disjunctions on the Thai-Malay Peninsula also seem to be responsible for cladogenesis in the *bernardus* clade of *Charaxes* butterflies (Müller et al. 2010) and cryptic genetic differentiation in the tiger subspecies *Panthera tigris corbetti* (Luo et al. 2004), a freshwater prawn (de Bruyn et al. 2005), and many other taxa.

Dispersal of Lineages Into, Out Of, and Among the Philippine Islands Has Been Common

Lowered Pleistocene sea levels are thought to have connected groups of Philippine islands known as Pleistocene Aggregate Island Complexes (PAICs) (Brown & Diesmos 2002). Genetic evidence suggests low dispersal among PAICs in mammals, including bats (Esselstyn & Brown 2009,

Heaney et al. 2005). The Philippines have apparently been colonized via almost every possible route, including Sulawesi, Borneo, the Asian mainland, Taiwan, and Palawan. Most Philippine avian taxa have their most recent ancestors in Borneo (Jones & Kennedy 2008, Lohman et al. 2010, Sheldon et al. 2009), and colonization of the Philippines via Palawan by birds appears to have been uncommon (Oliveros & Moyle 2010). Mammals and birds have colonized from the north via Taiwan (Esselstyn & Oliveros 2010, Oliveros & Moyle 2010), but nonvolant taxa such as freshwater crabs apparently have not (Shih et al. 2009). Once colonized, the Philippines were conducive to in situ diversification (**Figure 3**) (Esselstyn & Brown 2009, Jones & Kennedy 2008, Lohman et al. 2010).

Rivers That Flowed Through Sundaland Affected Ancient Patterns of Dispersal in Freshwater and Other Organisms

Changing patterns of river flow had substantial effects on the extents of estuarine, mangrove, and peat swamp habitats. Dodson and colleagues (1995) found strong support for the hypothesis that Sundaland paleodrainage rearrangements and exposure of the Sunda Shelf, resulting from Pleistocene climate change, affected catfish (*Hemibagrus nemurus*) population connectivity predicted by the inferred paleodrainage basins of Molengraaff & Weber (1921), as updated by Voris (2000) and others. Fish sampled from within the Riau Pocket floristic province (Corner 1960), including the Kapuas River (western Borneo), Johor River (southern peninsular Malaysia), and Palembang (Sumatra), shared identical haplotypes, but were dissimilar to populations sampled from nearby rivers on the same landmasses. Paleodrainage connectivity between Australia and New Guinea during Pleistocene sea level minima permitted connectivity across paleo-Lake Carpentaria on the Sahul Shelf (de Bruyn & Mather 2007, de Bruyn et al. 2004). Pleistocene sea level changes also facilitated faunal interchange in terrestrial invertebrates from this region (Azuma et al. 2006, Lohman et al. 2008).

Wallace's Line and Lydekker's Line Are Permeable Faunal Boundaries

Despite the general trend, many taxon disjunctions do not follow Wallace's Line. Examples are supertramp groups such as the beetle genus *Rhantus* (Balke et al. 2009) and the avian family Campephagidae (Jønsson et al. 2008), both of which have crossed Wallace's Line multiple times. In many groups of animals, single dispersal events across Wallace's Line (or its modification, Huxley's Line) and Lydekker's Line have been documented (see below). In contrast, distributional discontinuities have been found in groups, such as plants and marine organisms, that are regarded as widespread throughout the IAA, prompting discussion of a marine Wallace's Line and a floral Huxley's Line (Atkins et al. 2001, Barber et al. 2000).

Colonization of Wallacea Can Give Rise to Radiation

The fauna of Wallacea is depauperate compared with continental faunas (Mayr 1944). However, continental faunas are generally better studied, and the species diversity of oceanic islands has often been underestimated, for example, in Philippine birds (Lohman et al. 2010, Oliveros & Moyle 2010). Many of these faunas, especially from Sulawesi and the Philippines, show a high degree of species-level endemism [more than 90% in Sulawesi nonvolant mammals (Groves 2001)] and even higher levels in organisms with low dispersal abilities (e.g., Butlin et al. 1998). This high level of endemism from adaptive radiation following colonization by a small number of migrant species (Esselstyn & Oliveros 2010) is characteristic of oceanic island biota.

Sulawesi and Borneo Are Cradles of Diversity

Both islands are the sites of extensive in situ speciation. Sulawesi harbors a unique and highly endemic melting-pot biota with Asian and Australasian lineages—a product of the ongoing collision of two ancient continents and several different terranes. Within two ancient lake systems on the island, several aquatic groups of animals underwent adaptive radiations, resulting in endemic species flocks of vertebrates (fishes) and invertebrates (mollusks, crustaceans) and forming Wallacean freshwater biodiversity hotspots (Chia & Ng 2006, von Rintelen et al. 2011). In Sulawesi, terrestrial radiations have occurred in shrews (Esselstyn et al. 2009), tarsiers (Merker et al. 2009), grasshoppers (Butlin et al. 1998), and other taxa.

Preliminary evidence suggests that barriers associated with tectonic boundaries along the fragments that constitute Sulawesi helped drive diversification (Merker et al. 2009). Estimated divergence times between species within many Sulawesi radiations seem to have occurred approximately 15 Mya (Esselstyn et al. 2009), shortly after several of the terranes that comprise the island began to conjoin (Hall 2011).

Mountain ranges of peninsular Malaysia, Sumatra, and northwestern Borneo may have served as rainforest refugia. Surrounding lowlands were considerably drier in the Plio-Pleistocene, and montane areas consequently host genetically diverse populations of many organisms (Cannon & Manos 2003, Lim et al. 2011, Moyle et al. 2005, Quek et al. 2007). Tropical montane refugia are thought to have preserved old lineages and spurred the genesis of new taxa with restricted ranges (Fjeldså & Lovett 1997), and the examples cited above provide novel Southeast Asian examples of this global pattern.

Land Bridges That Were Exposed During Periods of Low Sea Level Caused Vicariance in Marine Taxa

The IAA, encompassing the Coral Triangle, is the planet's biologically richest marine region (Crandall et al. 2008, DeBoer et al. 2008, Mendoza et al. 2010). Studies on marine organisms frequently identify deep and fine-scale population genetic structuring that do not reflect the contiguous marine environment (Crandall et al. 2008, DeBoer et al. 2008). Vicariant isolation due to historically low sea levels is thought to have caused divergence among taxa, particularly between Indian and Pacific Ocean populations (Barber et al. 2000, Benzie 1998, Crandall et al. 2008, DeBoer et al. 2008). Similar patterns of highly divergent populations from northern Papua have been identified in several invertebrate taxa (e.g., DeBoer et al. 2008), possibly reflecting the role of the Halmahera Eddy in limiting water exchange, and thus gene flow, across the Maluku Sea. Many taxa display molecular signatures consistent with range expansions onto continental shelves as sea levels rose during the Pleistocene (Crandall et al. 2008). Wallace's Line is apparently also a dispersal barrier for some marine taxa (Lourie & Vincent 2004) and for some freshwater organisms with marine larvae (Wowor & Ng 2008).

THE RELATIVE IMPORTANCE OF DISPERSAL AND VICARIANCE IN THE INDO-AUSTRALIAN ARCHIPELAGO REASSESSED: SULAWESI AND BEYOND

"[Sulawesi's] fauna presents the most puzzling relations, showing affinities to Java, to the Philippines, to the Moluccas, to New Guinea, to continental India, and even to Africa; so that it is almost impossible to decide whether to place it in the Oriental or the Australian region" (Wallace 1876, p. 389).

Much of the dispersal/vicariance debate in the IAA has centered on the origin of taxa on Sulawesi. Molecular data have revealed that Sulawesi taxa are frequently basal groups clustering

either with Asian (e.g., Randi et al. 1996) or occasionally Australian taxa (e.g., Sparks & Smith 2004). The early diverging position of these taxa has been interpreted as evidence for these taxa being paleo-endemics on Sulawesi, with a vicariant origin either through the opening of the Makassar Strait or by tectonic dispersal on mobile terranes from the Australian margin (Michaux 2010). This interpretation, however, ignores the temporal dimension. Most studies involving Sulawesi taxa with an origin in Asia clearly suggest dispersal (e.g., Evans et al. 2003, Larson et al. 2005), and where diversification dates have been estimated, these range from the Miocene to the Plio-Pleistocene (Esselstyn et al. 2009, Merker et al. 2009, Müller et al. 2010). Few studies dating the divergence time of Sulawesi taxa claim an origin of these by vicariance from the west, which is temporally constrained by the opening of Makassar Strait approximately 45 Mya in the Eocene (Hall 2009). Only a handful of investigations infer that Sulawesi taxa diversified after the opening of Makassar Strait, with estimates ranging from 29–32 to 7–14 Mya (e.g., Takehana et al. 2005). Only some groups of mite harvestmen (Clouse & Giribet 2010) seem to have diverged early enough to meet the geological constraints and currently represent the most plausible case for a vicariant origin of Sulawesi taxa from Asia.

There is less evidence for a tectonic dispersal scenario of taxa rafting on Sulawesi's constituent terranes from elsewhere. Considerable uncertainty exists in assigning dates to the separation of continental fragments from Australia/New Guinea (Oligo-Miocene) and their collision with western Sulawesi (Mio-Pliocene) to form present-day Sulawesi, and it is unclear whether they were emergent (Hall 2009, 2011). A few studies have found Sulawesi taxa derived from or in a sister group relationship with Australian relatives (e.g., Sparks & Smith 2004), but vicariance has only been explicitly suggested for pachychilid snails on grounds of being biologically more plausible than dispersal (von Rintelen & Glaubrecht 2005).

Vicariance hypotheses have been less controversial in other areas of the IAA. At the Isthmus of Kra, the few studies that have explicitly estimated divergence time support a vicariant scenario (de Bruyn et al. 2005, Patou et al. 2010). Pre-Pleistocene vicariance of Sundaland taxa has been suggested repeatedly and usually against the prior expectation of younger Pleistocene patterns (Clouse & Giribet 2010, Gorog et al. 2004, Shih et al. 2009). Vicariant speciation is seldom regarded as an exclusive mechanism. The studies cited above also infer that dispersal is an important process at the species and/or population level. However, this summary may be biased toward an animal perspective. Muellner et al. (2008), for example, dismissed vicariance as playing a significant role in the present IAA distribution of the plant family Meliaceae.

BIOGEOGRAPHY AND CONSERVATION IN SOUTHEAST ASIA

Unfortunately, the naturally fragmented island habitats of the IAA make them particularly vulnerable to disturbance. Islands generally support smaller populations that are more prone to inbreeding and more easily affected by natural disasters, habitat loss, and predation by introduced predators. For example, less than one-fifth of the world's birds are island endemics, but these constitute 90% of avian extinctions (Johnson & Stattersfield 1990). Moreover, terrestrial habitats on the Sunda Shelf are currently in a vulnerable, refugial state after land area decreased by 50% after the Pleistocene (Cannon et al. 2009). Unfortunately, this insular biota is undergoing unprecedented human threat while simultaneously experiencing a natural, geography-induced population bottleneck. As a result, Southeast Asia has the highest tropical deforestation rates and highest proportions of threatened plant, mammal, reptile, and bird species of any tropical area (Koh & Sodhi 2010).

Anthropogenic pressures on natural habitats are particularly intense in Southeast Asia (Sodhi & Brook 2006). Proximity to countries that import significant amounts of tropical timber and animal products for consumption and traditional medicine creates a powerful economic incentive

to despoil and pillage natural habitats. Koh & Sodhi (2010) highlight conservation research priorities and changes in governance and forest management that can help curb biodiversity loss in the region.

Biogeographic studies can assist conservation efforts by using genetic data to identify morphologically cryptic species and geographic areas harboring unusually high or unique genetic diversity. Species thought to be widespread are frequently given low conservation priority, but cryptic species-level diversity is frequently detected when DNA sequence data are used in biodiversity research (Bickford et al. 2007). Cryptic species have even been split from large and supposedly well-studied mammals, including Asian elephants and clouded leopards (Buckley-Beason et al. 2006, Fernando et al. 2003). Within the IAA, several studies have identified cryptic avian species in the Philippines (Lohman et al. 2010, Oliveros & Moyle 2010), but studies that include taxa from multiple regions are few, in part because the logistics of sampling in more than one country are challenging and costly. It remains unknown whether the tropics harbor more cryptic species than temperate zones and whether some taxa are particularly prone to cryptic speciation (Bickford et al. 2007). An early attempt to examine these questions analyzed patterns in the number of published papers rather than patterns in the actual number of cryptic species described by those papers (Pfenninger & Schwenk 2007).

Molecular genetic approaches can also identify areas that harbor species with uniquely high genetic diversity or distinctiveness. Nascent model-based approaches can be used to infer historical demographic and distributional changes in response to past climates (Lim et al. 2011). This information can, in turn, be used to predict distributional changes in response to current climate change. These novel statistical phylogeographic methods will provide a powerful toolkit for addressing the considerable challenges facing biogeographers working in the IAA.

METHODOLOGICAL ADVANCES WILL REFINE FUTURE INVESTIGATIONS

Attempts to reconstruct the biogeographic history of taxa distributed throughout the IAA face unique problems. Terranes have fragmented (e.g., Borneo and West Sulawesi), conjoined (e.g., Sulawesi and New Guinea), and moved along idiosyncratic trajectories (e.g., Palawan) at different points in geological time. Area relationships are therefore poorly represented as a branching tree and better depicted as a coalescent network (Webb & Ree 2011). Comparing biogeographic patterns among taxa using a method that reconciles bifurcating trees is likely to misrepresent the actual history of the areas involved (Holloway 1998). Moreover, landmasses in the IAA have changed in size and proximity over time, which likely affected demographic parameters such as population sizes and extinction/dispersal probabilities.

Popular methods for reconstructing ancestral ranges (e.g., Ronquist 1997) make some assumptions that are not upheld in the IAA. Many taxa in the IAA inhabit more than one terrane, which creates polymorphism when geographic areas are treated as characters in an ancestral area analysis; most reconstruction methods cannot accept polymorphic characters (Webb & Ree 2011). Additionally, dispersal and extinction are expected to be the dominant forces influencing insular distributions (Cowie & Holland 2006), but dispersal-vicariance analysis and other methods that assume vicariance assign a higher cost to dispersal than to vicariance and are therefore likely to misinterpret data (Sanmartín et al. 2008). Many biogeographic analysis methods do not incorporate tree topological uncertainty into the analysis and fail to account for stochastic variability inherent in the coalescent process (Sanmartín et al. 2008). When making comparisons across multiple trees, failure to distinguish coalescent variability from actual differences in divergence times can mislead (Hickerson et al. 2007).

Coalescence: a retrospective method to infer the history of alleles back to their most recent common ancestor

A suite of new model-based methods helps circumvent many of these shortcomings. Novel methods for reconstructing range evolution and ancestral areas allow models to incorporate biologically relevant parameters, including different island sizes/carrying capacities that can change through time, and different dispersal, cladogenesis, and extinction rates among islands (Ree & Smith 2008, Sanmartín et al. 2008, Webb & Ree 2011). Ecological niche modeling, paleoclimatic inference, or geological reconstructions can be used to generate two or more biogeographic hypotheses for the distribution of suitable habitats or island terranes at some point in the past. Alternative models of historical population structure or phylogenetic history are then generated from these biogeographic hypotheses. These models are then challenged with simulated and real data in Bayesian (Sanmartín et al. 2008) or Maximum Likelihood (Ree & Smith 2008, Webb & Ree 2011) frameworks. In addition, Approximate Bayesian Computation can be employed to evaluate cross-taxon models of simultaneous divergence that take into account stochastic differences in coalescent times among taxa (Hickerson et al. 2007).

SUMMARY POINTS

1. The IAA is the most geologically dynamic geographic region in the tropics, and the 20,000+ islands that comprise the area have moved considerably over tens of millions of years.

2. Over timescales of thousands of years, repeated sea level changes have exposed the sea floor among adjacent islands, causing groups of islands on the Sunda Shelf and in Philippine Pleistocene Aggregate Island Complexes to fuse and then separate. Past climates were probably different from those of the present day, and habitats that joined different landmasses may have been savannah-like and not forested.

3. Biotas on either side of Wallace's Line were brought into close proximity relatively recently (approximately 5 Mya; **Figure 2**), but the demarcation is not absolute, as taxa have dispersed across the line with varying frequencies.

4. Sulawesi was formed after the collision of landmasses that originated in different locales, and radiation of its highly endemic biota seems to have been spurred by barriers associated with its constituent terranes.

5. Natural habitats in the IAA are among the most threatened in the world, and intensive conservation efforts are essential to the continued existence of this region's biotic novelty and wealth.

6. Recent advances in statistical phylogeography will help overcome analytical difficulties of biogeographic inference in the IAA, but increased geographical sampling effort of more taxa is essential for continued progress.

FUTURE ISSUES

1. Despite advances made in Cenozoic reconstructions of Sunda Shelf geology, similarly detailed information for New Guinea and the Philippines is lacking. Dated geological reconstructions of these unique, multiterrane areas would stimulate further phylogenetic and phylogeographic work.

2. Increased sampling of geographic areas (islands) and taxa (particularly plants) is needed to answer basic biogeographic questions in IAA biogeography (Webb & Ree 2011). For example, why does Wallace's Line delimit animal distributions better than plant distributions?

3. Habitat destruction in the IAA is proceeding at twice the pace of other tropical areas, fuelled in large part by a rapidly expanding human population (Sodhi & Brook 2006, Woodruff 2010). At current rates of habitat loss, some projections estimate extinction of up to 85% of the region's species by 2100 (Sodhi et al. 2010). Curbing human population growth, protecting pristine habitats, and restoring degraded areas are all necessary to preserve the region's biological integrity.

4. Statistical phylogeographic approaches that incorporate coalescent stochasticity and a hypothesis-testing framework (Knowles 2009) will greatly advance future biogeographic studies.

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Uses bathymetry data to reconstruct maps of IAA topography and freshwater drainage during periods of lower sea level.

Succinct and eloquent explanation of the anomalous faunal patterns observed by Wallace.

Introduces analytical methods to overcome key problems of biogeographic reconstruction peculiar to the IAA.

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