The University of Chicago

Taxonomic, Phylogenetic, and Trait Beta Diversity in South American Hummingbirds

Ben G. Weinstein,[1,*] Boris Tinoco,[1] Juan Luis Parra,[2] Leone M. Brown,[3] Jimmy A. McGuire,[4] F. Gary Stiles,[5] and Catherine H. Graham[1]

1. Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York 11794;   2. Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia, Medellín, Colombia;   3. Department of Biology, Tufts University, Medford, Massachusetts 02155;   4. Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, California 94720;   5. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia

ABSTRACT: Comparison of the taxonomic, phylogenetic, and trait dimensions of beta diversity may uncover the mechanisms that generate and maintain biodiversity, such as geographic isolation, environmental filtering, and convergent adaptation. We developed an approach to predict the relationship between environmental and geographic distance and the dimensions of beta diversity. We tested these predictions using hummingbird assemblages in the northern Andes. We expected taxonomic beta diversity to result from recent geographic barriers limiting dispersal, and we found that cost distance, which includes barriers, was a better predictor than Euclidean distance. We expected phylogenetic beta diversity to result from historical connectivity and found that differences in elevation were the best predictors of phylogenetic beta diversity. We expected high trait beta diversity to result from local adaptation to differing environments and found that differences in elevation were correlated with trait beta diversity. When combining beta diversity dimensions, we observe that high beta diversity in all dimensions results from adaption to different environments between isolated assemblages. Comparisons with high taxonomic, low phylogenetic, and low trait beta diversity occurred among lowland assemblages separated by the Andes, suggesting that geographic barriers have recently isolated lineages in similar environments. We provide insight into mechanisms governing hummingbird biodiversity patterns and provide a framework that is broadly applicable to other taxonomic groups.

Keywords: clade turnover, gradients, isolation, environment, elevation.

Introduction

Beta diversity, the change in species identities across sampled locations (sensu Anderson et al. 2011), has been used to identify the spatial, temporal, and environmental patterns that result from different ecological, evolutionary,

* Corresponding author; e-mail: bweinste@life.bio.sunysb.edu.

and biogeographic processes. Historically, beta diversity research has focused on taxonomic beta diversity (species composition turnover; Whittaker 1960; Condit et al. 2002), but taxonomic beta diversity does not account for shared evolutionary history or similarity in functional morphology among species (Faith 1992; Graham and Fine 2008). Recent efforts to identify and interpret differences among spatial patterns of these three beta diversity dimensions (taxonomic, trait, and phylogenetic) have yielded new insights into the origin and maintenance of biodiversity (Bryant et al. 2008; Graham and Fine 2008; Devictor et al. 2010; Fine and Kembel 2011; Morlon et al. 2011; Swenson 2011*a*; Huang et al. 2012; Lansing et al. 2012). However, a general a priori approach as to why and when beta diversity dimensions differ has yet to emerge. The lack of a predictive approach represents a gap in our knowledge and impedes connections between idiosyncratic studies in different systems. We propose an approach to evaluate geographic and environmental mechanisms influencing regional patterns of taxonomic, phylogenetic, and trait beta diversity. We test hypotheses for mechanisms generating the causes of occurrence of each combination of beta diversity dimensions using the ecologically diverse Neotropical hummingbird clades.

There are eight possible combinations of high versus low taxonomic, phylogenetic, and trait beta diversity between assemblages (fig. 1) Due to phylogenetic constraints on niche and trait evolution, we anticipate that, in most cases, taxonomic, phylogenetic and trait dimensions of beta diversity across a region will be similar (e.g., all low or all high; Cadotte et al. 2009; Safi et al. 2011; Swenson 2011*b*; Fritz and Rahbek 2012). However, beta diversity dimensions may be decoupled, where decoupling is identified by greater differences in one dimension than expected by chance based on differences in other dimensions. We expect greater differences in taxonomic beta diversity
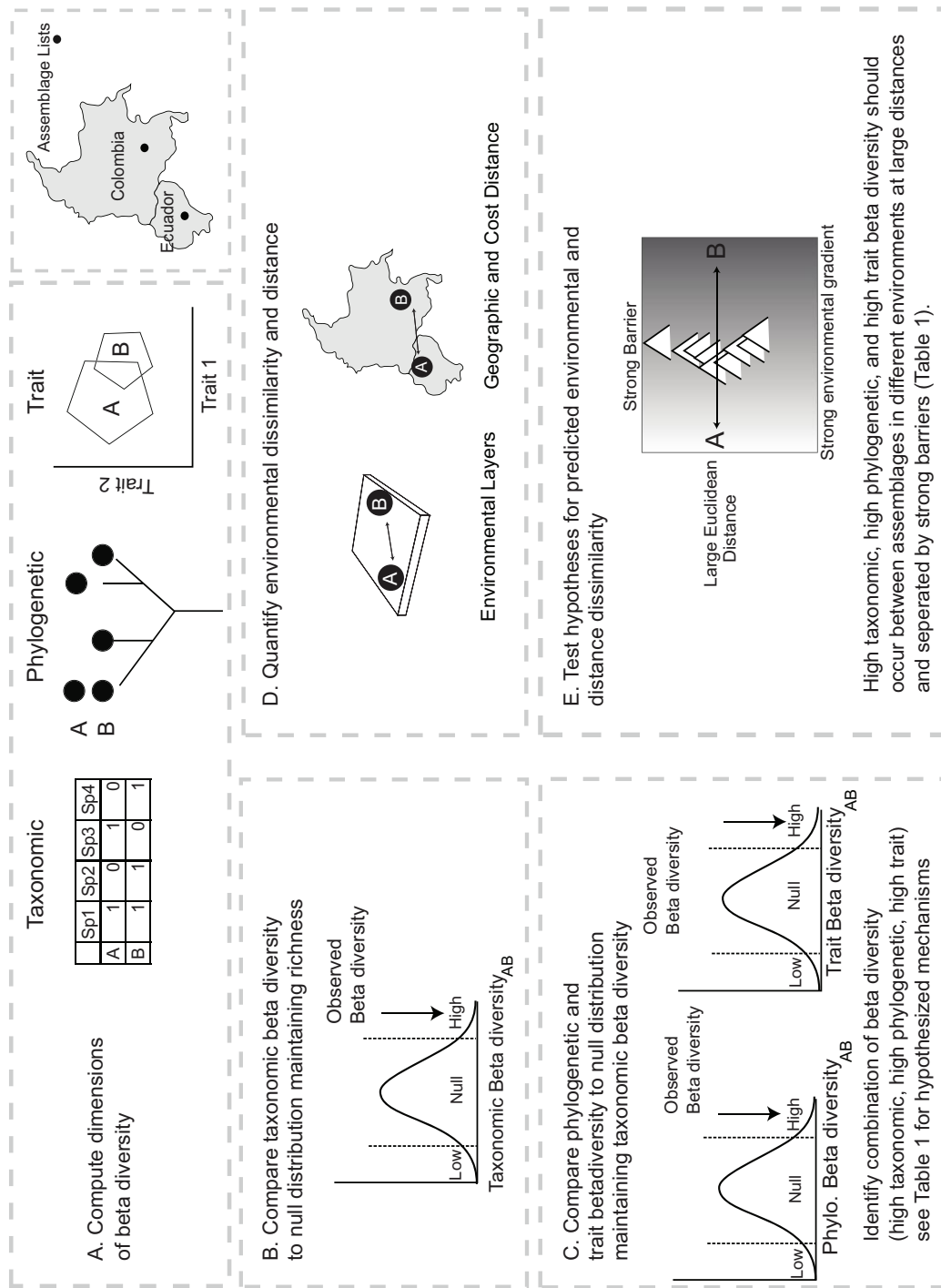
Figure 1: Conceptual figure outlining the five major steps of the analytical approach. First, we calculate taxonomic, phylogenetic, and trait dissimilarity between all pairwise combinations of assemblages (*A*). Second, we compared observed taxonomic beta diversity to a null model controlling for richness (*B*). Third, we compared the observed phylogenetic and trait beta diversity to a null model that maintains both richness and taxonomic beta diversity (*C*). Based on these null models, we delineated different combinations of beta diversity (e.g., high taxonomic, high phylogenetic, high trait). Fourth, we quantified the environmental dissimilarity and geographic distance between assemblages (*D*). Finally, we used these results to test hypotheses of predicted mechanisms for each combination of beta diversity (*E*).

than expected by chance if recent geographic barriers are limiting dispersal (Condit et al. 2002; Fine and Kembel 2011; Kraft et al. 2011; Myers et al. 2013), whereas we expect decoupling associated with phylogenetic beta diversity to be most influenced by historical factors such as historical connectivity or environmental stability (Bryant et al. 2008; Morlon et al. 2011; Jetz and Fine 2012), and decoupling associated with trait beta diversity resulting from local adaptation (Cornwell et al. 2006; Kraft et al. 2007; Rosenblum et al. 2010; Lansing et al. 2012). Specifically, given two assemblages that occur in similar environments, we hypothesize that (1) adaptation to similar environments with no dispersal limitation will lead to low taxonomic, low phylogenetic, and low trait beta diversity; and (2) recent speciation due to geographic isolation, but with historical connectivity, will lead to assemblages with high taxonomic, low phylogenetic, and low trait beta diversity because sister (or closely related) taxa will replace each other on either side of recent geographic barriers (Graham et al. 2009). If assemblages in similar environments are currently and historically isolated, there may be long branch lengths among species in these assemblages, leading to (3) high taxonomic and high phylogenetic beta diversity but low trait beta diversity due to similar ecological roles of species in a given environment and convergent adaptation (i.e., traits are labile and driven by adaptation to environmental factors). Finally, convergent adaptation between recently connected, but historically isolated assemblages should result in (4) low taxonomic, high phylogenetic, and low trait beta diversity.

In contrast to similar environments, assemblages in differing environments should have higher-than-expected trait beta diversity resulting from local adaptation to differing selection pressures. We expect that trait beta diversity will change independent of phylogenetic similarity when there is a strong environmental filter or recent adaptive radiation (Losos 2008). Therefore, we hypothesized that (5) current geographic and potential historical barriers will result in a pattern of high phylogenetic, high taxonomic, and high trait beta diversity, and (6) beta diversity among assemblages that were recently connected but historically isolated and in different environments should have low taxonomic beta diversity, high phylogenetic beta diversity, and high trait beta diversity. These assemblages should occur along environmental gradients in the absence of large current geographic barriers. Finally, (7) low taxonomic, low phylogenetic, but high trait beta diversity should occur between assemblages with no dispersal limitation and high trait lability; and (8) high taxonomic, low phylogenetic, and high trait beta diversity should result from recent geographic isolation of historically connected assemblages coupled with labile traits responding to environmental change. While our framework outlines all possible combinations of beta diversity dimensions, we do not necessarily expect all combinations to be important, or possible, in our system. The rate of diversification, the pattern of trait evolution, and the geographic configuration of barriers will vary between systems, and thereby effect which combinations of beta diversity dimensions are most prominent.

Hummingbirds of the northern Andes are an ideal group to evaluate these hypotheses. There are nine clades in the region, each with a distinct biogeographic history, distribution, and set of traits (Stiles 2008; Parra et al. 2011; Graham et al. 2012). The basal clades of hermits, mangoes, and emeralds are predominately lowland and largely diversified within Amazonia (Bleiweiss 1998; McGuire et al. 2007). The origin and diversification of the coquettes and brilliants coincided with the uplift of the Andes. The mountain gem and bee clades diversified in Central and North America, and representatives of these clades have moved into the Andes and associated lowlands. The combination of diversification within environments and colonization from outside the region create different patterns of taxonomic, phylogenetic, and trait beta diversity among assemblages. Previous work has shown that taxonomic beta diversity in the northern Andes and associated lowlands is generally greater than phylogenetic beta diversity on either side of the Andes, given a null model of taxonomic turnover, highlighting the potential role of isolation in generating patterns of beta diversity across different dimensions (Graham et al. 2009). Here we compare the three dimensions of beta diversity (taxonomic, trait, and phylogenetic) at a broad geographic scale and evaluate our predictive framework with hummingbirds. We expect our approach can be employed across an array of taxonomic groups and geographic and environmental contexts.

Methods

Overview of Approach

Our approach for exploring the dimensions of beta diversity consists of five steps. First, we used commonly employed beta diversity metrics to calculate taxonomic, phylogenetic, and trait dissimilarity between all pairwise combinations of assemblages (fig. 1*A*). We then delineate high and low beta diversity in this system by taking the 30% highest and lowest quantiles. To test whether these assemblage comparisons were different from random, we compared observed taxonomic beta diversity to a null model controlling for richness (fig. 1*B*). Third, we compared the observed phylogenetic and trait beta diversity to a null model which maintains both richness and taxonomic beta diversity (fig. 1*C*). Based on these null models, we delineated different combinations of beta diversity

Table 1: Patterns of environment and distance for each dimension of beta diversity

Beta diversity dimension	High	Low
Taxonomic	Assemblages in different environments separated by large distances	Assemblages in similar environments and separated by small distances
Phylogenetic	Strong historic isolation between assemblages or weak trait labiality limiting adaptation to the new environments	Weak historical isolation or recent connectivity between assemblages or strong trait lability permitting adaptation to new environments
Trait	Assemblages in different environments	Assemblages in similar environments

(e.g., high taxonomic, high phylogenetic, high trait). Fourth, we quantified the environmental dissimilarity and geographic distance between assemblages (fig. 1D). Finally, we used these results to test hypotheses of predicted mechanisms for each combination of beta diversity (fig. 1E, table 1).

Hummingbird Data

Our taxonomy followed the current version of the South American Classification Committee (Remsen et al. 2010). Our data set included 219 hummingbird assemblages containing 126 species across Ecuador and Colombia (fig. A1; figs. A1, B1–B5 available online; McGuire et al. 2007, 2009; Graham et al. 2009; Altshuler et al. 2010; Parra et al. 2010). Lists from eco-lodges with a high density of hummingbird feeders were excluded, as the presence of these artificial resources may cause range extensions. Each species was projected on to a map and occurrence in an assemblage was corroborated by comparing localities to known distributions based on field guides. For data-poor areas, species were also compared to expert range maps and citizen science data to support data cleaning (Sullivan et al. 2009). We used a densely sampled regional phylogeny that includes each of the 126 hummingbird species evaluated in this study and has been used extensively to analyze phylogenetic community structure in this system (McGuire et al. 2007; Parra et al. 2010; Graham et al. 2012).

We compiled measurements of three traits in adult males: body mass, wing chord (i.e., closed-wing length), and length of exposed culmen (Graham et al. 2012). The three traits represent important morphological interfaces for hummingbird flight, physiology, feeding, and behavior. Body mass is related to thermoregulatory adaptations to high elevation habitats, as well as aggressive interactions among territorial species (Altshuler and Dudley 2002; González-Gómez et al. 2011a, 2011b). Wing chord is a component of hovering flight, which becomes more difficult at high elevations due to lower air density (Altshuler et al. 2004; Stiles et al. 2005). Bill length is associated with resource use, foraging efficiency, and the matching between bill lengths and corolla lengths in hummingbird pollinated plants (Feinsinger et al. 1979; Smith et al. 1996; Temeles et al. 2002). These three traits show a predicted trait environment-relationship when all species in an assemblage are considered: body mass increases with elevation, wing chord increases with elevation and bill length decreases with elevation (high-elevation flowers have short corollas; Stiles 2008). All three traits can be well described by a Brownian motion model of trait evolution, indicating phylogenetic signal (Blomberg's $K \sim 1$ for all traits; Graham et al. 2012). Within-species trait variation was lower than among-species variation, indicating that intraspecific variation should not distort our beta diversity analysis. Morphological data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.1qg13 (Weinstein 2014).

Environmental Data

Based on previous analyses of the relationship between phylogenetic structure of hummingbird assemblages and the environment (Graham et al. 2009, 2012; Parra et al. 2010, 2011), we chose three variables to describe environmental gradients: annual precipitation, elevation, and vegetation structure. Elevation and climate were extracted from the Shuttle Radar Topography Mission data (30-m resolution) and the Worldclim database (accessed September 11, 2013; Hijmans et al. 2005), respectively. Since elevation is highly correlated with temperature (Pearson's $r = 0.98$), we used elevation because of its higher spatial resolution. Vegetation structure was quantified using the annual horizontal mean of Quick scatterometer data (30-m resolution), which is a measure of surface roughness and provides inference on biomass density and forest height and spacing and has been shown to be an informative variable for modeling species distributions in the region (Buermann et al. 2008; Parra et al. 2011).

Geographic Distance

We measured geographic isolation by calculating Euclidean distance and cost distance among all localities. Euclidean distances were computed for all combinations of localities

in R (R Development Core Team 2012) using the package maptools (Bivand 2012). Cost distance represents the environmentally weighted friction of moving between two points in a landscape and has been shown to be a strong predictor of dispersal limitation and population genetic structure (McRae and Beier 2007; Wang et al. 2009). Calculating cost distances among locations requires (1) construction of environmentally weighted cost surface and (2) calculation of a least-cost path between two locations. We used elevation to build our cost surface because it is a proxy for environmental turnover, and large changes in elevation can be barriers to dispersal in hummingbirds (Chaves and Smith 2011). We built a unique cost surface for each assemblage based on the difference in elevation from a given assemblage to each of the cells in our study region. We then calculated the least-cost path between all pairwise localities using the R package gDistance (Etten 2011).

Beta Diversity Metrics

For taxonomic beta diversity, we calculated Sorenson's index for each pairwise comparison of assemblages (Whittaker 1960). For phylogenetic beta diversity, we used 1-PhyloSor, which computes the proportion of unshared branch lengths between species in each assemblage comparison (Bryant et al. 2008). Trait beta diversity was calculated by standardizing the trait matrix, performing a principal components analysis and then measuring the nearest taxon distance for each species between an assemblage (mean nearest taxon distance [MNTD]; Webb et al. 2008; Swenson et al. 2012b). We chose this approach because it is a simple representation of the trait spacing between species and is computationally tractable. Since there is a wide variety of beta diversity metrics, we compared our results to several alternate methods, including the phylogenetic community dissimilarity (PCD) metric, a recent integrative metric of taxonomic and tree-based dissimilarity (Ives and Helmus 2010). We also compared MNTD to tree-based methods (Petchey and Gaston 2007) and convex hulls for our observed 219 assemblages (Villéger et al. 2013). The results using PCD, tree-based methods, and convex hulls are qualitatively similar to those obtained using our approach (app. B; apps. A and B available online).

We performed randomization tests to test the significance of the correlations between environmental and distance dissimilarity with the beta diversity dimensions. We used the nonparametric test proposed by Ives and Helmus (2010) instead of Mantel tests, because Mantel tests can suffer from inflated Type I errors (Raufaste and Rousset 2001). We first estimated Spearman's correlation between each environmental and distance variable and the beta

diversity values. We then randomized the labels of the assemblages for the environmental or distance variables 10,000 times, each time correlating the permuted data to the actual beta diversity values. The highest correlation in each of 10,000 permutations was recorded and used as a null distribution for the highest observed correlation. To generate the null distribution for the second-highest observed correlation, we removed one variable at random for each of the 10,000 permutations and recorded the new highest correlation. We repeated this method for all 18 combinations of taxonomic, phylogenetic, and trait beta diversity values and the six distance and environmental variables. We then compared the true correlation value to the null distribution of correlation values. Significant correlations were delineated as outside the lower fifth or upper ninety-fifth quantile of the null distribution.

Evaluating Hypotheses Associated with Combinations of Diversity Dimensions

We divided the dissimilarity values into all three-way combinations of beta diversity (e.g., high taxonomic, high phylogenetic, high trait; table 1), and used these assemblage comparisons to evaluate our environment and distance measures predictions for the combinations of beta diversity dimensions. We compared observed taxonomic beta diversity to a null distribution of comparisons between randomly generated assemblages with the same richness as the observed data (fig. 1A). We then compared our observed Sorenson value with the null distribution and considered it high if it was greater than the ninety-fifth quantile and low if less than the fifth quantile (fig. 1B). Values between the fifth and ninety-fifth quantiles were considered not different from randomly sized assemblages of similar richness. A null model of phylogenetic and trait beta diversity was generated by maintaining both richness and the number of shared species in observed assemblages but randomizing species identity (fig. 1C). We compared the observed taxonomic and phylogenetic beta diversity of a comparison to 500 generated null assemblages and designated higher-than-expected beta diversity between assemblages when observed values were greater than the ninety-fifth quantile of null values and lower-than-expected beta diversity when observed values were less than the fifth quantile of the null values.

We evaluated how well environmental dissimilarity and geographic distance variables predicted each combination of beta diversity by comparing the observed median value for each predictor with the median of 1,000 random draws, where the number of comparisons in each draw was equal to the number of comparisons in each hypothesis (fig. 1D). We chose the median rather than the mean because the environmental and distance variables, especially cost

distance, have very long positive tails, and the mean is not an accurate summary of the distribution. We used the medians of the randomly sampled data to form a null distribution to compare to our observed medians. If the observed median was outside the fifth or ninety-fifth quantile of the null distribution, we considered the median value significantly different than the overall data set. Finally, we mapped the assemblage comparisons to compare patterns of spatial beta diversity within this system. We stress that this analysis focuses on the emergent patterns of the dimensions of beta diversity rather than on any individual assemblage comparisons.

Results

We analyzed the taxonomic, phylogenetic, and trait beta diversity among 219 hummingbird assemblages in northern South America. Beta diversity was correlated between the taxonomic and phylogenetic dimensions ($r = 0.89$) and taxonomic and trait dimensions ($r = 0.64$). Phylogenetic and trait beta diversity dimensions were also correlated ($r = 0.58$); however, after accounting for taxonomic beta diversity, the partial correlation between phylogenetic and trait beta diversity was 0.29 (Spearman's r, $n = 23,871$, $P < .01$). For taxonomic beta diversity, 23.8% of the randomized compared assemblages were more similar than expected given a null model of richness, and 45.9% were less similar than expected (app. A). For phylogenetic beta diversity, 3.2% of the compared assemblages were less similar than expected, and 29.1% were more similar than expected given a null model of taxonomic beta diversity. For trait beta diversity, 6.0% of the compared assemblages were less than expected, and 6.1% were more similar than expected given a null model of taxonomic beta diversity.

Using all pairwise combinations, environmental parameters were stronger predictors of beta diversity than distance metrics across all dimensions (table 2). In particular, all dimensions of beta diversity were correlated with changes in elevation, while precipitation and canopy structure explained a smaller, but significant, amount of variation in each of the three dimensions. Cost distance was a stronger predictor of taxonomic beta diversity than either Euclidean or cumulative elevation distance, the latter of which was not significant. Neither Euclidean nor cumulative elevation distance metrics strongly explained phylogenetic nor trait beta diversity (table 2). To test predicted patterns of environmental dissimilarity with combinations of the beta diversity dimensions, we chose the two best predictors for environmental (elevation, annual precipitation) and distance metrics (Euclidean, cost distance).

We found mixed support for our hypothesized relationship between environmental and distance variables

Table 2: Environmental and distance correlates of beta diversity

	Taxonomic	Phylogenetic	Trait
Elevation	.61	.70	.39
Precipitation	.32	.29	.18
Canopy structure	.11	.10	.10
Euclid	.11	.09	.10
Cost distance	.30	.25	.16

Note: Spearman's coefficients for environment dissimilarity and distance metrics for the dimensions of beta diversity. Randomization tests with 1,000 permutations showed that all correlations were significant. We chose the top two variables for environment and distance to compare to our combination of beta diversity dimensions.

and each measure of beta diversity. Our results supported the prediction that assemblages separated by large distances would have high taxonomic beta diversity (table 1). Assemblage comparisons that had high taxonomic beta diversity also had higher median Euclidean and cost distance than the median of the entire data set. Assemblage comparisons that had low taxonomic beta diversity had lower median distance than the median of the entire data set (fig. 2). In contrast, there was no consistent relationship between phylogenetic beta diversity and either measure of distance. Assemblage comparisons with high phylogenetic beta diversity also had high dissimilarity in elevation and precipitation, and assemblages with low phylogenetic beta diversity had low dissimilarity in elevation and precipitation. Assemblage comparisons with high trait beta diversity had greater dissimilarity in elevation and annual precipitation, while assemblage comparisons with low trait beta diversity were more similar in elevation and annual precipitation. Low trait beta diversity in precipitation was not different from random.

When we combined taxonomic, phylogenetic, and trait dimensions of beta diversity into the eight three-way combinations of beta diversity dimensions (i.e., high taxonomic, high phylogenetic, and high trait), 1,145 of the 23,871 (4.8%) comparisons were significantly high or low for all three beta diversity dimensions (fig. 2). These comparisons were used to address hypotheses of the combinations of beta diversity dimensions (fig. 3). Seven of the eight possible combinations of taxonomic, phylogenetic, and trait beta diversity were observed (fig. 4). High taxonomic, low phylogenetic, high trait beta diversity did not occur among any assemblage comparisons. Three of the eight combinations were consistent with our predictions for both environmental dissimilarity and distance. Three of the eight combinations were consistent with our predictions for either environmental dissimilarity or distance. Two combinations were observed in less than 10 assemblage comparisons.
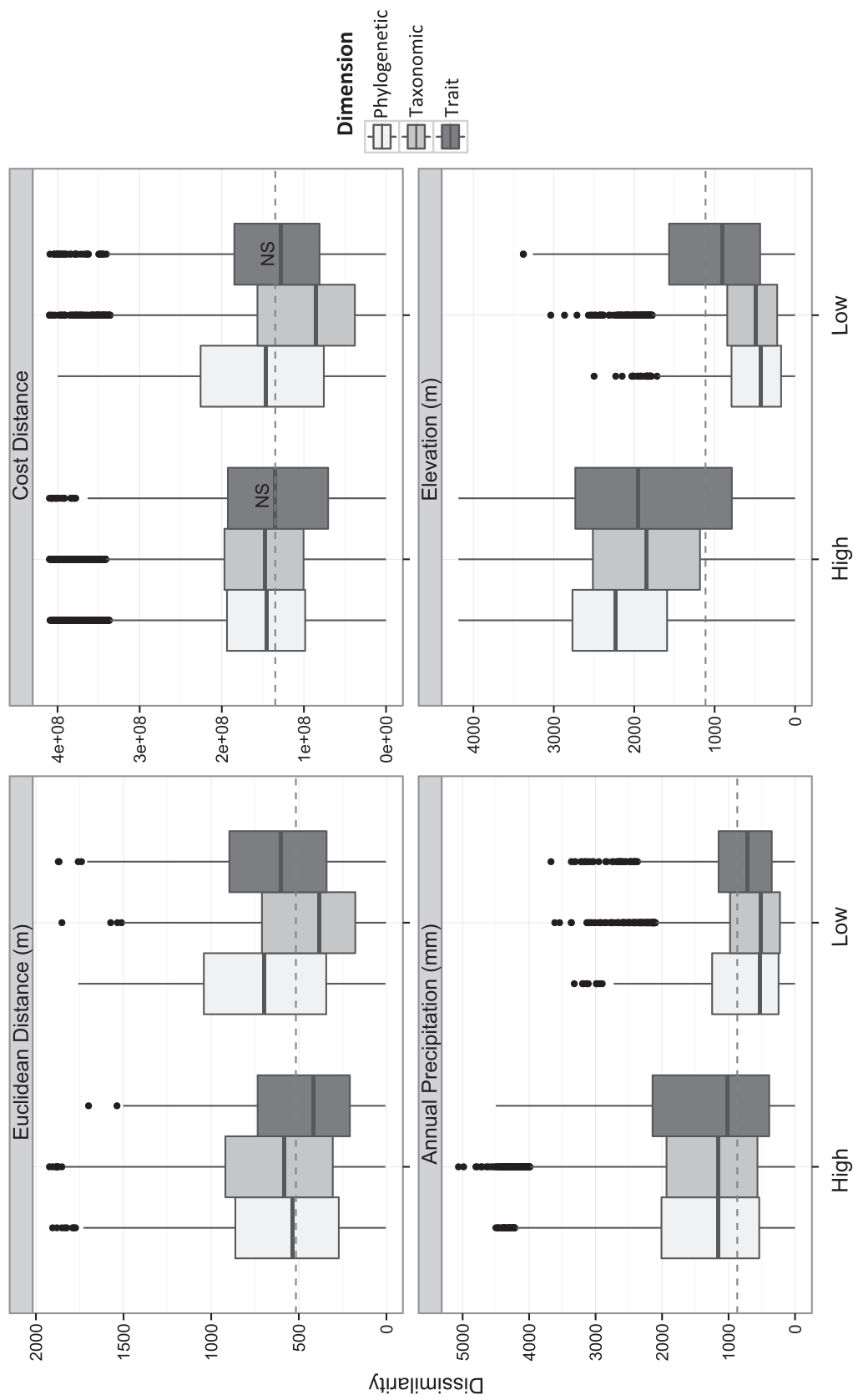
Figure 2: Summary of the environmental dissimilarity and distance measures for each beta diversity dimension. The dashed line represents the median value of all comparisons in the entire data set. Due to the long tail of the cost distance data, we eliminated the outliers from this boxplot by excluding all values greater than the ninety-fifth quantile. Dimensions of beta diversity (taxonomic, phylogenetic, and trait) are considered high or low based on a null model of community assembly. Variables that are not significantly different from the entire data set ($P > .05$) are labeled NS.
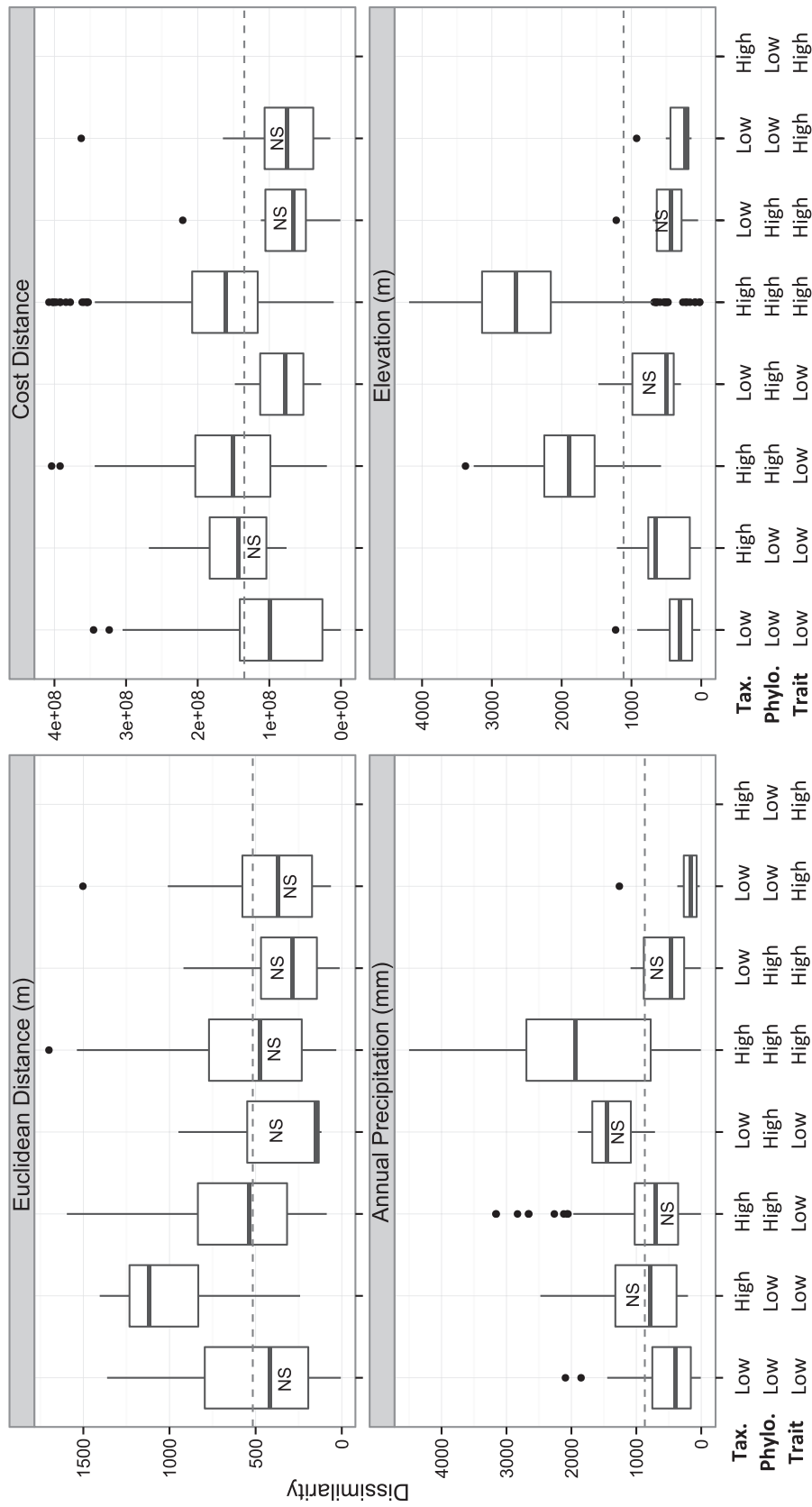
Figure 3: Summary of the environmental dissimilarity and distance measures for the combinations of beta diversity dimensions. The dashed line represents the median for the entire data set. Due to the long tail of the cost distance data, we eliminated the outliers from this boxplot by excluding all values greater than the ninety-fifth quantile. The labels at the bottom denote the three-way combination of beta diversity dimensions (order = taxonomic, phylogenetic, and trait). Dimensions of beta diversity are considered high or low based on a null model of community assembly. Variables that are not significantly different from the entire data set ($P > .05$) are labeled NS.

|	1. Species adapted to similar env. (traits conserved); limited recent or historic isolation	2. Species adapted to similar env. (traits conserved); recent isolation	3. Species adapted to similar env. (convergence); strong current and historic isolation	4. Species adapted to similar env. (convergence); limited recent but strong historic isolation	5. Species adapted to different env. (traits conserved); strong recent and historic isolation	6. Species adapted to different env. (traits conserved); limited recent but historic isolation	7. Species adapted to different env. (traits labile) with limited isolation	8. Species adapted to different env. (traits labile); recent isolation
Taxon.	Low	High	High	Low	High	Low	Low	High
Phylo.	Low	Low	High	High	High	High	Low	Low
Trait	Low	Low	Low	Low	High	High	High	High
Prevalence n = 23871	47	13	181	3	756	8	8	0
Diss.	Low Dist ✓ Low Env ✓	High Dist ✓ Low Env ✓	High Dist ✓ Low Env ✗	Low Dist ✓ Low Env NA	High Dist ✓ High Env ✓	Low Dist ✓ High Env NA	Low Dist NA High Env ✗	High Dist High Env NA
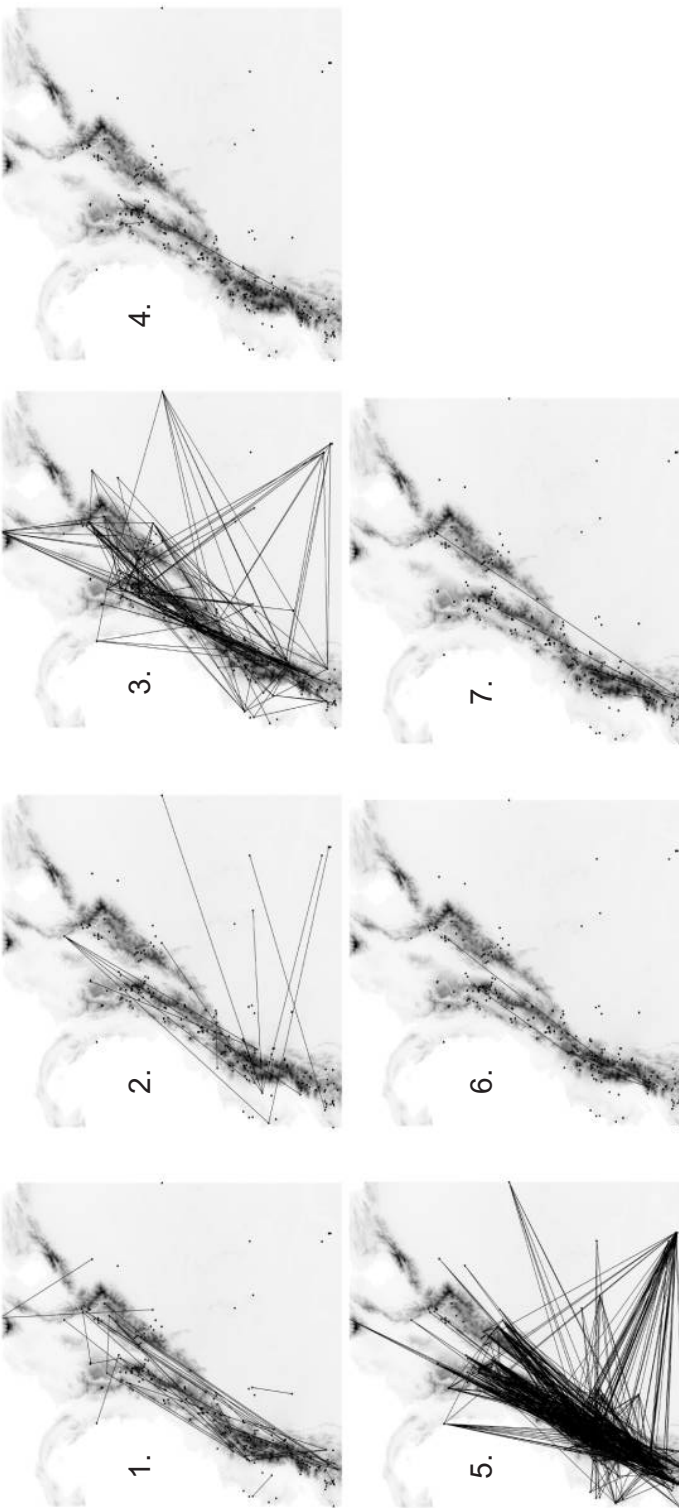
Figure 4: The mechanistic explanations for the eight combinations of beta diversity dimensions (taxonomic, phylogenetic, and trait). Beta diversity dimensions are delineated into high or low taxonomic beta diversity based on a null model of richness. Phylogenetic and trait dimensions are delineated into high or low based on a null model of taxonomic beta diversity. The predicted environmental and distance dissimilarity is shown along with check mark if supported by at least one variable in distance or environmental dissimilarity. The bottom panel depicts the study area and black lines connecting each pair of assemblages for each beta diversity combination.

Low beta diversity in all dimensions resulted where there was less-than-expected change in elevation and precipitation, whereas high beta diversity resulted where there was greater-than-expected change in elevation and precipitation. Where phylogenetic beta diversity was high, combinations with low trait beta diversity still showed a pattern of low environmental change. Assemblages with high taxonomic, low phylogenetic, and low trait beta diversity were located among lowland comparisons on either side of the Andes. These assemblages had large distances, but little environmental change. Combinations of beta diversity dimensions between assemblages in differing environments were predicted to be associated with high trait beta diversity. This was supported only for assemblages with high beta diversity in all dimensions, which showed the largest distances and changes in environments (fig. 4). Spatially, these patterns occurred most often between low-elevation assemblages and high-elevation assemblages on the Andean western slope (fig. 4). The additional three combinations of beta diversity that included high trait beta diversity did not show large changes in environment.

Discussion

The relative importance of environmental and geographic factors varied across the three dimensions of diversity. Environmental distance was correlated with beta diversity across all three dimensions, while geographic distance was only correlated with taxonomic beta diversity. The variation in relative importance of these predictors indicates that different processes likely influence the dimensions of diversity. Taxonomic beta diversity was related to both cost distance and environmental dissimilarity, suggesting that dispersal limitation, potentially combined with allopatric speciation and environmental filtering, influences patterns of assemblage turnover (Cavender-Bares et al. 2004; Emerson and Gillespie 2008; Pavoine and Bonsall 2011; Lansing et al. 2012; Myers et al. 2013). Previous work within biomes, such as tropical rain forests, found that Euclidean distance has a strong influence on beta diversity (Condit et al. 2002; Tuomisto et al. 2003; Pellissier et al. 2010; Fine and Kembel 2011). In addition, the stronger predictive power of environmentally weighted distance compared to Euclidean distance is not a surprising result since the Andes are a known biogeographic barrier to current dispersal (Haffer 1969; Bleiweiss 1998; Chaves et al. 2007; Chaves and Smith 2011) and suggests that measures that incorporate landscape connectivity may be particularly important in understanding patterns of biodiversity.

We found support for most of our a priori expectations about the relationship between the three dimensions of beta diversity and environmental and distance dissimilarity. Comparisons with high taxonomic, phylogenetic, and

trait beta diversity had the highest environmental differences and geographic isolation as predicted. We infer that local adaptation to contrasting environments between isolated assemblages is an important mechanism generating spatial patterns of hummingbird beta diversity (Bleiweiss 1998; McGuire et al. 2007; Parra et al. 2010). High beta diversity exists between assemblages in all dimensions on both sides of the Andes, highlighting the role of the uplift of the Andes in the diversification of hummingbirds. The role of the uplift of mountain ranges in generating beta diversity is well established in avian evolutionary history and indicates the importance of allopatry and subsequent adaptation to differing environments in driving patterns of diversification (Fjeldså et al. 2012).

Consistent with the finding that environmental differences and isolation lead to high beta diversity across dimensions, we found low beta diversity across all dimensions are low when both environmental and geographic distances between assemblages was low. Beta diversity is low across all dimensions in the Andes, with only a few instances of this combination in lowland comparisons. The low phylogenetic beta diversity in the Andes highlights the recent nature of the Andean diversification; few lineages have colonized high-elevation environments resulting in low phylogenetic beta diversity because related species occur in all assemblages (Stiles 2004; Parra et al. 2010). In contrast, species from many clades occur in Amazonia; therefore, there is a greater chance that the species from different clades turnover between assemblages, resulting in relatively high phylogenetic beta diversity in this region as compared to the Andes.

Decoupling of one or more beta diversity dimensions provides potential insights into mechanisms influencing spatial patterns of diversity. Assemblage combinations where trait diversity is low relative to taxonomic and/or phylogenetic beta diversity indicates that morphologically similar species, potentially from different clades, inhabit different assemblages. Convergence in morphological characters may be responsible for these patterns. For example, comparisons with high taxonomic, high phylogenetic, and low trait beta diversity mainly occur between geographically distant lowland and Andean assemblages. In these cases, environmental distance was not lower than expected by chance. Convergence of behavioral and foraging roles could lead to this pattern, as most hummingbird assemblages include species with distinctive roles (e.g., trap-liner, territorial; Feinsinger and Colwell 1978; Stiles 1995; Altshuler 2006) and, generally, distinctive morphologies. These role-specific morphologies, however, vary by elevation because air density presents a significant constraint to high-elevation flight (Altshuler et al. 2004). Two exemplary species are *Discosura popelairii* and *Myrmia micrura*, which are distantly related but are small-bodied and

small-billed trap-liners. These species inhabit different environments; *D. popelairii* occurs in humid foothill montane forests and *M. micrura* in the dry southwestern lowland. Species converging on similar traits and behaviors could explain the occurrence of high taxonomic, high phylogenetic, and low trait beta diversity comparisons.

Comparisons with high taxonomic, low phylogenetic, and low trait beta diversity also occur between distant assemblages on either side of the Andes but in similar environments. In this case, related species with similar ecological roles replace each other in similar environments, consistent with the findings of (Graham et al. 2009). For example, *Glaucis*, *Threnetes*, and *Phaethornis* hermits all have morphologically similar sister species present in the western Choco lowlands and the eastern Amazonian lowlands. High taxonomic beta diversity relative to trait beta diversity is predicted in the tropics due to small range sizes, increased rates of speciation, and niche conservatism (Safi et al. 2011). These mechanisms would result in tight packing of related species over relatively short geographic distances but with biogeographic barriers between them (Haffer 1969). We find evidence for this proposed mechanism consistent with Safi et al.'s (2011) predictions.

Low taxonomic, high phylogenetic, and high trait beta diversity occurs along the Andean elevation gradient, which has rapid clade replacement over short distances. We show that clades that turn over across the gradient are also morphologically distinct, suggesting that different clades may have evolved specific adaptations for different conditions along the elevation gradient. The presence of a few very morphologically distinct species, most notably *Patagona gigas*, may explain the occurrence of these combinations with one assemblage along the inner Andean slopes. We expected that high environmental dissimilarity would be associated with low taxonomic, high phylogenetic, and high trait beta diversity, but this was not observed. The lack of association is likely because of the rapid turnover of species across a relatively continuous and steep gradient; such environmental changes are relatively small in comparison with our null model, which included assemblages in very different environments. Rapid turnover in vegetation communities along the gradient, not captured with our environmental measures, may also cause rapid replacement of species with different bill morphologies. For example, in hummingbird food plants, low-elevation nectar resources are dominated by *Heliconia* and Rubiaceae and replaced by Gesnericeae at midelevations and Ericaceae at high elevations. This shift also corresponds to decreasing floral corolla length, which could promote rapid taxonomic turnover across short geographic distances (personal communication, G. Stiles). In addition, low taxonomic diversity but high phylogenetic diversity could occur either where (1) assemblages were originally isolated for long periods of time, allowing local clade diversification, but then recently connected due to relaxed dispersal limitation; or (2) there was a recent local extinction of a phylogenetically distinct lineage. Furthermore, the relative nature of analysis does not distinguish between absolutely high phylogenetic diversity and more phylogenetic diversity than expected given taxonomic diversity. While we believe this is the most intuitive approach to combine beta diversity dimensions, it cannot distinguish between the absolute causes of phylogenetic beta diversity, which depend greatly on the evolutionary history and biogeography of the system.

While distance was informative in delineating combinations of beta diversity dimensions, neither of our distance measures incorporated past connectivity, which has been shown to be a better predictor of beta diversity than current connectivity (Graham et al. 2006; Baselga et al. 2012). The majority of hummingbirds evolved within the past 10 million years, concurrent with major uplifts in the Andes (McGuire et al. 2007). Thus, a historical cost surface, or a dynamic cost surface over time, may provide more robust insight into the phylogenetic beta diversity of this system. In particular, historical information may allow us to better understand how connectivity through time might influence decoupling between dimensions of beta diversity, where taxonomic beta diversity may be influenced by recent speciation event or colonization and phylogenetic beta diversity may be influenced by historical connectivity. A fruitful avenue for future research would be to integrate shifting climate, geology, and species distributions over time to quantify the influence of isolation and environment on current patterns of species richness and composition (Antonelli et al. 2009; Hoorn et al. 2010). Combining the predictive approach proposed here with time-calibrated phylogenies and geological data would further mechanistic explanations of community structure and biodiversity.

We found support for the majority of our hypothesized environmental and distance dissimilarities for each combination of taxonomic, phylogenetic, and trait beta diversity, indicating that our approach provides insight into mechanisms leading to biodiversity in this highly diverse and complex system. Where data are available, we expect our approach is applicable across taxonomic groups, and testing our hypotheses in other groups would be a productive step toward understanding how diversity is generated and maintained across systems.

Literature Cited

Altshuler, D., and R. Dudley. 2002. The ecological and evolutionary interface of hummingbird flight physiology. Journal of Experimental Biology 205:2325–2336.

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

Altshuler, D. L., R. Dudley, S. M. Heredia, and J. A. McGuire. 2010. Allometry of hummingbird lifting performance. Journal of Experimental Biology 213:725–34.

Altshuler, D. L., R. Dudley, and J. A. McGuire. 2004. Resolution of a paradox: hummingbird flight at high elevation does not come without a cost. Proceedings of the National Academy of Sciences of the USA 101:17731–17736.

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology letters 14:19–28.

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 Sciences of the USA 106:9749–9754.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Baselga, A., C. Gómez-Rodríguez, and J. M. Lobo. 2012. Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. PLoS ONE 7:e32341.

Bivand, R., and N. Lewin-Koh. 2012. maptools: tools for reading and handling spatial objects. R package version 0.8-29. http://CRAN.R-project.org/package=maptools.

Bleiweiss, R. 1998. Origin of hummingbird faunas. Biological Journal of the Linnean Society 65:77–97.

Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. J. Enquist, and J. L. Green. 2008. Colloquium paper: microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences of the USA 105(suppl.):11505–11511.

Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, B. Milá, and C. H. Graham. 2008. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. Journal of Biogeography 35:1160–1176.

Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. Ecology Letters 16:1234–1244.

Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PLoS ONE 4: e5695.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. American Naturalist 163:823–843.

Chaves, J. A., J. P. Pollinger, T. B. Smith, and G. LeBuhn. 2007. The role of geography and ecology in shaping the phylogeography of the speckled hummingbird (*Adelomyia melanogenys*) in Ecuador. Molecular Phylogenetics and Evolution 43:795–807.

Chaves, J. A., and T. B. Smith. 2011. Evolutionary patterns of diversification in the Andean hummingbird genus *Adelomyia*. Molecular Phylogenetics and Evolution 60:207–218.

Condit, R., N. Pitman, E. G. Leigh, J. Chave, J. Terborgh, R. B. Foster, P. Núñez, et al. 2002. Beta-diversity in tropical forest trees. Science 295:666–669.

Cornwell, W., D. Schwilk, and D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471.

Devictor, V., D. Mouillot, C. Meynard, F. Jiguet, W. Thuiller, and N. Mouquet. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecology Letters 13:1030–1040.

Emerson, B. C., and R. G. Gillespie. 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends in Ecology and Evolution 23:619–630.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61:1–10.

Feinsinger, P., and R. Colwell. 1978. Community organization among neotropical nectar-feeding birds. American Zoologist 18:779–795.

Feinsinger, P., R. K. Colwell, J. Terborgh, and S. B. Chaplin. 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. American Naturalist 113:481–497.

Fine, P. V. A., and S. W. Kembel. 2011. Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. Ecography 34: 552–565.

Fjeldså, J., R. C. K. Bowie, and C. Rahbek. 2012. The role of mountain ranges in the diversification of birds. Annual Review of Ecology, Evolution, and Systematics 43:249–265.

Fritz, S. A., and C. Rahbek. 2012. Global patterns of amphibian phylogenetic diversity. Journal of Biogeography 39:1373–1382.

Garland, T., Jr., and A. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155:346–364.

González-Gómez, P. L., N. Ricote-Martinez, P. Razeto-Barry, I. S. Cotorás, and F. Bozinovic. 2011*a*. Thermoregulatory cost affects territorial behavior in hummingbirds: a model and its application. Behavioral Ecology and Sociobiology 65:2141–2148.

González-Gómez, P. L., R. a. Vásquez, and F. Bozinovic. 2011*b*. Flexibility of foraging behavior in hummingbirds: the role of energy constraints and cognitive abilities. Auk 128:36–42.

Gotelli, N. 2000. Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621.

Graham, C. H. C., J. J. L. Parra, B. A. B. Tinoco, F. G. Stiles, and J. A. McGuire. 2012. Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages. Ecology 93:99–111.

Graham, C. H., and P. V. A. Fine. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. Ecology Letters 11:1265–1277.

Graham, C. H., C. Moritz, and S. E. Williams. 2006. Habitat history improves prediction of biodiversity in rainforest fauna. Proceedings of the National Academy of Sciences of the USA 103:632–636.

Graham, C. H., J. L. Parra, C. Rahbek, and J. A. McGuire. 2009. Phylogenetic structure in tropical hummingbird communities. Proceedings of the National Academy of Sciences of the USA 106(suppl.):19673–19678.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165:131–135.

Helmus, M. R., T. J. Bland, C. K. Williams, and A. R. Ives. 2007. Phylogenetic measures of biodiversity. American Naturalist 169:E68–E83.

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.

Hoorn, C., F. P. Wesselingh, H. ter Steege, M. A. Bermudez, A. Mora, J. Sevink, I. Sanmartín, et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330:927–931.

Huang, S., P. R. Stephens, and J. L. Gittleman. 2012. Traits, trees and taxa: global dimensions of biodiversity in mammals. Proceedings of the Royal Society B: Biological Sciences 279:4997–5003.

Ives, A. R., and M. R. Helmus. 2010. Phylogenetic metrics of community similarity. American Naturalist 176:E128–E142.

Jetz, W., and P. P. V. A. Fine. 2012. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. PLoS Biology 10:e1001292.

Kembel, S. W. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. Ecology Letters 12:949–960.

Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, et al. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science 333:1755–1758.

Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. American Naturalist 170:271–283.

Lansing, E., E. Change, E. Group, N. Z. Park, F. Royal, S. Juan, S. Utilization, et al. 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities 93:112–125.

Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology letters 11:995–1003.

McGuire, J. A., C. C. Witt, D. L. Altshuler, and J. V Remsen. 2007. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. Systematic Biology 56:837–856.

McGuire, J. A., C. C. Witt, J. V. Remsen, R. Dudley, and D. L. Altshuler. 2009. A higher-level taxonomy for hummingbirds. Journal of Ornithology 150:155–165.

McRae, B. H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences of the USA 104:19885–90.

Morlon, H., D. W. Schwilk, J. A. Bryant, P. A. Marquet, A. G. Rebelo, C. Tauss, B. J. M. Bohannan, et al. 2011. Spatial patterns of phylogenetic diversity. Ecology Letters 14:141–149.

Myers, J. A., J. M. Chase, I. Jiménez, P. M. Jørgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. Ecology Letters 16:151–157.

Parra, J. L., J. A. McGuire, and C. H. Graham. 2010. Incorporating clade identity in analyses of phylogenetic community structure: an example with hummingbirds. American Naturalist 176:573–587.

Parra, J. L., C. Rahbek, J. A. McGuire, and C. H. Graham. 2011. Contrasting patterns of phylogenetic assemblage structure along the elevational gradient for major hummingbird clades. Journal of Biogeography 38:2350–2361.

Pavoine, S., and M. B. Bonsall. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews of the Cambridge Philosophical Society 86:792–812.

Pellissier, L., K. Anne Bråthen, J. Pottier, C. F. Randin, P. Vittoz, A. Dubuis, N. G. Yoccoz, et al. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. Ecography 33:1004–1014.

Peres-neto, P. R., J. D. Olden, and D. A. Jackson. 2001. Environmentally constrained null models : site suitability as occupancy criterion. Oikos 1:110–120.

Petchey, O. L., and K. J. Gaston. 2007. Dendrograms and measuring functional diversity. Oikos 116:1422–1426.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raufaste, N., and F. Rousset. 2001. Are partial Mantel tests adequate? Evolution 55:1703–1705.

Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, J. F. M. Nores, M. B. Pacheco, T. S. S. Robbins, F. G. Stiles, et al. 2010. A classification of the bird species of South America. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm.

Rosenblum, E. B., H. Römpler, T. Schöneberg, and H. E. Hoekstra. 2010. Molecular and functional basis of phenotypic convergence in white lizards at White Sands. Proceedings of the National Academy of Sciences of the USA 107:2113–2117.

Safi, K., M. V Cianciaruso, R. D. Loyola, D. Brito, K. Armour-Marshall, and J. A. F. Diniz-Filho. 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2536–2544.

Scheiner, S. M. 2012. A metric of biodiversity that integrates abundance, phylogeny, and function. Oikos 121:1191–1202.

Smith, C., J. Stevens, E. Temeles, P. Ewald, R. Hebert, and R. Bon-

kovsky. 1996. Effect of floral orifice width and shape on hummingbird-flower interactions. Oecologia (Berlin) 106:482–492.

Stiles, F. 1995. Behavioral, ecological and morphological correlates of foraging for arthropods by the hummingbirds of a tropical wet forest. Condor 97:853–878.

Stiles, F. G. 2004. Phylogenetic constraints upon morphological and ecological adaptation in hummingbirds (Throchilidae): why are there no hermits in the Paramo? Ornitologia Neotropical 15:191–198.

———. 2008. Ecomorphology and phylogeny of hummingbirds: divergence and convergence to adaptations to high elevations. Neotropical Ornithology 19:511–519.

Stiles, F. G., D. L. Altshuler, and R. Dudley. 2005. Wing morphology and flight behavior of some North American hummingbird species. Auk 122:872.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

Swenson, N. G. 2011*a*. Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. PLoS ONE 6:e21264.

Swenson, N. G. 2011*b*. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. American Journal of Botany 98:472–480.

Temeles, E., Y. Linhart, and M. Masonjones. 2002. The role of flower width in hummingbird bill length–flower length relationships. Biotropica 34:68–80.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2–22.

Tuomisto, H., K. Ruokolainen, and M. Yli-halla. 2003. Floristic variation of western Amazonian forests. Science 299:241–244.

van Etten, J. 2011. gdistance : distances and routes on geographical grids. R package version 1.1-5. http://CRAN.R-project.org /package = gdistance.

Villéger, S., G. Grenouillet, and S. Brosse. 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Global Ecology and Biogeography 22:671–681.

Wang, I. J., W. K. Savage, H. Bradley Shaffer, and H. B. Shaffer. 2009. Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (*Ambystoma californiense*). Molecular Ecology 18:1365–74.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100.

Weinstein, B., B. Tinoco, J. L. Parra, L. M. Brown, J. A. McGuire, F. G. Stiles, and C. H. Graham. 2014. Data from: Taxonomic, phylogenetic and trait beta diversity in South American hummingbirds. American Naturalist, Dryad Digital Repository, http:// dx.doi.org/10.5061/dryad.1qg13.

Whittaker, R. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.

Associate Editor: Susan Harrison
Editor: Troy Day

A violet-tailed sylph (*Aglaiocercus coelestis*). Photo credit: Dr. Donald Powers, George Fox University.