Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages

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Abstract. Phylogenetic community ecology combines phylogenetic hypotheses with local species composition and functional-trait information to evaluate historical and contemporary mechanisms influencing local assemblage structure. Most studies assume that, if functional traits are conserved, then patterns of trait variation should match patterns of phylogenetic structure within local assemblages. Here we evaluated if we could predict trait structure by assuming that environmental filtering or biotic interactions work primarily on phylogenetically conserved functional traits. We investigated patterns of phylogenetic assemblage structure and functional-trait variation in bill length, wing length, and body mass in 236 hummingbird assemblages (126 species) across two major gradients in northern South America: elevation and precipitation. While mean trait values for assemblages vary predictably based on empirical knowledge of hummingbird biology, the distribution of trait values within assemblages do not correspond to those predicted based on phylogenetic signal and phylogenetic structure. Instead, we were able to identify instances where assemblages have high levels of morphological variation despite their close evolutionary relatedness and vice versa. Our results provide support for both filtering and biotic interactions across gradients, as has been documented in other studies.

Key words: Andes; competition; environmental filtering; functional trait; gradient; phylogenetic structure; South America.

INTRODUCTION

Community assembly theory predicts that, at a given site, a series of nested mechanisms that act across various spatial and temporal scales will influence local community composition (Keddy 1992, Weiher and Keddy 1995, Weiher et al. 1998). Webb et al. (2002) proposed a framework that combines phylogenetic and functional-trait data to evaluate the relative role of two of the most important mechanisms in assembly theory: environmental filtering and biotic interactions. Environmental filtering is the persistence of a species in a given environment based on a given trait or set of traits and should result in a relatively limited set of trait values in a local assemblage. If environmental filtering is the predominant mechanism structuring a local assemblage, and traits are conserved on the phylogeny, then closely related species are predicted to co-occur in a given assemblage (phylogenetic clustering). Biotic interactions, such as competitor- or enemy-mediated negative density dependence, should result in co-occurring species that have relatively different trait values, which should

lead to evenly spaced morphologies. A pattern of prevalent trait conservatism with assemblages composed of relatively distantly related species (i.e., phylogenetic evenness) would be consistent with biotic interactions influencing assemblage structure. If functional traits are not conserved, there is no expected match between phylogenetic and phenotypic structure. To date, evaluation of this theory, particularly the link between the distribution of functional traits within assemblages and patterns of phylogenetic structure, remains somewhat inconclusive. Several studies have documented the predicted correspondence between trait conservatism, patterns of phylogenetic structure, and trait spacing (e.g., Cavender-Bares et al. 2004, Kraft and Ackerly 2010); however, a weak, complex, or random correspondence between spacing of conserved traits and phylogenetic structure has also been uncovered (e.g., Cadotte et al. 2009, Swenson and Enquist 2009, Kraft and Ackerly 2010, Kluge and Kessler 2011). To explore this discrepancy, we developed a priori predictions about patterns of functional-trait diversity and its variation based on existing knowledge about phylogenetic assemblage structure, trait evolution, and environment–trait relationships in South American hummingbirds. Specifically, we evaluated if we could predict trait structure by assuming that environmental

filtering or biotic interactions are working primarily on functional traits that are phylogenetically conserved.

Hummingbirds represent a model system to develop and test predictions regarding variation in functional traits. They are a highly diverse (~335 species) family of New World nectar specialists that originated in humid lowland environments in South America and radiated into higher elevation environments and drier regions (Bleiweiss 1998, McGuire et al. 2007, 2009). As many as 25–30 species may co-occur in a given assemblage (Rahbek and Graves 2000). Graham et al. (2009) showed that the phylogenetic structure of hummingbirds changed from even (i.e., distant relatives co-occur) to clustered (i.e., close relatives co-occur) along the elevational gradient formed by the Andes Mountains and along a moisture gradient between humid and dry lowland forests. They attributed this pattern to environmental filtering such that only species with specific traits can occur at high elevations (e.g., Altshuler 2006, Stiles 2008) and in dry environments. Phylogenetic evenness is consistent with empirical observations of intense competition among co-occurring species of hummingbirds (e.g., Feinsinger and Colwell 1978, Wolf 1978). While Graham et al. (2009) proposed these hypotheses to explain patterns of phylogenetic structure, they did not evaluate if patterns of functional-trait variation across assemblages were consistent with these hypotheses.

To evaluate the role of environmental filtering and biotic interactions in hummingbird assemblages, we considered three functional traits: body mass, wing chord (length of the closed wing), and exposed culmen (length of the exposed portion of the bill). These traits all vary predictably across the elevational gradient, but less is known about trait variation across moisture gradients. Body mass is related to surface area-to-volume ratios, which mediate heat loss; therefore, body mass is expected to increase in regions with cooler climates (McNab 1971, Carpenter 1976, Calder 1994, Altshuler and Dudley 2006). Hovering flight is one of the most expensive means of locomotion (Feinsinger et al. 1979, Altshuler et al. 2004, Stiles 2008). At high elevations, hovering flight is more difficult due both to lack of oxygen and a decrease in air density (Feinsinger et al. 1979, Altshuler et al. 2004, Altshuler and Dudley 2006), which results in montane birds having larger wings (Feinsinger et al. 1979, Altshuler and Dudley 2002, Stiles 2008). The length and shape of the beak has long been known to be associated with resource use by hummingbirds and the efficiency with which nectar is extracted from flowers (Wolf et al. 1972, Hainsworth 1973, Temeles et al. 2009), but it remains unclear why one form or another might be at a selective advantage at different elevations.

Given empirical patterns of phylogenetic assemblage structure, known trait–environment relationships and trait conservatism (tested herein), we evaluated if we could predict patterns of morphological metrics that measure environmental filtering or interactions (Fig. 1). Morphological metrics indicative of environmental filtering include the range and variation of trait values in a given assemblage where low values indicate that only a subset of trait values are present in a given environment (Ricklefs and Travis 1980, Weiher et al. 1998, Cornwell and Ackerly 2009). We predicted that environmental filtering in harsh environments, including cool high-elevation regions and seasonally dry regions, should result in decreased trait variance (VAR) values because only species with certain trait values would be expected to occur in these environments. Wing chord and body mass should be particularly influenced by environmental filters at high elevations given flight and physiological limitations associated with these traits. Morphological metrics indicative of competition include two measures of spacing among traits in a given assemblage: standard deviation of nearest neighbor distances (SDNNr) and standard deviation of the nearest distances along a single direction (SDNDr). If competition is prevalent, traits are phylogenetically conserved, and assemblages are composed of species evenly distributed across a phylogeny (i.e., phylogenetic evenness), then co-occurring species should have evenly spaced morphologies (i.e., low SDNNr and SDNDr). In the humid lowlands, where assemblages generally have an even pattern of phylogenetic structure, we predicted that trait values would be evenly spaced. Nevertheless, given extensive empirical evidence for biotic interactions across most hummingbird assemblages, we might also expect even morphological trait spacing across assemblages, even those that occur in harsh environments (Gutiérrez-Zamora et al. 2004, Rico-G. 2008). Bill length, which is directly related to resource use, should be particularly influenced by biotic interactions and, as a result, we expected even spacing in this trait.

MATERIALS AND METHODS

Data

Assemblage composition.—We compiled a database of hummingbird assemblages using lists (presence/absence data) from published references in peer-reviewed journals, gray literature, and non-published reports to environmental organizations including BirdLife International and Aves and Conservación (Appendix A). The taxonomy was updated to reflect the current version of the South American Classification Committee (Remsen et al. 2010). All georeferences of assemblages were checked using the elevation recorded with a given assemblage and then confirmed using digital elevation data or gazetteers. We only included sites that had at least four species for which we had complete information on the phylogenetic relatedness among species and morphological measures for all traits of each species.

The composition of hummingbird assemblages is known to vary both through time and space (Feinsinger et al. 1988, Hilty 1997), and there was some variation in how a given location was sampled. The average area

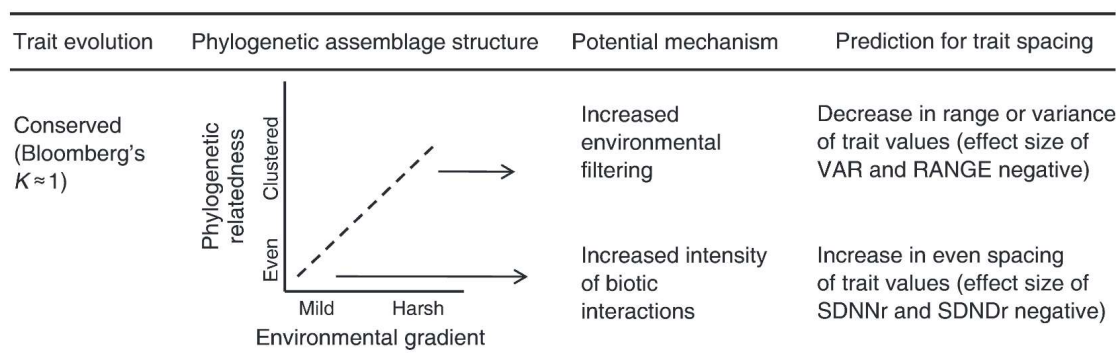| Trait evolution	Phylogenetic assemblage structure	Potential mechanism	Prediction for trait spacing
Conserved (Bloomberg's $K \approx 1$)	Phylogenetic relatedness — Clustered / Even; Environmental gradient — Mild / Harsh	Increased environmental filtering	Decrease in range or variance of trait values (effect size of VAR and RANGE negative)
		Increased intensity of biotic interactions	Increase in even spacing of trait values (effect size of SDNNr and SDNDr negative)

FIG. 1. Conceptual figure of the approach taken in this paper. Assuming that environmental filtering and biotic interactions are mediated by functional traits, we can predict trait spacing based on phylogenetic spacing in assemblages when traits are conserved. When traits are not conserved, we cannot predict phenotypic spacing from phylogenetic spacing. Effect size is a measure of the magnitude and direction of the observed spacing relative to a null expectation.

covered by sites was 1.95 km^2 (median = 1, range = 0.07–12) and the average recorded elevational range covered was ~290 m (median = 160, range = 0–1900). Species richness was not strongly related to either the area (Pearson's $r = 0.03$) or elevational range (Pearson's $r = -0.02$) covered. The area and elevational range reported in the studies from which species lists sometimes included descriptions of the general area where the inventory took place (e.g., Cotopaxi National Park, 3400 to over 5800 m). To identify errors and minimize overly long lists (i.e., taken from a large area or elevation range), each species in each assemblage were checked by local experts and the authors to ensure that it was within its known elevational and geographic range. Finally, we acknowledge that we cannot definitively demonstrate that competition-mediated co-occurrence or environmental filtering occur at the spatial scale of each assemblage. In total, we evaluated 236 assemblages across Ecuador and Colombia, which included 126 species of hummingbirds; 108 of these were used in Graham et al. (2009).

Environmental data.—Based on previous analyses of the relationship between phylogenetic structure of hummingbird assemblage structure and the environment (Graham et al. 2009, Parra et al. 2010), we chose four variables: mean annual temperature, annual precipitation, precipitation of the driest quarter, and vegetation structure. The three climate variables were taken from the Worldclim database (Hijmans et al. 2005). Vegetation structure was quantified using the annual horizontal mean of Quick scatterometer (QSCAT) data, which is a measure of surface roughness and provides insight on vegetation structure and complexity (Buermann et al. 2008). Elevation, also an important variable related to hummingbird flight, is correlated with temperature (Pearson's $r = 0.98$), so we retained only temperature. Given that our study was done at the equator and at a regional scale, latitudinal trends in temperature are minimal.

Our analyses also required evaluating assemblages based on environmental classes. We created classes using four uncorrelated and transformed (using the z score transformation) Worldclim environmental variables: annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality. We used the ISOCLUSTER and MLCLASSIFY algorithms in ArcInfo (ArcInfo Workstation Version 8.1; ESRI 2001) to identify 20 environmental classes across South America, seven of which were in our study region. We then combined several similar and geographically small classes to generate four environmental classes for our study region: humid, warm lowlands (wet lowlands); warm, seasonally dry lowlands (dry lowlands); humid mid-elevations; and high, cool elevations (high elevation; Fig. 2).

Trait values.—We compiled information about three traits in adult males: body mass, length of exposed culmen, and length of closed wing (wing chord). Wing chord and body mass have been used to calculate wing disc loading (Weis-Fogh 1972, 1973, Epting 1980), a measure that is negatively correlated with elevation (Feinsinger et al. 1979, Altshuler and Dudley 2002). Recent studies, however, have shown that measures of the distribution of area across the wing are better indicators of flight ability and behavior (Altshuler et al. 2004, Stiles et al. 2005); therefore, we did not calculate wing disc loading, and instead used only wing chord. Data were gathered from a variety of published and unpublished sources (Appendix B). For each species–trait combination we removed possible mistaken measures by plotting histograms and visually identifying obvious outliers. The weighted means and standard deviations of these traits are provided in Appendix B. There are species for which distinct morphological differences exist between subspecies (Stiles 1983, 1996), but we did not have repeated measurements of species by geographic region to evaluate such variation. However, the standard deviation of a trait value within a species is much lower than the standard deviation of the trait across all species (body mass, within-species mean SD = 0.27, among-species SD = 2.67; exposed culmen, within-species mean SD = 0.67, among-species
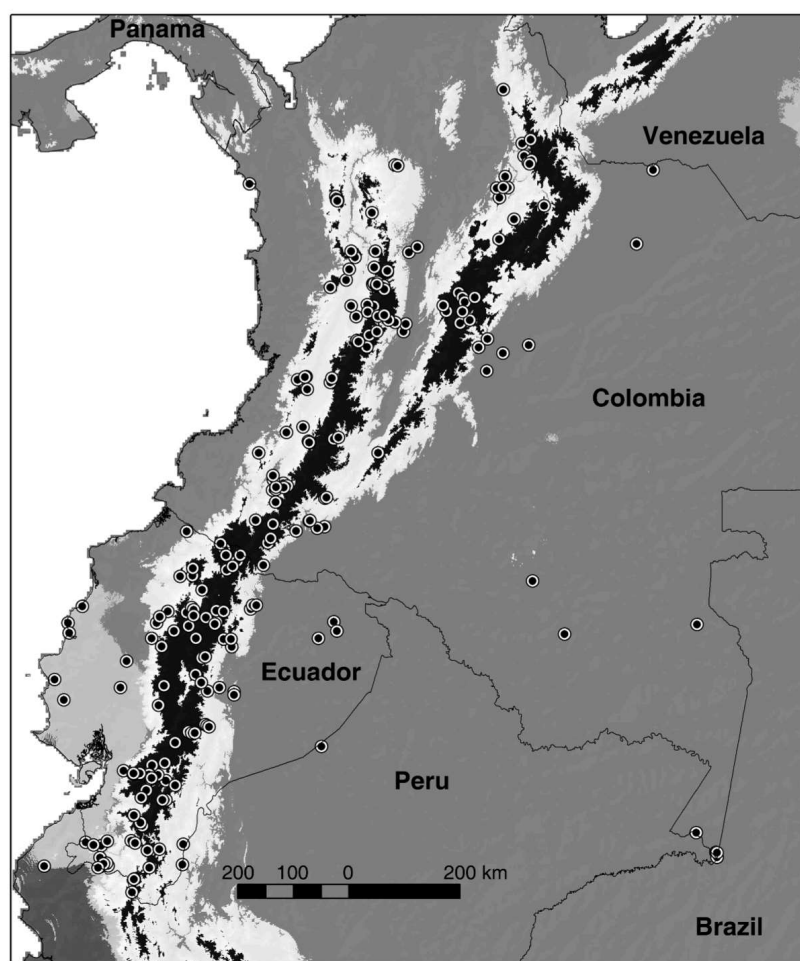
FIG. 2. Study area, showing environmental classes resulting from the unsupervised classification: black is the cool–high environment, white is mid-elevation, medium gray is low–wet, and light gray is low–dry. Dots represent hummingbird assemblages used in this study.

SD = 7.57; wing chord, within-species mean SD = 1.29, among-species SD = 14.07). Therefore, given the broadscale nature of our study, we believe that intraspecific variation is unlikely to overly influence our results.

Phylogenic information.—Our molecular phylogeny included each of the 126 hummingbird species evaluated in this study. Phylogenetic relationships were estimated using DNA sequences from three nuclear genes (adenylate kinase intron 5 [AK1], beta fibrinogen intron 7 [Bfib], and ornythin decarboxylase intron 6 [ODC]), and two mitochondrial genes (NADH dehydrogenase subunit 2 and 4 [ND2, ND4]), comprising 4906 aligned base pairs. The phylogeny was estimated using a Bayesian analysis (MrBayes 3.1; Ronquist and Huelsenbeck 2003) with separate partitions applied to each nuclear gene, and to each codon position within the mitochondrial genes and their flanking tRNAs (12 total partitions). Appropriate substitution models for each partition were determined using the Akaike Information Criterion (AIC) as implemented in the program ModelTest 3.06 (Posada and Crandall 1998). The resulting tree is well

resolved and supported, with 79% of nodes receiving posterior probabilities of 95% or greater (Appendix C). All sequences are deposited in GenBank (see Appendix F), and the matrix used in this study was deposited in TreeBase.

Analyses

Trait evolution.—We measured phylogenetic signal of each of the three traits using the K statistic (Blomberg et al. 2003) in the R package Picante (Kembel et al. 2010). Phylogenetic signal, as measured by Blomberg's K, evaluates if trait variation among species can be better approximated by their phylogenetic distance as compared to trait data that have been randomly shuffled across the phylogeny. K values close to one indicate that trait similarity among species is proportional to their common evolutionary history (as expected under Brownian motion). K values smaller than one indicate high levels of divergence, and larger values indicate stasis. The significance of the K statistic is evaluated using a randomization approach where the values of K

are calculated for 999 data sets where the tips of the tree are randomly shuffled.

Phylogenetic metrics.—We calculated the net relatedness index (NRI) and nearest taxon index (NTI) developed by Webb et al. (2002). NRI quantifies the mean phylogenetic distance and NTI quantifies the mean minimum phylogenetic distance using all possible pairs of species in a given assemblage. The difference between the observed mean and mean minimum phylogenetic distances and expected mean and mean minimum phylogenetic distances, respectively, is divided by the standard deviation of the expected value of each, where the expected value is generated with 999 simulated assemblages using the independent swap null model (Gotelli 2000, Helmus et al. 2007, Webb et al. 2008). This null model is preferred relative to other null models because phylogenetic structure is not influenced by phylogenetic signal in species prevalence (Kembel 2009). We used all species in assemblages to create assemblages for our null model because we wanted to detect filtering across the gradient. Positive values of NRI and NTI indicate phylogenetic clustering, and negative values indicate phylogenetic evenness (Webb 2000). All indices were calculated using the package Picante (Kembel et al. 2010) and R (R Development Core Team 2009).

Morphological spacing metrics.—We calculated all metrics following Cornwell and Ackerly (2009), Ingram and Shurin (2009), and Kraft and Ackerly (2010). We excluded two species with very extreme morphologies: the Sword-billed Hummingbird (*Ensifera ensifera*), which has an ~8 cm exposed culmen, and the Giant Hummingbird (*Patagona gigas*), which weighs between 18 and 24 g (these traits are at least three times greater than the average values for other hummingbirds used in our analyses). Such large morphological discrepancies could bias the outcome of subsequent analyses, especially the expected values of spacing metrics. To evaluate the role of environmental filtering, we quantified the range (RANGE) and variance (VAR) of trait values, but because VAR and RANGE are highly correlated (wing chord, $r = 0.95$; exposed culmen, $r = 0.91$; body mass, $r = 0.94$) we retain VAR in subsequent analyses. To quantify spacing among traits, we used three measures designed to capture biotic interactions based on classic competition theory, which states that similar or identical species are unlikely to co-occur (MacArthur and Levins 1967, Weiher et al. 1998). Our first measure of trait spacing measured the standard deviation of nearest neighbor distances (SDNN) of trait values. As our second measure of trait spacing, we calculated SDNN normalized to range (SDNNr). However, given strong correlation between SDNN and SDNNr (wing chord, $r = 0.86$; exposed culmen, $r = 0.92$; body mass, $r = 0.89$) we retained SDNNr, which we refer to as trait similarity. Finally, we measured how evenly spaced traits are across the entire assemblage (as opposed to only the nearest neighbor) by quantifying the standard

deviation of nearest distances along a single direction normalized to range (SDNDr, referred to as even spacing). For each assemblage, we calculated the observed morphological spacing metric and the average and standard deviation for the same metric based on 999 communities assembled randomly from the regional pool. For the simulated communities, we sampled species with equal probability from the regional pool, which we defined as all species present in the data set. To calculate the effect size of an observed metric for each assemblage, we subtracted the mean metric of the simulated assemblages from the observed value and divided by the standard deviation of the simulated assemblages. Negative effect size values for VAR indicate environmental filtering, and negative effect sizes for SDNNr and SDNDr are consistent with limiting similarity and even spacing of traits, respectively, which are indicative of competition. Note that the standardized effect sizes of the trait-spacing metrics are analogous to the phylogenetic structure metrics. All morphological spacing metrics were calculated using the R script from Kraft and Ackerly (2010).

Both morphological and phylogenetic patterns might be caused by the same species co-occurring across our study area. To explore this possibility, we used a Sorenson similarity index to quantify similarity across assemblages in a given environmental class. When the index has a value of one, assemblages are identical; low values indicate that assemblages are generally composed of nonoverlapping species. While we acknowledge there are many ways to quantify community similarity (see, for example, Legendre et al. 2005, Tuomisto 2010, Anderson et al. 2011), we simply wanted to determine whether patterns of phylogenetic or trait structure were generally based on the same species across multiple assemblages; we are not attempting to evaluate beta diversity per se in the system.

Statistical analyses for evaluation of mechanisms influencing morphological structure.—In order to ensure that traits responded to gradients in a biologically realistic manner, we used a simple linear model with the mean trait values of a given assemblage as the dependent variable and precipitation and temperature as the independent variables. We also tested for interaction between these two variables.

When assemblage size is small, it is difficult to obtain significant phylogenetic structure, especially phylogenetic evenness (i.e., the power of these tests is relatively low; Kraft et al. 2007); therefore, we evaluated our predictions about the relationship between morphological spacing metrics and phylogenetic metrics across environmental gradients in two ways. First, we used a continuous approach, based on correlations and regressions, where significance at the individual assemblage level should not influence our results. Second, to better understand how trait spacing varied across different environments, we used a categorical approach, in which categories were based on environmental classes where
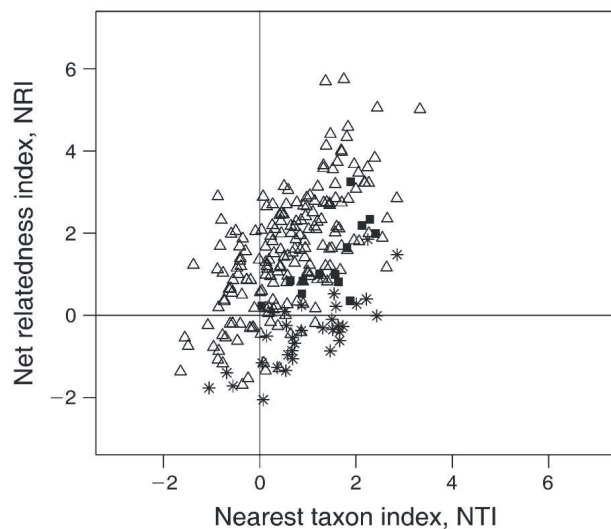
FIG. 3. The relationship between the net relatedness index (NRI) and the nearest taxon index (NTI). Key to symbols: open triangles, high elevation; black squares, low–dry; stars, low–wet. Lines indicate values where there is no phylogenetic structure. The lower right quadrat and upper left quadrat indicate cases where NTI and NRI provide conflicting signals.

assemblages showed consistent patterns of phylogenetic relatedness.

For our continuous approach we conducted Pearson's correlation analyses between phylogenetic structure metrics (NRI and NTI) and both morphological spacing metrics, as well as mean morphological assemblage values. These correlations allowed us to determine direction and strength of univariate relationships between phylogenetic structure and different morphological spacing metrics. We followed these analyses with a series of generalized additive models (GAMs) with the morphological-spacing metric as the dependent variable and either NRI or NTI and four environmental variables (mean temperature, annual precipitation, precipitation of the warmest quarter, and vegetation complexity) as independent variables. We used NTI in analyses that evaluate SDNNr because both of these metrics measure nearest neighbor distances. Morphological-spacing metrics based on multiple species included VAR and SDNDr, and these were evaluated with NRI. Given that we were interested in quantifying the extent to which patterns of phylogenetic structure predict trait spacing for conserved traits, we conducted the following three GAMs for each morphological metric: (1) all four environmental variables and the phylogenetic metric as predictor variables, (2) only the environmental variables as predictors, and (3) only the phylogenetic metric as a predictor. We evaluated the deviance explained by each model to determine the influence of the phylogenetic structure metric on morphological structure in the context of environmental factors.

In our second set of analyses, we used Wilcoxon signed-rank tests to determine if, for assemblages grouped according to environmental classes and phylogenetic structure, a given morphological spacing metric differed from the null hypothesis that the average of the observed values of each morphological metric was equal to the average of the null expectation (following Cornwell and Ackerly 2009, Kraft and Ackerly 2010). Given that our goal was to predict values of trait spacing based on phylogenetic structure (and trait conservatism), we identified environmental classes in which assemblages exhibited consistent patterns of phylogenetic structure, and determined morphological spacing metrics in these assemblages. Based on Graham et al. (2009), and corroborated here, consistent patterns of phylogenetic structure occur in the wet lowlands, high elevations, and dry lowlands, three of the classes identified in our environmental classification (see environmental variables described above in the subsection *Environmental data*). We did not evaluate humid, mid-elevations because strong patterns of phylogenetic structure as measured by NRI and NTI are not apparent in this environment. Assemblages in the wet lowlands were, on average, at 350 m in elevation (range = 9–960 m) with 3075 mm of annual precipitation (range = 1410–4850 mm), and a mean temperature of 25°C (range = 21°–27°C). Assemblages in the high elevations were, on average, at 3030 m (range = 2180–4190 m), with cool temperatures (mean = 11°C, range = 4°–15°C). Finally, assemblages in the dry lowlands occurred at a mean elevation of 406 m (range = 14–861 m), annual precipitation was relatively low (mean = 1007 mm, range = 256–2137 mm), and temperatures warm (mean = 24°C, range = 21°–28°C).

RESULTS

Trait evolution

As predicted based on multivariate analyses of morphological similarity within hummingbird clades (Stiles 2008), we found that divergence could be predicted from evolutionary distance among species (body mass, $K = 1.06$; length of closed wing, $K = 0.99$; length of exposed culmen, $K = 1.38$; $P < 0.001$ in all cases).

Phylogenetic community structure

The patterns of phylogenetic structure across environmental gradients for the 236 assemblages in Ecuador and Colombia were consistent with those found by Graham et al. (2009) for Ecuador only; those assemblages that were phylogenetically clustered (positive NRI values) tended to be at high elevations and in the seasonally dry lowlands, while assemblages with even NRI were in the wet lowlands. The correlation between NTI and NRI was moderate (0.5) but significant. In general, NRI was more likely to identify lowland assemblages as evenly spaced than NTI (Fig. 3). Ninety-nine of 101 assemblages (98%) in the high

TABLE 1. Correlation coefficients between trait metrics and phylogenetic structure indices (net relatedness index, NRI; and nearest taxon index, NTI) in 126 hummingbird species in northern South America.

Trait and index	Correlation coefficient	
	NRI	NTI
Wing chord		
Mean	0.45***	−0.11
VAR	0.42***	0.13*
SDNDr	−0.35***	−0.11
SDNNr	0.10	0.11
Exposed culmen		
Mean	−0.76***	−0.27***
VAR	−0.21***	−0.29***
SDNDr	−0.12	−0.12
SDNNr	−0.29***	−0.19*
Body mass		
Mean	−0.08	−0.30***
VAR	−0.29***	−0.22***
SDNDr	0.10	0.18*
SDNNr	−0.14*	−0.13*

Note: Abbreviations are: VAR, trait variance; SDNDr, standard deviation of the nearest distances along a single direction; and SDNNr, standard deviation of nearest neighbor distances.

* $P < 0.05$; *** $P < 0.001$.

elevations were phylogenetically clustered as measured by NRI (51 significantly clustered at $P < 0.05$), and 84% were clustered based on NTI (8 significantly clustered at $P < 0.05$). All 13 assemblages in the dry lowlands were clustered based on both NRI and NTI, though assemblage size was small resulting in limited significance. In this environment, 4 and 3 assemblages were significantly clustered at $P < 0.05$ for NRI and NTI, respectively. Finally, in the wet lowlands, 24 assemblages were even (only 3 were significant at $P < 0.05$), and 9 were clustered (not significantly) for NRI. In contrast, for NTI, only 3 were even and 30 clustered, 4 of which were significantly clustered ($P < 0.05$).

Morphological spacing metrics

Body mass and wing chord were positively correlated ($r = 0.73$), whereas other correlations among traits were low (body mass and exposed culmen, $r = 0.26$; wing chord and exposed culmen, $r = −0.32$). Correlations among the morphological metrics (VAR, SDNNr, and SDNDr) varied between 0.10 and 0.56 and were mostly below 0.50 (Appendix D).

Pairwise similarity values for species composition within a given environmental class were low (Sorenson similarity; low–dry, mean = 0.34, SD = 0.22; high, mean = 0.31, SD = 0.18; and low–wet, mean = 0.29, SD = 0.23) indicating that observed patterns of trait and phylogenetic structure are likely not driven by the same or a small subset of species. Further, the limited similarity among assemblages indicates that spatial autocorrelation does not drive patterns observed in our study.

Evaluation of mechanisms influencing morphological structure

Trait means for each assemblage varied across the elevational gradient as predicted based on existing empirical work on hummingbird trait–environment relationships. As predicted, body mass and wing chord were negatively related to both temperature and precipitation ($R^2 = 0.24$ and $R^2 = 0.53$, respectively; $P < 0.01$), and exposed culmen was positively related to these two variables ($R^2 = 0.56$, $P < 0.01$).

Overall, the correlation between NRI or NTI and morphological spacing metrics was low, though many of the correlations (14 out of 16) were significant (Table 1). For exposed culmen and body mass, most correlations between phylogenetic metrics and morphological spacing metrics were negative, i.e., as communities become more clustered (positive NRI), morphological spacing metrics decreased. This indicates that in more phylogenetically clustered assemblages there was more constant spacing among trait values (low SDNNr and SDNDr) and increased filtering (low VAR). For wing chord, this pattern was only found for trait evenness (SDNDr) and not for VAR or trait similarity (SDNNr). VAR in particular had a relatively high positive correlation with NRI for wing chord ($r = 0.42$). Results from GAMs generally showed a very weak relationship between morphological spacing metrics and the phylogenetic metric (NRI when VAR or SDNDr was the dependent variable, and NTI when SDNNr was the dependent variable; Table 2). When NRI or NTI was removed from a model, there was little change in the deviance explained by the model (mean change = 2.2%; Table 2).

TABLE 2. Deviance-explained values from general additive models relating trait spacing metrics to phylogenetic structure indices and environmental variables.

Spacing metrics and phylogenic structure	Full model	Model without index	Index alone
VAR			
Wing chord	29.8	29.1	17.3
Exposed culmen	30.4	31.9	6.4
Body mass	44.4	41.8	18.2
SDNDr			
Wing chord	25.1	24.6	1.2
Exposed culmen	14.0	12.5	3.9
Body mass	18.2	15.9	0.4
SDNNr			
Wing chord	19.5	12.6	7.2
Exposed culmen	25.1	25.1	3.5
Body mass	27.0	20.1	8.7

Notes: The dependent variable is the morphological spacing metric. Full model includes all four environmental variables (mean temperature, annual precipitation, precipitation of the warmest quarter, and vegetation complexity), and the index of phylogenetic structure (NRI or NTI); model without NRI/NTI includes only environmental variables (model without metric); and NRI/NTI alone is the model with only the phylogenetic structure index as a predictor (index alone). NRI was used in models for VAR and SDNDr, and NTI was used for SDNNr. See Table 1 for key to abbreviations.

TABLE 3. Wilcoxon-signed rank test for each trait in the three "extreme" environmental classes.

Phylogenetic structure	Environmental class		
	Low–dry, clustered (n = 21)	Cool–high, clustered (n = 99)	Low–wet, even (n = 24)
Wing chord			
Mean	−1.32***	1.43***	−0.24
VAR	−0.12	0.15	−0.66***
SDNDr	−0.03	−0.16**	0.91**
SDNNr	−0.29	0.06	0.24
Exposed culmen			
Mean	0.24	−0.78***	1.8***
VAR	0.61	−0.04	−0.18
SDNDr	−0.32*	−0.41***	−0.04
SDNNr	0.18	−0.40***	0.32
Body mass			
Mean	−0.99**	0.4***	0.62*
VAR	−0.31*	−0.36***	0.11
SDNDr	−0.02	−0.07	−0.02
SDNNr	−0.42	−0.21**	−0.07

Notes: Values indicate average effect sizes for each metric and environmental class. Phylogenetic structure is based on NRI. Numbers in parentheses show the number of assemblages in each group.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The largest changes in deviance between models with and without the phylogenetic metric were SDNNr for wing chord and body mass, for which models of the percent deviation declined by 6.9% in each case (Table 2). Further, neither NRI nor NTI alone explained much deviance in any trait metric (mean deviance explained = 7.4%; Table 2), although deviation explained by NRI alone for VAR of wing chord and body mass was relatively high (17.3% and 18.2% variation explained, respectively; Table 2).

Wilcoxon results were consistent with results from regression analyses. Mean wing chord (calculated based on all species within a local assemblage) was significantly longer than expected by chance in the cool environment (Table 3). Wing chord was also significantly shorter in low–dry environments. Mean length of the exposed culmen was significantly shorter than expected by chance in cool dry environments and significantly longer in warm wet environments. All tests were significant for mean assemblage body mass; mean body mass was relatively low in low–dry environments, and higher in cool–high environments and low–wet environments. When these results are considered along with the regression and correlation analyses, the mean assemblage-level trait values change predictably across environmental gradients based on hummingbird ecology, and thus, are likely useful functional traits for analyses of trait spacing.

We predicted that VAR would be lower under environmental filtering in harsh environments (dry lowlands and high elevation) where assemblages are phylogenetically clustered based on NRI. For body mass, VAR was significantly lower in dry lowlands and

high elevations, consistent with our prediction of environmental filtering in harsh environments. VAR was also significant and low in wet lowlands for wing chord, contrary to our expectation of lack of environmental filtering in this environment. There were no significant differences in VAR across environmental classes for exposed culmen. In terms of morphological spacing metrics, we predicted that spacing would be most even in the phylogenetically even communities of the wet lowlands. This prediction was not supported. In fact, SDNDr for wing chord, which measures if a trait is evenly spaced along a single dimension, showed less even spacing than expected by chance in the wet lowlands. All other instances of significance for SDNNr and SDNDr were negative (suggestive of even spacing) and were strongest for exposed culmen for cool–high elevations where both SDNNr and SDNDr were significant. Finally, in several instances, trait-spacing metrics that measure both filtering and even spacing were significant. For body mass in high environments, morphological metrics are indicative of both environmental filtering (negative VAR) and limiting trait similarity (negative SDNNr).

DISCUSSION

Hummingbird assemblages varied from being phylogenetically clustered in harsh environments to even in wet lowlands, which is considered the ancestral habitat for hummingbirds (also see Graham et al. 2009). We found that the traits of co-occurring species in clustered assemblages were surprisingly even, despite the fact that they showed relatively strong phylogenetic signal. These results appear to contradict the common assumption in community phylogenetics that if important ecological traits are known and are phylogenetically conserved, then phylogeny should be a useful tool for predicting community trait structure. Nonetheless, our results for some traits support a key prediction in community ecology that dates back to Darwin; the more closely related species are, the more strongly they will compete. While a strong abiotic filter can result in phylogenetic clustering and a limited range of trait values, biotic interactions among close relatives should result in trait evenness. Further, trait evenness can also arise simply from the shape of a phylogenetic tree (Davies et al. 2012). These instances indicate that it is essential to combine both trait and phylogenetic information to evaluate potential mechanisms influencing local assembly structure (also see Kembel 2009, Swenson and Enquist 2009, Mayfield and Levine 2010).

Given trait conservatism, we predicted that environmental filtering would be strongest in phylogenetically clustered assemblages, which generally occur in harsh environments in the dry lowlands or at high elevations (also see Graham et al. 2009). The only trait in which trait spacing could be predicted from the phylogenetic structure of assemblages was body size. At high elevations and in dry environments, variance (VAR) in

body size was reduced. These results suggest that, at high elevations, larger body mass may reduce thermal stress produced by cold climates. In addition, body mass influences hummingbird foraging and flight behavior and is related to other morphological characteristics, including larger wings for efficient flight at high elevations (Altshuler and Dudley 2002, Stiles 2008). However, in contrast to our expectation, we found evidence for filtering for wing chord in low, warm environments, and not at high elevations.

Metrics indicative of biotic interactions measuring even spacing (SDNDr) and limited similarity (SDNNr) in morphological traits are likely driven by competition in hummingbirds; ample empirical evidence indicates that hummingbirds compete aggressively for nectar resources (Feinsinger and Colwell 1978, Wolf 1978, Paton and Carpenter 1984, Brown and Bowers 1985, Dearborn 1998). We found no evidence for even spacing (SDNDr) of any trait in phylogenetically even assemblages in low–wet environments, possibly because assemblages are made up of distant relatives whose habits and morphologies are already differentiated allowing them to coexist. Thus, the spacing among co-occurring species may not be the result of competition, but the result of independent evolutionary trajectories. Alternatively, given that NRI measures overall relatedness among individuals in an assemblage, and not specifically close relatives that are more likely to interact, it might not be capturing interactions that influence trait spacing. In contrast, NTI, which is based on nearest neighbors, indicated that lowland assemblages were clustered. This result is consistent with those shown by Parra et al. (2010) where some clades (hermits in particular) are overrepresented (occurred more than expected by chance) in phylogenetically even assemblages according to NRI.

We found that trait spacing generally became more even (both SDNNr and SDNDr) in phylogenetically clustered assemblages, which are prevalent in harsh environments. This may indicate that biotic interactions are particularly intense when the range of trait values (i.e., VAR) in a given assemblage is reduced, forcing traits to be evenly spaced across the existing, somewhat limited, morphospace. The efficiency with which hummingbirds extract resources from flowers is partly determined by the morphological fit between flower corolla length and hummingbird culmen length (Hainsworth 1973, Stiles 1975, Gutiérrez-Zamora et al. 2004, Temeles et al. 2009). In stressful environments, such as mountains, efficient use of resources may be particularly important, and this could lead to relatively closely matched culmen–corolla lengths (Stiles 2008), which in turn may explain the even dispersion of bill size in high cold environments. At high elevations, body masses of co-occurring hummingbirds were less similar when nearest neighbors (SDNNr) were considered but were random in terms of overall even spacing (SDNDr) of this trait. This may be explained by the fact that there

are two dominant clades at high elevations, brilliants and coquettes; the brilliants tend to have large body sizes, whereas coquettes tend to be smaller (Stiles 2008). In most assemblages there are at least two species from each of these clades (Parra et al. 2010), so the likelihood that there are two species with similar body sizes is relatively high.

By evaluating wing chord, body mass, and culmen length across environmental gradients, we gained significant insight into how traits mediate patterns of co-occurrence in hummingbird assemblages across broad environmental gradients in northern South America. However, we found that patterns of morphological variation cannot be directly predicted from measures of phylogenetic structure and trait lability, a result consistent with several recent studies suggesting that mechanisms inferred from phylogenetic and morphological spacing metrics are not always congruent (Kraft et al. 2008, Ingram and Shurin 2009, Swenson and Enquist 2009, Uriarte et al. 2010). These incongruencies could be caused by methodological issues associated with choosing functional traits, quantifying trait conservatism, and evaluating trait and phylogenetic spacing, or by conceptual issues mostly focused on the temporal, spatial, and phylogenetic scale of analyses.

For a variety of methodological reasons, particular traits might not capture the mechanisms influencing assemblage composition. Traits might not be functionally important in terms of environmental filtering or biotic interactions, or an important trait that governs assemblage composition may not have been considered. In hummingbirds, mean values for all traits we evaluated varied as hypothesized across elevational gradients, and the importance of these traits for both biotic interactions and environmental filtering is backed by extensive empirical work. Nonetheless, additional morphological traits such as wing loading (wing area in relation to body size) or foot morphology, which are known to influence foraging behavior (Altshuler et al. 2004, Stiles 2008), could provide additional insights. Differentiating among the simultaneous effects of the multiple influencing mechanisms of community organization (i.e., filtering or biotic interactions) poses another methodological challenge. Trait conservatism might not discriminate among multiple patterns of trait evolution, or phylogenetic structure metrics might integrate multiple mechanisms that cannot be captured by a series of functional traits (Kraft and Ackerly 2010). For instance, Bloomberg's K measures the correlation between path length and the amount of trait variation, but does not provide information on the rate of evolution of traits or the magnitude of its variation; faster evolving traits could show more variation, even if that variation is correlated to the phylogeny (Revell et al. 2008). Another assumption of Bloomberg's K analyses is that the correlation between path length and trait variation is equal for all members of the clade analyzed; if there is among-clade variation, this is not captured. To evaluate

this possibility, we calculated Bloomberg's *K* for individual clades within hummingbirds and found considerable variation among clades in the correlation between path length and trait variation (Appendix E). These results indicate that there may be a need to account for evolutionary lability of traits in a more detailed manner in studies of community phylogenetics (e.g., Ackerly 2009, Pavoine et al. 2010, Losos 2011). In terms of phylogenetic structure metrics, Parra et al. (2010) showed that patterns of structure in hummingbird assemblages, not apparent in assemblage-wide summary metrics of phylogenetic structure (i.e., NRI, NTI), could be detected using node-based analyses. Finally, there is often limited power to detect nonrandom patterns of trait spacing in individual assemblages (Kraft et al. 2007).

Some of the discrepancies we uncovered between our a priori expectations and patterns of trait spacing hummingbirds may be related to scaling; assemblage composition is influenced by multiple mechanisms acting at different spatial, temporal, and phylogenetic scales (Cavender-Bares et al. 2006, Lovette and Hochachka 2006, Swenson et al. 2006, 2007, Parra et al. 2010). For instance, environmental filtering can select for species with similar ecologies, which may mean that they are likely to be strong competitors. We observe this pattern for body mass, which is consistent with both filtering and competition, potentially acting in a hierarchical fashion. In general, mean body mass of co-occurring species increases at higher elevations suggesting that temperature–body mass relationships impose an important ecological filter on what species occur at high elevation. Body mass likely also influences biotic interactions; it is implicated in the foraging efficiency for nectar in hummingbirds (Hainsworth and Wolf 1972, Temeles et al. 2010) and in the dominance relationships among co-occurring hummingbirds (Feinsinger 1976, Altshuler 2006). The limiting similarity principle predicts that there is a limit to how similar competing species can be (MacArthur and Levins 1967); thus, if species are competing, we expect an even spacing among them (such as measured by SDNDr). Evenness of traits may occur in assemblages composed of primarily distant relatives or those where close relatives co-occur; however, it is perhaps more likely in assemblages of the latter where competition may be stronger. Current metrics of phylogenetic structure are not designed to capture this hierarchy. Additionally, phylogenetic assemblage structure in local assemblages may reflect the biogeographic history of a given group (Moen et al. 2009) and not necessarily the trait-based assembly processes mediated through functional traits. In this case, phylogenetic assemblage structure likely captures historic processes that generate the species pool, but may not capture processes that structure local assemblages. This would explain why NRI and NTI explained little variation in trait spacing metrics in our GAM analyses.

In light of growing evidence that both environmental filtering and biotic interactions, as well as the evolutionary and biogeographic mechanisms, likely influence patterns of assemblage composition, it remains a challenge to identify the relative importance of different mechanisms in structuring local assemblages (Emerson and Gillespie 2008, Cavender-Bares et al. 2009, Vamosi et al. 2009). Both phylogenetic and morphological data are required to address this challenge. By contrasting phylogenetic and morphological patterns of assemblage structure, we were able identify instances where groups have high levels of morphological evenness despite their close evolutionary relatedness and the inverse. As such, our results provide useful insights into the relative importance of different mechanisms structuring assemblages and areas for future research. However, our results also emphasize the need to evaluate patterns of phylogenetic structure and trait variation in a more comprehensive manner.

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Supplemental Material

Appendix A

A list of sources used to generate lists of hummingbird assemblage composition (*Ecological Archives* E093-180-A1).

Appendix B

Morphological values of three traits of adult male hummingbirds (*Ecological Archives* E093-180-A2).

Appendix C

Additional detail on phylogenic information (*Ecological Archives* E093-180-A3).

Appendix D

Pearson correlation coefficients among the three trait metrics used in this study (*Ecological Archives* E093-180-A4).

Appendix E

Clade based values of Bloomberg's *K* for the major hummingbird clades (*Ecological Archives* E093-180-A5).

Appendix F

Species names, genebank catalog number, and genetic markers used to create the hummingbird phylogeny used in this study (*Ecological Archives* E093-180-A6).