A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly of Neotropical forest birds

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Summary

1. Methods that assess patterns of phylogenetic relatedness, as well as character distribution and evolution, allow one to infer the ecological processes involved in community assembly. Assuming niche conservatism, assemblages should shift from phylogenetic clustering to evenness with decreasing geographic scale because the relative importance of mechanisms that shape assemblages is hypothesized to be scale-dependent. Whereas habitat filtering is more likely to act at regional scales because of increased habitat heterogeneity that allows sorting of ecologically similar species in contrasting environments, competition is more likely to act at local scales because low habitat heterogeneity provides few opportunities for niche partitioning.

2. We used species lists to assess assemblage composition, data on ecologically-relevant traits, and a molecular phylogeny, to examine the phylogenetic structure of antbird (Thamnophilidae) assemblages at three different geographical scales: regional (ecoregions), intermediate (100-ha plots) and local (mixed-flocks). In addition, we used patterns of phylogenetic beta diversity and beta diversity to separate the factors that structure antbird assemblages at regional scales.

3. Contrary to previous findings, we found a shift from phylogenetic evenness to clustering with decreasing geographical scale. We argue that this does not reject the hypothesis that habitat filtering is the predominant force in regional community assembly, because analyses of trait evolution and structure indicated a lack of niche conservatism in antbirds.

4. In some cases, phylogenetic evenness at regional scales can be an effect of historical biogeographic processes instead of niche-based processes. However, regional patterns of beta diversity and phylogenetic beta diversity suggested that phylogenetic structure in our study cannot be explained by the history of speciation and dispersal of antbirds, further supporting the habitat-filtering hypothesis.

5. Our analyses suggested that competitive interactions might not play an important role locally, which would provide a plausible explanation for the high alpha diversity of antbirds in Amazonia.

6. Finally, we emphasize the importance of including trait information in studies of phylogenetic community structure to adequately assess the mechanisms that determine species co-existence.

Key-words: antbirds, niche conservatism, phenotypic structure, phylogenetic community structure, phylogenetic signal

Introduction

Studying the phylogenetic structure of assemblages allows one to bridge ecology and evolutionary biology to understand the processes mediating species' coexistence (Webb *et al.* 2002; Cavender-Bares *et al.* 2004, 2009; Cavender-Bares, Keen & Miles 2006; Emerson & Gillespie 2008; Vamosi *et al.* 2009). Because closely related species often have similar ecological niches (Peterson, Soberon & Sanchez-Cordero 1999; Kozak & Wiens 2006; Warren, Glor & Turelli

2008), interspecific competition can produce assemblages whose constituent species are less related than expected by chance (i.e. phylogenetic evenness or overdispersion). Alternatively, habitat filtering might result in the coexistence of species that are more closely related than expected by chance (i.e. phylogenetic clustering) because close relatives often possess traits that allow them to persist in particular environments (Webb *et al.* 2002).

Because the relative importance of the processes involved in community assembly likely varies in a scale-dependent fashion, patterns of phylogenetic structure of assemblages are expected to change with spatial scale (Cavender-Bares, Keen & Miles 2006; Swenson *et al.* 2007; Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009). Habitat filtering is hypothesized to structure assemblages predominantly at regional scales, where high habitat heterogeneity allows species with similar environmental requirements to sort across contrasting habitats (Weiher & Keddy 1995; Swenson *et al.* 2007; Cavender-Bares *et al.* 2009). In contrast, at smaller spatial scales, habitat homogeneity can increase the strength of interspecific competition, making it the predominant limitation for coexistence. Consequently, if closely related species are more ecologically similar than distant relatives, then regional assemblages should show phylogenetic clustering as a result of habitat filtering, whereas assemblages at smaller scales should show increased phylogenetic evenness resulting from competitive exclusion of close relatives.

Several studies have used patterns of phylogenetic structure to infer the role of competitive interactions and habitat filtering on community assembly. For example, mammal and plant species coexisting locally are often less related than expected by chance, suggesting that competitive interactions influence local assemblages (Bryant *et al.* 2008; Cardillo, Gittleman & Purvis 2008; Cooper, Rodríguez & Purvis 2008). However, because these studies neither evaluated the phenotypic structure of assemblages nor examined trait evolution, they relied on the assumptions that phylogenetic similarity reflects ecological similarity and that closer relatives are stronger competitors. Because these assumptions are not always met (Cahill *et al.* 2008; Losos 2008), analyses of phylogenetic structure in concert with studies of the distribution of ecologically-relevant traits among species within and among assemblages, and of the evolution of such traits, can provide a clearer understanding of assembly processes. This is exemplified by studies showing that (1) regional assemblages tend to be phylogenetically clustered and local ones tend to be phylogenetically even; (2) species co-occurring locally often exhibit ecologically-relevant traits that are less similar than expected by chance; and (3) such traits are often phylogenetically conserved (Cavender-Bares *et al.* 2004; Cavender-Bares, Keen & Miles 2006; Slingsby & Verboom 2006; Swenson *et al.* 2006, 2007). Thus, ecological similarity of close relatives resulting from niche conservatism likely allows their regional coexistence as a result of habitat filtering and prevents their local coexistence as a consequence of competition.

Although several authors have interpreted patterns of phylogenetic structure of assemblages with reference only to processes such as competition and habitat filtering, such patterns might also reflect evolutionary and biogeographic processes (Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009; Kembel 2009). For example, speciation within regions and low historical dispersal rates across regions may lead to phylogenetic clustering in regional assemblages, whereas speciation across different regions and high dispersal rates across regions are likely to result in phylogenetic evenness (Emerson & Gillespie 2008). Thus, the role of alternative mechanisms influencing assemblage structuring cannot be inferred only from the phylogenetic structure of assemblages, even if such structure is considered with analyses of trait evolution and phenotypic structure (Kembel 2009). Accordingly, characterizing assemblages based on indices of beta diversity and phylogenetic beta diversity (i.e. a measure of geographical turnover in phylogenetic diversity; Cavender-Bares *et al.* 2009) can allow separating the influence of niche-based assembly processes (competition, habitat filtering) from that of evolutionary and biogeographical factors that can lead to similar patterns of phylogenetic structure (Graham & Fine 2008). Specifically, high beta diversity (i.e. high species turnover across regions) together with low phylogenetic beta diversity (i.e. low turnover of lineages) may indicate that phylogenetic structure of assemblages primarily reflects speciation across regions, although these assemblages might be secondarily structured by niche-based processes (Graham & Fine 2008). In contrast, high beta diversity together with high phylogenetic beta diversity may indicate low lineage dispersal across regions (Graham & Fine 2008). The only study applying a phylogenetic beta diversity approach to examine the forces involved in assemblage structuring revealed that patterns of phylogenetic structure can be partly accounted for by dispersal limitation (Graham *et al.* 2009).

Despite the important contribution of ornithology to classic community ecology (MacArthur 1958; Cody 1974), studies using phylogenetic approaches to study bird assemblages are scarce (Vamosi *et al.* 2009). Avian ecologists were among the first to use proxies for the degree of evolutionary relatedness among species (i.e. taxonomic ratios) to address questions about community assembly (e.g. Connor & Simberloff 1978; Grant & Abbott 1980), but only two studies have implemented explicitly phylogenetic approaches. The first one found that wood-warbler species (Parulidae) coexisting locally in North America are less related than expected by chance, suggesting that interactions among closely related species sharing ecological traits hinder coexistence, whereas coexistence of distantly related species is facilitated by ecological and behavioral divergence (Lovette & Hochachka 2006). The second (Graham *et al.* 2009) found that local hummingbird (Trochilidae) assemblages in Ecuador are phylogenetically even in the lowlands suggesting competition, but clustered in the highlands suggesting habitat filtering. However, neither of these studies evaluated the evolution of ecologically-relevant traits in a phylogenetic framework.

The high species richness of antbirds (Thamnophilidae), especially in Amazonian forests, where as many as 40 species may coexist locally (Terborgh *et al.* 1990; Blake 2007), represents a great challenge for explaining diversity and coexistence patterns in birds. This Neotropical radiation comprises nearly 220 species occurring mostly in the lowlands from Mexico to Argentina (Zimmer & Isler 2003). Antbirds vary substantially in body size, plumage, vocalizations, social systems, microhabitat use, and foraging behavior, including extreme cases of specialization (Zimmer & Isler 2003). Here, we integrate information on phylogenetic relationships, phenotypic variation, and species composition of antbird assemblages at different spatial scales to provide insights concerning the processes governing community assembly. Specifically, we use analyses of phylogenetic structure to test the hypothesis that habitat filtering shapes species assemblages at regional scales, whereas competitive interactions predominate at local scales. This hypothesis predicts that under phylogenetic niche conservatism, regional assemblages should exhibit phylogenetic clustering, whereas local assemblages should exhibit phylogenetic evenness. Further, we characterize beta diversity of species and phylogenetic lineages in regional assemblages to consider the effects of speciation and dispersal, which can produce similar patterns of phylogenetic structure to those expected under niche-based assembly processes. We do not assume that ecological niches are conserved, but rather test for phylogenetic niche conservatism using comparative methods and combine such tests with analyses of the phenotypic structure of assemblages. Our results illuminate the processes that govern community assembly at different scales and provide a new perspective on the exceptionally high diversity of Neotropical avian assemblages.

Materials and methods

PHYLOGENETIC ANALYSIS

We used DNA sequences from one nuclear intron (β-Fibrinogen Intron 5) and three mitochondrial genes (ND2, ND3, and Cytochrome B) to reconstruct phylogenetic relationships among 142 species of antbirds for which samples were available. Sequences for 48 species are first reported here (GenBank accession numbers HM637104-HM637286; in Table S1) with the rest obtained from Brumfield & Edwards (2007) and Brumfield *et al.* (2007). We performed a maximum-likelihood (ML) analysis using the GTR + I + G model of nucleotide substitution implemented in RAxML (Stamatakis 2006) and converted the resulting ML tree into an ultrametric tree using the nonparametric rate smoothing algorithm implemented in the package APE (Paradis, Claude & Strimmer 2004) for R (R Development Core Team, 2005). We also used the program BEAST to estimate phylogeny and branch lengths simultaneously in a Bayesian framework with a relaxed molecular clock approach (Drummond & Rambaut 2007). Results obtained with both methods were similar, so we present analyses based on the ML ultrametric tree. Because the tree will be presented in a forthcoming publication with more comprehensive taxonomic sampling, it is not depicted here but the topology is available as supplementary material (Supplement S1).

PHYLOGENETIC STRUCTURE OF ASSEMBLAGES

Definition of assemblages and species pools

We examined phylogenetic structure of antbird assemblages at three different spatial scales: regional, intermediate, and local. The regional scale comprises assemblages composed of species occurring within different ecoregions in Amazonia. Ecoregions are large areas containing distinct assemblages, defined based on broad-scale patterns of floristic and zoogeographic variation (Olson *et al.* 2001). We focused on the Amazonian portion of the Tropical and Subtropical Moist Broadleaf Forests Biome because this was the area for which we had the most complete information on assemblages, and in which antbirds reach their highest diversity. The list of species occurring in each Amazonian ecoregion was extracted from an updated distributional and taxonomic database (Isler 1997) by overlapping shape files for each ecoregion (http://www.worldwildlife.org/science/data/item6373.html) onto the distributional data using the program ArcGIS v 9.3.

At the intermediate scale, we defined assemblages as the group of species coexisting in 100-ha plots, the smallest area that adequately reflects α-diversity of Neotropical forest birds (Terborgh *et al.* 1990). Analyses at this scale are based on data from (1) western Amazonia: three plots from Ecuador (English 1998; Blake 2007) and one from Peru (Terborgh *et al.* 1990); (2) central Amazonia: six plots from Manaus (TEAM Project unpublished data) and two from the Rio Tapajós, Brazil (Wunderle, Pinto-Henriques & Willig 2006); (3) eastern Amazonia: one plot from French Guiana (Thiollay 1994); and (4) Central America: one plot from Panama (Robinson, Brawn & Robinson 2000), four from Costa Rica (TEAM Project, unpublished data), and one from Honduras (D. L. Anderson, unpublished data; Fig. 1).

Finally, at the local scale, we studied mixed-species flocks occurring at single localities. Mixed-species flocking is a common social system among forest birds, in which antbirds commonly participate (Munn 1985). At this scale, opportunities for resource partitioning are presumably limited; accordingly, flock assembly appears to be strongly influenced by competition (Graves & Gotelli 1993). The data sets we used were lists of antbird species co-occurring in 25 canopy and seven understorey mixed-species flocks at Cocha Cashu Biological Station, southeastern Peru (Munn 1985) and in five understorey flocks near Manaus (Develey & Stouffer 2001).

To assess the phylogenetic structure of assemblages at each scale, we established pools of species that could potentially occur in each assemblage. The species pool at the regional scale included all antbird species coexisting within the area of endemism (i.e., an area in which there is congruence among the geographical ranges of taxa with a shared history of isolation and diversification; Cracraft 1985) in which the ecoregion is located. At the intermediate scale, the species pool was the species list for the ecoregion in which each plot was embedded. At the local scale, the pool included all species known to join either canopy or understorey mixed-species flocks at each locality.

Quantifying the phylogenetic structure of assemblages

We used Phylocom version 4.0.1b (Webb, Ackerly & Kembel 2008) to calculate two metrics of phylogenetic structure based on the ML ultrametric tree, the Net Relatedness Index (NRI) and the Nearest Taxon Index (NTI); values of NRI or NTI greater than zero indicate phylogenetic clustering and values lower than zero indicate phylogenetic evenness (Webb *et al.* 2002). To calculate indices for each assemblage, we used 1000 randomly constructed assemblages based
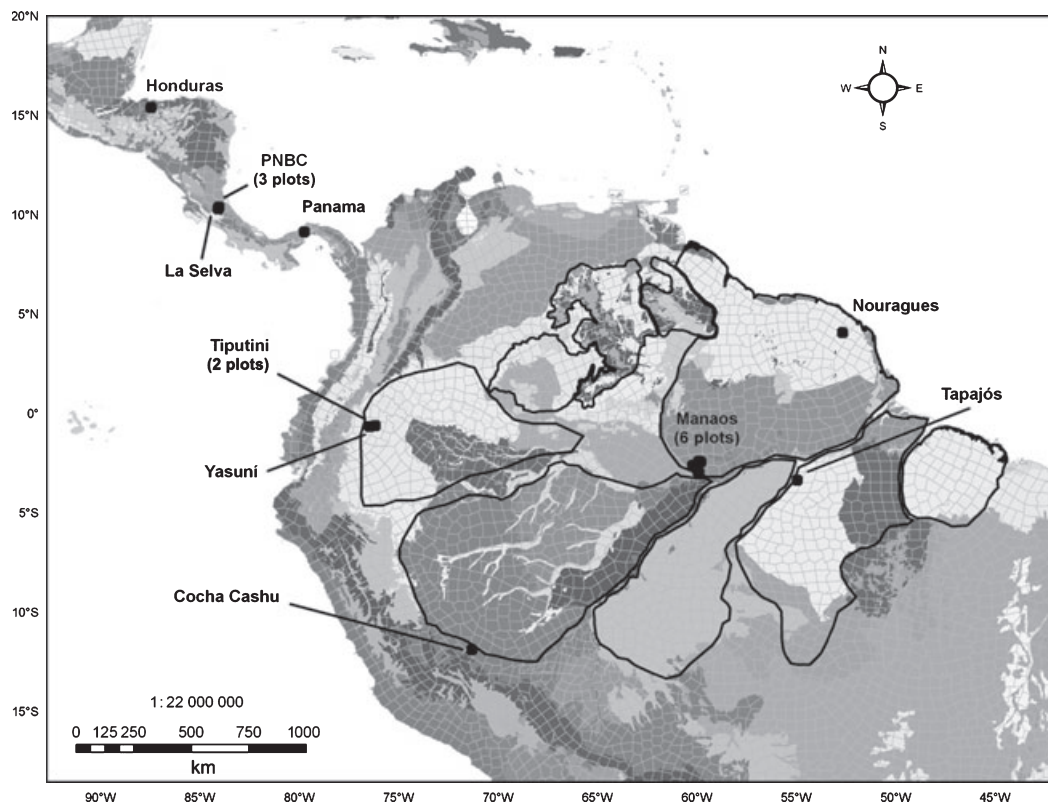
Fig. 1. Map of the Neotropics showing the location of sites used to evaluate the phylogenetic structure of antbird assemblages. Black dots and their labels indicate assemblages at the mixed-flock and 100-ha-plot scales. The areas in gray show the delimitation of ecoregions; sectors for which antbird distributions have been characterized are delimited with solid gray lines, and areas of endemism are delimited with solid black lines.

on the relevant species pool; similar results were obtained using different randomization approaches (see Webb, Ackerly & Kembel 2008). We also characterized phylogenetic structure using the Phylogenetic Species Variability (PSV) index (Helmus *et al.* 2007); results obtained with both methods were similar, so we only present analyses based on the NRI and NTI because they showed an increased statistical power (results based on the PSV are available in supplementary Table S2).

Beta diversity and phylogenetic beta diversity

To evaluate whether observed patterns of phylogenetic structure at the regional scale may have resulted from niche-based assembly processes or rather from speciation and dispersal processes, we used an approach that combines Sorensen's index of beta diversity with a modified Sorensen's index that describes phylogenetic beta diversity (Graham & Fine 2008). The latter index calculates turnover among assemblages after replacing the identity of each species within assemblages with a measure of its phylogenetic distinctiveness as indexed by branch lengths with respect to the root of the phylogeny (Bryant *et al.* 2008). If speciation has occurred mainly across ecoregions, then sister species are unlikely to co-occur in the same ecoregion, resulting in phylogenetic evenness at this scale. In addition, under this scenario one would expect high beta diversity and low phylogenetic beta diversity because species turnover across ecoregions within areas of endemism would be high, but the species being turned over across ecoregions would be close relatives. Alternatively, when phylogenetic structure at the regional scale reflects limited dispersal of lineages, one would expect high beta diversity and phylogenetic beta diversity

among ecoregions within areas of endemism because each ecoregion would contain distinct clades that have diversified within it. Finally, if observed values of beta diversity and phylogenetic beta diversity do not differ from null values obtained by constructing random assemblages from the species pool, phylogenetic structure at the regional scale is unlikely to be a result of speciation and historical dispersal processes, suggesting that niche-based hypotheses may be more plausible. To examine these scenarios, observed beta and phylogenetic beta diversity were compared to null values calculated from 1000 random assemblages constructed using an independent swap algorithm employing the R packages Picante (Kembel *et al.* 2010) and Vegan (Oksanen *et al.* 2010). Finally, we used one-way ANOVAs to compare the mean observed and null values of beta diversity and phylogenetic beta diversity.

PHENOTYPIC STRUCTURE OF ASSEMBLAGES AND TRAIT EVOLUTION

Selection of traits and data collection

Analyses of trait evolution and phenotypic structure were based on a selection of 51 traits (Table 1). Included were both α and β traits, a designation analogous to local (α) and regional (β) measures of biodiversity (Ackerly & Cornwell 2007; Swenson *et al.* 2007). Alpha (α) traits are those that might allow local species coexistence and should show variation among species locally. Beta (β) traits are those that might allow species to overcome habitat filters at regional scales and should vary among regional assemblages but should be similar within assemblages.

Table 1. Traits used to evaluate phenotypic structure and trait evolution across the antbirds. Each trait is listed together with the factor extracted from PCA to which it was related. The percentage of variation explained by each factor is also shown

Type of trait	Trait dataset	PCA	% Variation explained by PCA	Traits
α	Morphological	PC1	40·1%	Wing length; length of primary 10; length of secondary 10; tarsus length; hallux length
		PC2	30·8%	Bill length; bill width; bill depth
		PC3	22·4%	Rectrix 1 length; rectrix 1 width
	Vocal	PC1	33·5%	Max frequency of loudsong (MaxF); min frequency of loudsong (MinF); band width (MaxF−MinF); max frequency of middle note (MaxF-M); max frequency of final note (MaxF-F); peak frequency; maximum frequency of penultimate note.
		PC2	17·9%	Number of notes; pace (duration of pace/number of notes−1); duration of first note; duration of second note; duration of final note
		PC3	12·6%	Duration of loudsong; duration from the beginning of first note to the beginning of final note
		PC4	10·1%	Second frequency change (MaxF-F/MaxF-M); third frequency change (MaxF-F/MaxF-Pen)
		PC5	8·1%	First frequency change (MaxF-M/MaxF−1); Maximum frequency of first note (MaxF−1)
	Ecological	N/A	N/A	Foraging Stratum
β	Macroecological	PC1	31·1%	Annual mean temperature; mean diurnal range (mean of monthly (max temp−min temp)); isothermality; temperature seasonality (SD*100); max temperature of warmest month; min temperature of coldest month; temperature annual range; mean temperature of wettest quarter; mean temperature of driest quarter; mean temperature of warmest quarter; mean temperature of coldest quarter; annual precipitation; precipitation of wettest month; precipitation of wettest quarter; precipitation of coldest quarter
		PC2	24·3%	Aspect; slope; precipitation of driest month; precipitation of driest quarter; precipitation of warmest quarter
		PC3	22%	Precipitation seasonality (coefficient of variation); elevation

Because morphology reflects ecological variation that may be important for resource partitioning locally (Miles & Ricklefs 1984) or habitat filtering regionally (Ingram & Shurin 2009), we treat morphological variation as both an α and a β trait. To characterize morphology across the Thamnophilidae, we measured ten characters (Table 1) on museum specimens following Baldwin, Oberholser & Worley (1931) and using one specimen per each of 140 species. Foraging stratum, which is an important axis of local ecological differentiation in forest birds (Marra & Remsen 1997), was also considered an α trait. For each species, we assigned a value from one to five for foraging strata (Parker, Stotz & Fitzpatrick 1996), with one assigned to terrestrial species and five to canopy species. Species that forage at two different strata received the corresponding intermediate value. Finally, considering that species might compete for acoustic space (Ryan & Brenowitz 1985; Luther 2009), and that thamnophilid songs show evolutionary divergence in response to interactions between sympatric species (Seddon 2005), vocal traits were also treated as α traits. To characterize vocal variation, we measured 18 traits related to frequency ($n = 10$) and temporal aspects ($n = 8$) of songs (Table 1) following Seddon (2005) on spectrograms generated for a single loudsong recording of each thamnophilid species obtained from Isler & Whitney (2002); these vocal traits are important for species recognition in antbirds (Isler, Isler & Whitney 1998; Seddon 2005). We assume that intraspecific variation in morphology and vocalizations is substantially smaller than interspecific variation and that one individual is sufficient to provide an approximate species value for the purposes of our analyses. This simplifying assumption, which we validated following Harmon & Losos (2005) for morpho-

logical variation in 87 species (Table S3), was necessary to coarsely characterize a large number of species for multiple traits across the family (Seddon 2005; Tobias & Seddon 2009).

The β traits related to macroecology used in our analyses were climatic and topographic variables characterizing areas where species occur (i.e. a multivariate description of realized niches; Kearney 2006). This includes 19 climatic variables related to temperature and precipitation at $1\ km^2$ resolution obtained from WorldClim (Table 1; Hijmans *et al.* 2005) and three topographic variables: elevation, obtained from WorldClim, and slope and aspect calculated in ArcGIS. We extracted the value of each variable from localities available in Isler's (1997) database in ArcGIS and then calculated an average value per variable per species.

We reduced each multivariate data set (i.e. morphology, vocalizations, macroecological variables) to uncorrelated sets of variables using principal component analyses (PCA; Table 1) based on the correlation matrices. We then used varimax-rotated factor scores as independent variables for subsequent analyses of phenotypic structure and trait evolution.

We examined the phenotypic structure and the degree of phylogenetic conservativeness for different sets of characters at different scales. At the regional scale we considered only β traits, whereas at the intermediate and highly local scales we considered only α traits.

Phenotypic structure of assemblages

We determined whether traits of coexisting species are more or less similar than expected by chance using two methods. First, we used

Phylocom to calculate the standardized effect size of the variance (SES(Variance)) of each trait following Rabosky *et al.* (2007) based on 1000 random assemblages constructed using an independent swap algorithm; values greater than 0 indicate that species within assemblages are more similar than expected by chance (phenotypic clustering) and values lower than 0 indicate that species within assemblages are less similar than expected by chance (phenotypic evenness).

We also used Mantel tests implemented in the Ecodist package (Goslee & Urban 2007) to correlate matrices of species co-occurrence distances with matrices of trait distances between species (Cavender-Bares, Keen & Miles 2006). Co-occurrence matrices were calculated using the species.dist function in Picante using Schoener's index. Trait Euclidean distance matrices were calculated using the dist function in R. In these analyses, a positive correlation indicates that co-occurring species are phenotypically even, whereas a negative correlation indicates phenotypic clustering. We examined significance of correlations using 1000 randomizations of the co-occurrence matrices. Based on the predicted roles of competition and habitat filtering, we expected β traits to show phenotypic clustering at the regional scale and α traits to exhibit phenotypic evenness at the highly local and intermediate scales.

Analyses of trait evolution

To assess whether α and β traits are evolutionarily conserved or labile in antbirds, we conducted two tests using the multiPhylosignal function in Picante. We first employed a randomization test for phylogenetic signal (Blomberg, Garland & Ives 2003), which calculates the variance of the independent contrasts of each trait across the phylogeny and compares it with a null distribution of the variance of trait's independent contrasts obtained from 1000 randomizations of the traits among species. Observed variances lying on the first or last 25 quantiles of the 1000 randomizations were considered evidence of significant phylogenetic signal or antisignal, respectively. We then used the K statistic (Blomberg, Garland & Ives 2003) to quantify the strength of the phylogenetic signal of traits relative to signal expected for traits evolving under Brownian motion. If K equals zero, differences in traits between species are proportional to the branch lengths separating them on the phylogeny. If K is greater than one, then traits are considered conserved because close relatives are more similar than expected under Brownian motion evolution; if K is lower than one, then traits are considered labile. Because K values are calculated based on a set of traits reduced to one variable using PCA, we were not able to associate significance values to them; however, we consider the trends of these values for different traits as an indication of conservatism or lability (Blomberg, Garland & Ives 2003).

Results

PHYLOGENETIC STRUCTURE OF ASSEMBLAGES

Quantifying the phylogenetic structure of assemblages

In contrast to our initial expectations, regional antbird assemblages were composed of species that are more distantly related phylogenetically than expected by chance, whereas local assemblages were generally composed of close relatives (Fig. 2). No significant phylogenetic structure was observed at the intermediate scale (Fig. 2). In general, the NRI showed the same patterns as the NTI for the understorey mixed-flocks and the intermediate scale, but the indices were not consistent for the canopy mixed-flocks at the local scales (random for NTI and significantly even for NRI) and for regional scale assemblages (even for NTI and random for NRI; Fig. 2).

Beta diversity and phylogenetic beta diversity

Phylogenetic beta diversity and beta diversity indices were not higher or lower than expected for randomly constructed assemblages (Fig. 3; Table S5). Because phylogenetic beta diversity is expected to be lower and beta diversity to be higher than expected by chance if closely related species are distributed in different ecoregions as a result of allopatric speciation, these results suggest that the observed pattern of phylogenetic structure at this scale (i.e. phylogenetic evenness) cannot be attributed to effects of speciation. In addition, because high beta and phylogenetic beta diversity among assemblages would be expected as a result of speciation within ecoregions and when close relatives have similar dispersal limitations, historically-limited dispersal cannot explain our results either.

PHENOTYPIC STRUCTURE OF ASSEMBLAGES AND TRAIT EVOLUTION

Phenotypic structure of assemblages

As predicted by the habitat-filtering hypothesis, both methods used to evaluate the phenotypic structure of assemblages showed that species co-occurring regionally were more similar than expected by chance in the three macroecological traits, but not in morphometrics (Table 2). At the 100-ha scale, both methods indicated that most of the α traits showed random phenotypic structure (Fig. 4). However, the SES(Variance) indicated that vocal measures related to frequency and temporal parameters of loudsongs (see Tables 1 and S4 for detailed results of all principal components analyses) were phenotypically even in Central American (principal component 1, PC1), Central Amazonian (PC2) and West Amazonian assemblages (PC5), and phenotypically clustered in Central America (PC2, PC3). In addition, morphological measurements related to bill length and shape (PC2) showed phenotypic evenness in central Amazonian assemblages and a measurement related to wing, tarsus, and hallux size (PC1) showed phenotypic clustering in the western Amazonian assemblages. Finally, in contrast with the prediction of the competition hypothesis, species coexisting locally did not show phenotypic evenness for any of the traits evaluated, except for a principal component related to frequency change in loudsongs in understorey mixed-flocks in Manaus and Cocha Cashu (PC 4; Fig. 4). In general, both methods used to assess phenotypic structure yielded similar results, but analyses based on the the SES(Variance) revealed a larger amount of significant patterns than analyses based on the Mantel test. The most extreme example of differences between analyses
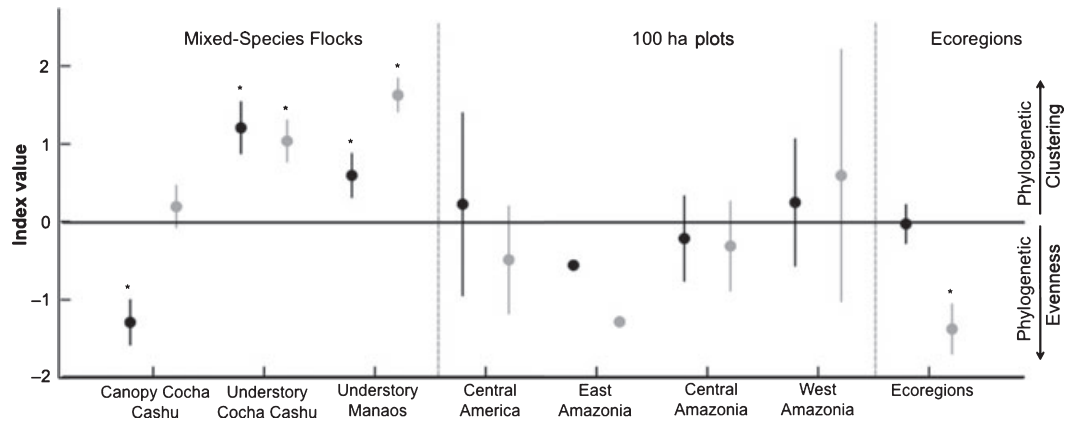
Fig. 2. Indices of phylogenetic community structure and their 95% confidence intervals (NRI in black and NTI in gray) for each of the geographic scales evaluated, suggesting phylogenetic clustering at the local scale (left), random assembly at the intermediate scale (center), and phylogenetic evenness according to the NTI and random dispersion according to the NRI at the regional scale (right). Asterisks indicate indices that were significantly different from zero (random) based on either the 95% confidence intervals or the associated *P*-value for individual index values.
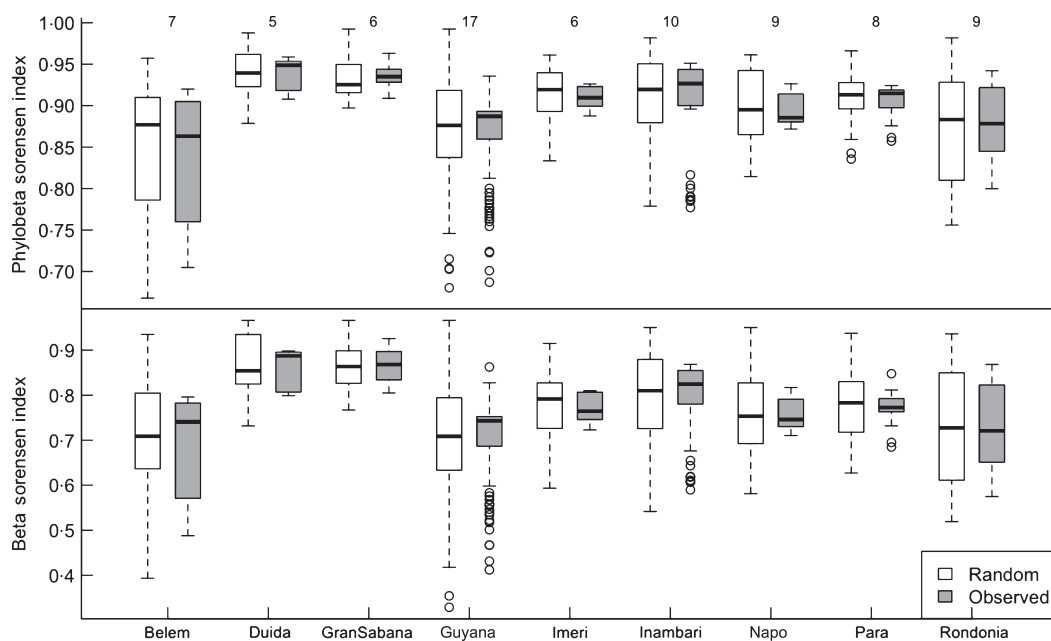

Fig. 3. Phylogenetic beta diversity (top) and beta diversity (bottom) Sorensen indices across ecoregions within each of the nine areas of endemism considered for analyses of phylogenetic community structure. Because there are no differences between observed (gray) and null (white) values, patterns of phylogenetic structure are unlikely to be a result of speciation and dispersal processes. Numbers above bars indicate the number of ecoregions within each area of endemism.

was in canopy mixed-species flocks in Cocha Cashu; in these assemblages, half of the traits showed phenotypic evenness and the other half showed phenotypic clustering using the SES(Variance), but all traits showed random phenotypic structure using the Mantel test (Fig. 4; Table 2). In sum, macroecological variables tended to be phenotypically clustered in regional assemblages, which is consistent with the habitat-filtering hypothesis. At the other scales, traits did not show the pattern of phenotypic dispersion predicted by the competition hypothesis.

Analyses of trait evolution

Both α and β traits showed significant phylogenetic signal in antbirds (Table 3), indicating that closely related species are more similar than expected by chance. Two sets of traits did not conform to this pattern: (1) a summary of the second and third frequency change measurements of vocalizations (i.e. PC4 of the vocal data set; Table 1) showed marginally significant phylogenetic antisignal; and (2) a composite variable related to aspect, slope, and temperature and precipitation in

Table 2. Results of Mantel tests correlating phylogenetic and phenotypic distance matrices suggest phenotypic clustering for β traits at the regional scale and non-significant phenotypic structure at the local and intermediate scales for α traits. Significant correlation coefficients are indicated in bold font. PC indicates each of the factors obtained from the PCA for each of the data sets. F.S. refers to the foraging stratum trait

		α Traits									β Traits		
		Morphological traits			Vocal traits					Ecological F.S.	Macroecological traits		
		PC1	PC2	PC3	PC1	PC2	PC3	PC4	PC5		PC1	PC2	PC3
Local													
Cocha Cashu understorey	r	0·13	0·15	**0·29**	−0·15	0·15	0·03	0·20	0·16	N/A	N/A	N/A	N/A
	p	0·42	0·50	**0·04**	0·24	0·11	0·87	0·39	0·58	N/A	N/A	N/A	N/A
Manaus understorey	r	−0·10	−0·90	−0·10	−0·16	−0·12	0·13	0·14	0·16	N/A	N/A	N/A	N/A
	p	0·68	0·10	0·79	0·70	0·37	0·79	0·88	0·52	N/A	N/A	N/A	N/A
Cocha Cashu canopy	r	−0·05	−0·75	−0·64	−0·04	−0·16	0·30	0·29	0·16	N/A	N/A	N/A	N/A
	p	0·99	0·10	0·15	1·00	0·26	0·25	0·45	0·72	N/A	N/A	N/A	N/A
Intermediate													
Central Amazonia	r	0·00	0·01	−0·01	0·026	0·01	0·06	−0·002	0·05	−0·005	N/A	N/A	N/A
	p	0·91	0·86	0·81	0·55	0·89	0·12	0·96	0·15	0·91	N/A	N/A	N/A
Central America	r	−0·13	0·07	−0·14	0·08	0·04	0·08	−0·07	0·04	−0·27	N/A	N/A	N/A
	p	0·26	0·73	0·39	0·54	0·83	0·60	0·72	0·96	0·07	N/A	N/A	N/A
Western Amazonia	r	**−0·14**	0·02	0·10	−0·06	−0·003	0·04	0·02	−0·11	−0·02	N/A	N/A	N/A
	p	**0·03**	0·86	0·12	0·34	0·97	0·58	0·79	0·24	0·82	N/A	N/A	N/A
Regional													
Ecoregions	r	0·039	0·043	0·04	N/A	N/A	N/A	N/A	N/A	−0·01	**−0·45**	**−0·41**	**−0·30**
	p	0·45	0·45	0·45	N/A	N/A	N/A	N/A	N/A	0·89	**0·001**	**0·001**	**0·001**

dry and warm periods (PC2 of macroecological variables; Table 1) showed no significant phylogenetic signal.

Despite exhibiting phylogenetic signal, α and β traits tended to be evolutionarily labile because the resemblance between species was generally lower than expected under Brownian motion evolution (i.e. most traits exhibited $K < 1$; Table 3). Only two sets of traits were relatively conserved: a multivariate measure of wing, tarsus and hallux size (i.e. morphology PC1), and foraging stratum (Table 3). That closely related species are not more similar than expected under Brownian motion evolution and that some traits show at least marginally significant phylogenetic antisignal indicate a lack of phylogenetic niche conservatism in antbirds.

Discussion

THE ROLE OF COMPETITION AND HABITAT FILTERING

Under phylogenetic niche conservatism, the hypothesis that habitat filtering predominates at larger scales and competition at smaller scales, predicts that assemblages should shift from phylogenetic clustering regionally to phylogenetic evenness locally (Cavender-Bares et al. 2009). We found the exact opposite pattern: the phylogenetic structure of antbird assemblages shifted from significant phylogenetic evenness in Amazonian ecoregions to significant phylogenetic clustering in understorey mixed-species flocks, with no significant phylogenetic structure at the intermediate 100-ha plots.

Examining patterns of phenotypic structure and trait evolution can illuminate the unexpected relationship between phylogenetic structure and geographic scale. At the regional scale, the β traits related to macroecological variables (but not to morphology) were more similar among co-occurring species than expected by chance; this result was expected under habitat filtering and was unsurprising considering the nature of the data (i.e. macroecological variables are similar across localities within ecoregions). However, regional assemblages were composed of distant relatives. Because our analyses revealed that antbirds do not exhibit phylogenetic niche conservatism, this suggests that habitat filtering is important for assembly at regional scales, and that most ecologically-relevant traits are evolutionarily labile. Thus, distantly related species have likely converged on similar β traits that may allow their coexistence in particular environments at large scales (Fig. 4; Table 3). Had we not tested for niche conservatism and assumed it to exist (Bryant et al. 2008; Cardillo, Gittleman & Purvis 2008; Cooper, Rodríguez & Purvis 2008), we might have erroneously concluded that the coexistence of distant relatives within regional assemblages is a result of competition. This highlights the value of analyzing phylogenetic structure together with phenotypic structure and character evolution to understand the processes involved in community assembly (Cavender-Bares et al. 2009).

At the local scale, antbird assemblages were composed of closely related species. Given the high lability of α traits, competition could, in theory, allow closely related species to co-occur through ecological displacement (Table 3). This seems plausible for canopy mixed-species flocks in Cocha Cashu, where half of the traits showed weak but significant phenotypic evenness (Fig. 4). However, α traits did not exhibit significant phenotypic structure in understorey mixed-flocks (Fig. 4), suggesting that species coexisting at this scale might not compete as strongly as expected. Another potential explanation for this pattern is that some α traits might show
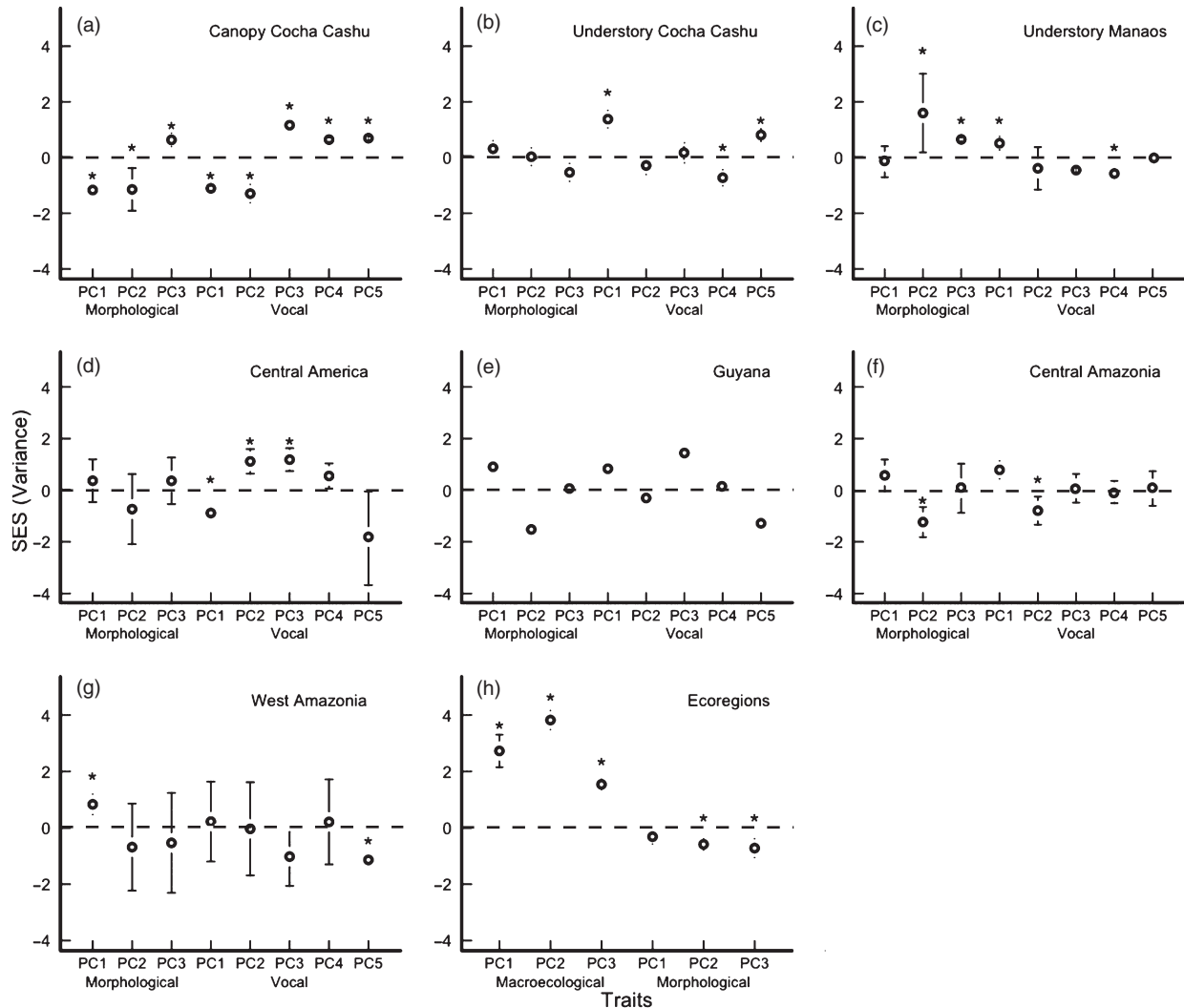
Fig. 4. Phenotypic structure of assemblages as indexed by the SES (Variance) and its 95% confidence intervals for each of the geographic scales evaluated (a–c Local, d–g Intermediate, h Regional), indicating phenotypic clustering for the macroecological traits in ecoregions, phenotypic evenness for half of the traits in Cocha Cashu canopy mixed-flocks, and essentially random phenotypic structure in all other assemblages. Asterisks indicate indices that were significantly different from zero (random) based on either the 95% confidence intervals or the associated *P*-value for individual index values.

significant divergence in sympatry, but that the reduction of variables to principal components in our analyses reduced the importance of individual variables and increased type II error. In addition, competition among close relatives might not be reflected in presence/absence patterns, but rather in species' abundances (Anderson, Lachance & Starmer 2004). It is also possible that we did not consider specific niche axes affected by competition (e.g. we lack quantitative assessments of microhabitat and foraging substrate). Unfortunately, the data available for these variables at the scales we targeted are limited to qualitative descriptions that were unsuitable for our analyses. Gathering quantitative comparable information in the field across different geographic regions will be necessary to detect subtle ecological differences among species and to shed light on the effects of interspecific competition shaping antbird assemblages. Also, extending our sampling of local assemblages to various sites in the Neotropics (analyses in this study were limited to two

sites) might allow us to increase our ability to detect competition at this scale.

In contrast to the patterns seen at the smallest and largest scales, all 100-ha plots lacked phylogenetic structure (Fig. 2). Significant phenotypic structure was also lacking for all of the traits analyzed at this scale (Fig. 4, Table 2). Plausible explanations are that effects of competition and habitat filtering mask each other (Helmus *et al.* 2007), or that assemblages are structured by species-neutral processes (Hubbell 2001). We did not analyze the phenotypic structure of macroecological traits at this scale because some of the variables we measured vary over relatively coarse spatial scales, and because the resolution of those that might vary within plots (e.g. elevation, aspect) was insufficient to finely characterize variation in traits among species. Studies characterizing species niches based on abiotic variables at finer resolutions may be able to detect effects of habitat filtering and competition.

Table 3. Results of the trait evolution analysis suggesting a general pattern of phylogenetic signal but evolutionary lability of ecological traits in the antbirds. *Indicates significant results for the phylogenetic signal test. PC indicates each of the factors obtained from the PCA of the morphological, vocal, and macroecological data sets. F.S. refers to the foraging stratum trait

	K	Evolution	Phylogenetic signal
Morphological			
PC1	1·1	Conserved	Signal*
PC2	0·62	Labile	Signal*
PC3	0·89	Labile	Signal*
Vocal			
PC1	0·96	Labile	Signal*
PC2	0·34	Labile	Signal*
PC3	0·68	Labile	Signal*
PC4	0·12	Labile	Antisignal
PC5	0·53	Labile	Signal*
Ecological			
F.S.	1·34	Conserved	Signal*
Macroecological			
PC1	0·36	Labile	Signal*
PC2	0·25	Labile	Random
PC3	0·34	Labile	Signal

OTHER EXPLANATIONS FOR PHYLOGENETIC STRUCTURE

As an alternative to the hypothesis of habitat-filtering and convergent evolution leading to coexistence of distant relatives within ecoregions, phylogenetic evenness at this scale may also arise as a consequence of the history of speciation and dispersal (Emerson & Gillespie 2008; Graham & Fine 2008). Specifically, phylogenetic evenness within ecoregions may arise if there is speciation across ecoregions within the same area of endemism, resulting in infrequent regional co-occurrence of closely related species. Such a scenario would predict beta diversity to be higher and phylogenetic beta diversity to be lower than expected by chance (Graham & Fine 2008; Graham *et al.* 2009). In addition, if traits involved in dispersal across ecoregions are evolutionarily labile, resulting in similar dispersal abilities in distant relatives, species colonizing ecoregions via dispersal will tend to be distantly related. This would predict both beta and phylogenetic beta diversity to be higher than the null expectation (Graham & Fine 2008). However, because phylogenetic beta diversity and beta diversity did not differ from null values, it appears that the patterns we uncovered cannot be ascribed to speciation and dispersal and that habitat filtering is a more plausible explanation of our results. Alternatively, interspecific competition could also result in phylogenetic evenness at the regional scale if species' ranges are limited by exclusion of ecologically similar species (Case *et al.* 2005; Gotelli, Graves & Rahbek 2010).

COMPARISONS TO OTHER STUDIES

A study on temperate wood-warbler assemblages showed that closely related species are less likely to co-occur, suggest-ing that competitive interactions influence assemblages locally (Lovette & Hochachka 2006). Our study supports such a hypothesis for canopy mixed-flocks using a trait-based approach. However, understorey mixed-flocks failed to reveal compelling evidence for competitive exclusion at local scales because these assemblages lacked phenotypic structure. Overall, this result hints at the possibility that competition might be more relaxed in tropical settings, allowing close relatives to coexist locally. This provides a plausible explanation for the high local diversity of birds in tropical forests, but more studies are needed to evaluate whether this pattern can be generalized to other taxa and sites.

In contrast to the parulid study noted above, our results and those of other studies in a variety of organisms show phylogenetic clustering at local scales (Webb 2000; Cavender-Bares, Keen & Miles 2006; Swenson *et al.* 2006; Helmus *et al.* 2007; Bryant *et al.* 2008). Most of these studies attribute local phylogenetic clustering to the effects of habitat filtering. However, our analyses of trait data suggest this is unlikely because they do not show evidence of phenotypic clustering as the habitat-filtering hypothesis would predict, and because close relatives tend to be phenotypically divergent.

In conclusion, by integrating ecology and evolutionary biology we have inferred the processes involved in community assembly that might account for diversity patterns in antbirds. Our findings support the hypothesis that habitat filtering is an important force in structuring antbird assemblages regionally. The lability of β traits in antbirds may explain coexistence of distantly related species within the same ecoregions, although competition between closely related species remains an alternative explanation for the pattern of phylogenetic evenness that should be tested. The local coexistence of close relatives coupled with the lack of evidence for phenotypic evenness at this scale suggests that antbirds might not compete strongly. This would provide a plausible explanation for the high local diversity of these birds in the Neotropics, although more data are needed to fully test for competition at local scales. In addition, it remains possible that habitat filtering based on traits that we did not examine can operate at small scales. In sum, further studies of the evolution and structure of finer ecological traits may allow us to more clearly separate the determinants of the structure of local antbird assemblages (Helmus *et al.* 2007). Finally, our study indicates that the assumption of phylogenetic niche conservatism has to be carefully considered, because it is clearly not general to all organisms (Losos 2008).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Supplement S1. Maximum-likelihood phylogeny of antbird (Thamnophilidae) species employed for analyses of phylogenetic structure and trait evolution in Newick format.

Table S1. List of species used to reconstruct the phylogenetic hypothesis used for all the analyses, including information of genes used, tissue collection catalogue numbers, and Genbank accession numbers.

Table S2. Results of the analysis of phylogenetic structure based on the Phylogenetic Species Variability (PSV) index. Results are similar to those of other analyses but power is reduced.

Table S3. Results of ANOVAS showing that intraspecific variation in morphology is significantly lower than interspecific variation, which validates the use of a single individual per species in analyses.

Table S4. Loadings for each of the principal components used for trait analyses.

Table S5. Results of ANOVAS showing no differences between random and observed mean values of phylogenetic beta and beta diversity indices within each area of endemism.

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