

Adaptive processes drive ecomorphological convergent evolution in antwrens (Thamnophilidae)

Gustavo A. Bravo,^{1,2,3,4} J. V. Rensen Jr.,^{1,2} and Robb T. Brumfield^{1,2}

¹Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana 70803

²Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803

³Current Address: Seção de Aves, Museu de Zoologia, Universidade de São Paulo (MZUSP), Caixa Postal 42.494, CEP 04218-970, São Paulo, SP, Brasil

⁴E-mail: gbravo1@usp.br

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Phylogenetic niche conservatism (PNC) and convergence are contrasting evolutionary patterns that describe phenotypic similarity across independent lineages. Assessing whether and how adaptive processes give origin to these patterns represent a fundamental step toward understanding phenotypic evolution. Phylogenetic model-based approaches offer the opportunity not only to distinguish between PNC and convergence, but also to determine the extent that adaptive processes explain phenotypic similarity. The *Myrmotherula* complex in the Neotropical family Thamnophilidae is a polyphyletic group of sexually dimorphic small insectivorous forest birds that are relatively homogeneous in size and shape. Here, we integrate a comprehensive species-level molecular phylogeny of the *Myrmotherula* complex with morphometric and ecological data within a comparative framework to test whether phenotypic similarity is described by a pattern of PNC or convergence, and to identify evolutionary mechanisms underlying body size and shape evolution. We show that antwrens in the *Myrmotherula* complex represent distantly related clades that exhibit adaptive convergent evolution in body size and divergent evolution in body shape. Phenotypic similarity in the group is primarily driven by their tendency to converge toward smaller body sizes. Differences in body size and shape across lineages are associated to ecological and behavioral factors.

KEY WORDS: Adaptation, antwren, convergent evolution, ecological correlates, phenotypic disparity, Thamnophilidae.

Phenotypic similarity among independent lineages is a pervasive pattern observed across taxa (Conway Morris 2009; Losos 2011). When such similarity is observed across lineages that have a relatively recent common ancestor, it is often described as phylogenetic niche conservatism (PNC; Losos 2008; Wiens et al. 2010; Crisp and Cook 2012), but when distantly related species independently evolve to become more similar to each other, the pattern is attributed to convergent evolution (Stayton 2006; Losos 2011). Although the use of comparative methods facilitates the detection of both patterns, identifying the evolutionary mechanisms responsible for them represents a major challenge (Losos 2008; 2011). For instance, PNC can result from fundamentally different processes, such as stabilizing selection, low genetic variation

underlying the traits, gene flow among lineages, lack of opportunities for colonizing new niches, and genetic drift (Wiens and Graham 2005; Losos 2008; Crisp and Cook 2012). Similarly, convergent evolution can be the consequence of coincidence, adaptation via natural selection (e.g., Grant et al. 2004), exaptation (Gould and Vrba 1982), genetic drift (Stayton 2008), a correlated response to selection on another character (reviewed by Larson and Losos 2004; Losos 2011), or a community-wide response to competition (Scheffer and van Nes 2006). Therefore, distinguishing PNC from convergent evolution, as well as identifying the driving forces behind them represents a fundamental step toward understanding the mechanisms underlying phenotypic diversity.



With the exception of a few groups, such as lizards in the genus *Anolis* (e.g., Losos 1990; Harmon et al. 2005; Kolbe et al. 2011; Mahler et al. 2013), and fish in the families Cichlidae (e.g., Rüber and Adams 2001; Hulsey et al. 2008; Muschick et al. 2012) and Gasterosteidae (e.g., McGee and Wainwright 2013), the mechanistic underpinnings of phenotypic similarity in vertebrate groups is still poorly understood. Moreover, despite the rapidly increasing number of phylogenetic studies, suggesting the existence of either conserved or convergent phenotypic similarity, sufficient evidence to identify the mechanisms involved is difficult to amass (Losos 2008, 2011; Wiens et al. 2010).

Statistically based phylogenetic comparative methods can be used to quantify the degree of ecological and phenotypic similarity among related species while accounting for phylogenetic relatedness; this allows distinguishing ancestral from derived similarity and identifying potential routes to the latter (e.g., Stayton 2006; Revell et al. 2007a; Sidlauskas 2008). Phylogenetic comparative methods do not only represent a powerful quantitative tool to test whether such similarity is consistent with PNC or convergent evolution, but they also offer the possibility of revealing the potential role of natural selection and adaptation in driving phenotypic evolution among close relatives (Cooper et al. 2010).

The *Myrmotherula* complex (i.e., genus *Myrmotherula* sensu Zimmer and Isler 2003) in the Neotropical family Thamnophilidae is a polyphyletic group (Hackett and Rosenberg 1990; Irestedt et al. 2004; Brumfield et al. 2007; Belmonte-Lopes et al. 2012; Bravo et al. 2012a) that consists of 35 species of sexually dimorphic small insectivorous forest birds that are relatively homogeneous in size and shape. The complex is ideal for the study of evolutionary processes that underlie relationships between ecology and morphology because these birds form a tight ecological assemblage with high levels of intrageneric sympatry and syntopy (Stotz 1990). The complex has been traditionally subdivided into at least three groups defined by male plumage types, which also exhibit some behavioral and ecological differences, such as foraging behavior and habitat preferences (Fig. 1; Hackett and Rosenberg 1990; Stotz 1990; Ridgely and Tudor 1994; Zimmer and Isler 2003). The first group consists of 10 species, commonly referred to as the “streaked antwrens” that occur mainly in the canopy and forest borders of lowland forests; some species join mixed-species flocks in the canopy (e.g., Pearson 1977; Powell 1979; Munn 1985; Stotz 1990). The second group contains 13 species, commonly known as the “gray/slaty antwrens” that occur in the understory and midstory of lowland and subtropical forests; most species join understory mixed-species flocks (e.g., Munn and Terborgh 1979; Stotz 1990; Whitney 1994; Whitney and Pacheco 1997). The third group consists of eight species known as the “stipple-throated antwrens” based on their spotted throat plumage. These species are dead-leaf foraging specialists,

and join understory mixed-species flocks (Hackett and Rosenberg 1990; Rosenberg 1990, 1993). They are now placed in the separate genus *Epinecrophylla* (Isler et al. 2006). Also, members currently placed in the genera *Isleria* and *Rhopias* show combinations of plumage, behavioral, and ecological characters that make their assignment into any of these ecomorphological groups difficult (Zimmer and Isler 2003). Some members of the genera *Formicivora*, *Terenura*, and *Myrmochanes* have been associated to the complex (e.g., Irestedt et al. 2004; Brumfield et al. 2007; Bravo et al. 2012b; Ohlson et al. 2013). The fivefold polyphyly in the complex (Hackett and Rosenberg 1990; Irestedt et al. 2004; Brumfield et al. 2007; Belmonte-Lopes et al. 2012; Bravo et al. 2012a) suggests different lineages within the complex have either converged into similar morphologies or have retained ancestral morphological features.

Here, we integrate a comprehensive species-level molecular phylogeny of the *Myrmotherula* complex with morphometric and ecological data within a comparative framework to test whether phenotypic similarity is due to PNC or to convergent evolution. Because body size and shape can be subject to different evolutionary processes (Miles and Ricklefs 1984), we take into account variation in body size and body shape separately to identify potential mechanisms for ecomorphological evolution in the complex. Also, we study ecological correlates of phenotypic diversification to assess their importance in explaining phenotypic similarity in the complex.

Materials and Methods

MOLECULAR DATA

We sampled 126 vouchered thamnophilid individuals, including two samples from 33 of the 35 species currently and formerly recognized in *Myrmotherula* (Remsen et al. 2013 [13 September 2013]), and at least one individual from 30 other thamnophilid genera (Table S1). This taxon sampling not only represents all subfamilies and tribes within the family (sensu Moyle et al. 2009; Bravo et al. 2012b), but also spans the family’s range of ecological and phenotypic variation. Samples of *Myrmotherula sunensis* and *M. fluminensis* were not available to us. One sample of *Formicivora littoralis* represents an unvouchered blood sample housed at Coleção de Ornitologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP; see Table S1 for acronym information). For outgroups, we included one representative of all other families in the infraorder Furnariides (Formicariidae, Rhinocryptidae, Grallariidae, Furnariidae, Conopophagidae, and Melanopareiidae; Moyle et al. 2009) and the family Pipridae in the infraorder Tyrannides (Tello et al. 2009).

We used standard methods described elsewhere (Groth and Barrowclough 1999; Barker et al. 2002; Brumfield and Edwards

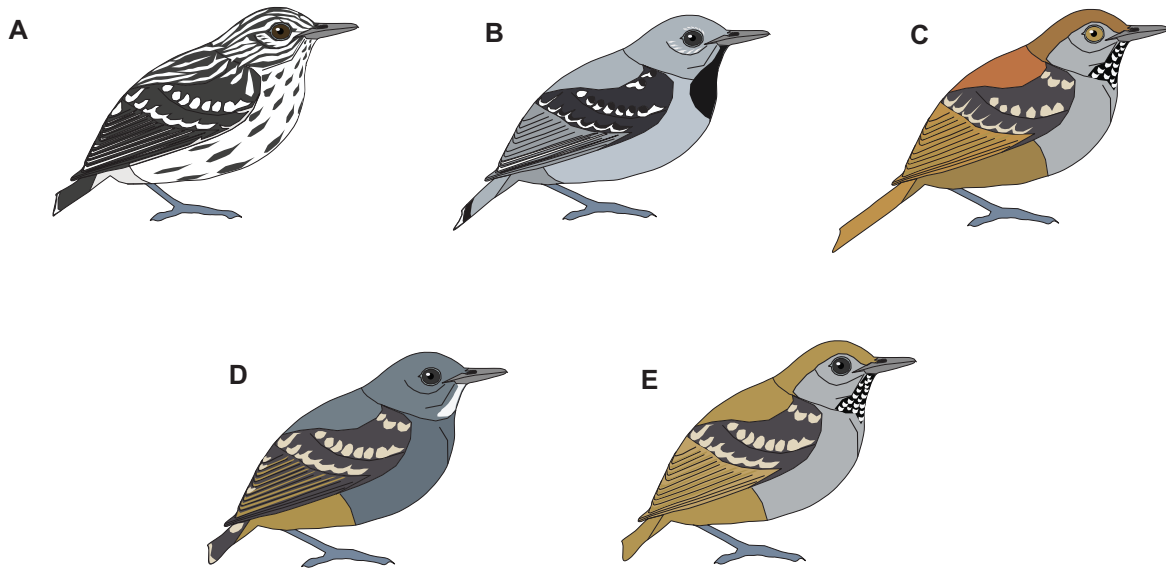


Figure 1. Plumage types traditionally recognized within the *Myrmotherula* complex. (A) Streaked assemblage (*Myrmotherula surinamensis*). (B) Gray assemblage (*M. minor*). (C) Stipple-throated assemblage (*Epinecrophylla haematonota*). (D) *Isleria guttata*. (E) *Rhopias gularis*.

2007; Brumfield et al. 2007) to extract total DNA from pectoral muscle and to amplify and obtain sequences for six genes. After combining newly obtained sequences with sequences from our previous work (Brumfield and Edwards 2007; Brumfield et al. 2007; Moyle et al. 2009; Gómez et al. 2010; Derryberry et al. 2011; Belmonte-Lopes et al. 2012; Bravo et al. 2012a,b), we were able to include sequences for all ingroup and outgroup individuals for three mitochondrial genes (cytochrome b—*cytb*, 1,045 bp; NADH dehydrogenase subunit 2—*ND2*, 1041 bp; and NADH dehydrogenase subunit 3—*ND3*, 351 bp) and one autosomal nuclear intron (β -fibrinogen intron 5— β F5; 568 bp). For a subset of 57 individuals that represent genus-level clades, we included sequences of two protein-coding nuclear genes (recombination activation gene 1—*RAG1*, 2872 bp; recombination activation gene 2—*RAG2*, 1152 bp).

We edited sequences using Sequencher 4.7 (Gene Codes Corporation, Ann Arbor, MI) and checked that protein-coding sequences did not include stop codons or anomalous residues. We aligned sequences using the program MAFFT version 6 (Kato et al. 2002), and obtained a concatenated dataset using Geneious Pro version 5.5 (Drummond et al. 2011). The final alignment included 7035 base pairs. Newly obtained sequences were deposited in GenBank (Accession numbers KM236249–KM236497).

PARTITION AND SUBSTITUTION MODELS

We estimated the optimal partitioning regime using the strategy described by Li et al. (2008) to designate partitions based on their similarity in evolutionary parameters. The data were fully partitioned (a different partition for each position of each cod-

ing gene [15] and the nuclear intron) and each of the 16 data blocks was optimized independently under a GTR+ Γ model using the maximum-likelihood (ML) method in RAxML (Stamatakis 2006). We selected six partitioning strategies based on similarities of substitution rates, base composition, and the gamma parameter among data blocks (Table S2). We used RAxML to obtain likelihood values for each partition strategy under the GTR+ Γ model and identified the most informative strategy using the Akaike information criterion (AIC). We established that the most informative partition scheme included 16 partitions (the nuclear intron and each codon position for each coding gene are treated separately; Table S2). For each partition, we evaluated the 24 substitution models available from MrModeltest 2.3 (Nylander 2004) based on parameter estimation in PAUP* (Swofford 2003), and identified the best substitution model via comparison of AIC (Akaike 1974; Table S3).

PHYLOGENETIC INFERENCE

We generated a phylogenetic hypothesis for the *Myrmotherula* complex under both ML and Bayesian frameworks using the most informative partition scheme. ML analyses were conducted with the GTR+ Γ model of nucleotide substitution and 1000 bootstrap replicates using RAxML 7.2.7 (Stamatakis 2006) on the Cipres Science Gateway version 3.1 (Miller et al. 2010). Bayesian inference analyses in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001) were conducted on the University of Oslo Biportal (Kumar et al. 2009). We performed the analysis with four runs and four MCMC chains, using 20 million generations with a sample frequency of 1000, a chain temperature of 1.75, and a

burn-in of 20%. The use of the “compare” and “slide” functions of AWTY online (Wilgenbusch et al. 2004) were used to assess the performance of Bayesian phylogenetic inference. The obtained Bayesian topology is available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.21sf7>.

We estimated a relative time-calibrated phylogeny in a Bayesian framework using the program BEAST version 1.6.1 (Drummond and Rambaut 2007). We used an uncorrelated log-normal model (UCLD; Drummond et al. 2006) with unlinked substitution models across partitions, and clock models linked by gene. Substitution parameters were based on results previously conducted in MrModeltest. Clock parameters used log-normal distributions with different means for each gene based on behavior of chains in preliminary runs. We used a Yule prior for tree shape with no restrictions on tree shape, and a randomly generated tree was used as a starting tree. Because subsequent analyses do not depend on estimation of absolute times but rather on relative times, no attempt to calibrate the tree based on absolute times was conducted. We ran analyses for a total of 200 million generations with a sampling frequency of 1000. We determined that replicate analyses converged (effective sample size values > 400) using Tracer version 1.5 (Drummond and Rambaut 2007). Using TreeAnnotator version 1.6.1 (Drummond and Rambaut 2007) and a burn-in of 20%, we estimated a posterior distribution of topologies and the maximum clade credibility (MCC) tree. A simplified version of the relative time-calibrated phylogeny is available from the Dryad Digital Repository .

MORPHOLOGICAL DATA

From 362 museum specimens (4.3 individuals/species; Table S4), we obtained weight data from labels and measured 10 ecomorphological variables representing the size and shape of the bill, wing, tail, tarsus, and feet. Five species were represented by fewer than four measured specimens (*Epinecrophylla fjeldsaai*, $n = 1$; *Myrmotherula ambigua*, $n = 1$; *M. behni*, $n = 1$; *Formicivora iheringi*, $n = 2$; and *Euchrepomis spodioptila*, $n = 2$), and one species, *Myrmotherula snowi*, was completely excluded from morphological analyses due to the lack of available specimens. The ecomorphological nature of selected traits in birds (sensu Williams 1972) has been addressed in various studies both from a taxonomic (e.g., Pearson 1977; Schulenberg 1983; Fitzpatrick 1985) and a community perspective (e.g., Ricklefs and Travis 1980; Miles and Ricklefs 1984; Corbin 2008). Strong associations have been documented between behavior, ecology, and external morphology of these traits. Bill morphology has been shown to correlate with prey item and attacking behavior (e.g., Greenberg 1981; Schulenberg 1983; Fitzpatrick 1985); wing morphology affects attack methods and associates with foraging substrate (e.g., Schulenberg 1983; Fitzpatrick 1985); tail morphology is tightly associated with specific foraging movements, such as

climbing (e.g., Norberg 1979; Claramunt et al. 2012), and affects maneuverability during foraging (Thomas and Balmford 1995); and morphology of feet and tarsi correlates with substrate utilization, searching movements, and perch types (e.g., Miles and Ricklefs 1984; Fitzpatrick 1985). For most species, we collected measurements from at least two adult males and two adult females. Measurements obtained were bill length, bill width, and depth at the level of the anterior border of the nostrils, wing length to the longest primary feather, wing length to the tenth primary feather, wing length to the first secondary feather, tail maximum length, central rectrix maximum width, tarsus length, and hallux length. All measurements were taken with a Mitutoyo Digimatic Point Caliper by GAB (for details see Baldwin et al. 1931; Claramunt 2010). Morphometric data were deposited as an associated document file in Microsoft Excel format in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.21sf7>. Using a log-transformed dataset for all individuals, we obtained mean estimates of each morphological trait for every species. Using the phytools version 0.1–6 package (Revell 2012) in the R language for statistical computing (R Development Core Team 2011), we performed a phylogenetic size correction that uses the residuals from a least squares regression analysis, while controlling for nonindependence due to phylogenetic history (Revell 2009). We used log-transformed body weight as a proxy for body size. We then reduced the multivariate dataset to an uncorrelated set of variables using phylogenetic principal component analyses (Revell and Collar 2009; Revell 2012). All subsequent analyses were conducted based on this reduced dataset, except when noted.

TESTING FOR PNC VERSUS CONVERGENT EVOLUTION

To characterize and test PNC and convergent ecomorphological evolution of the *Myrmotherula* complex, we performed a suite of analyses (Wiens and Graham 2005; Losos 2008, 2011; Revell et al. 2008; Wiens et al. 2010). First, we assessed whether body size and shape variation in the complex differs significantly from that of the Thamnophilidae. Second, we tested for adaptive scenarios of body size and shape evolution and fitted models of continuous trait evolution (Harmon et al. 2003, 2008). Third, we explicitly assessed whether ecomorphological variation among lineages within the complex are consistent with a pattern of adaptive convergent evolution (Ingram and Mahler 2013; Mahler et al. 2013). Finally, we assessed whether certain ecological features are correlated with the evolution of specific ecomorphological traits. Details about these analyses are provided below.

Body size and shape diversity

To assess whether members of the *Myrmotherula* complex exhibit constrained ecomorphological diversity, we first quantified

the size and shape components of ecomorphological variation within the family (i.e., all species included in the phylogenetic tree), and within all members in the *Myrmotherula* complex. A vector and a matrix describing size and shape variation, respectively, were estimated excluding body weight from the log-transformed averaged dataset following the approach described by Mosimann (1970) and Mosimann and James (1979). The size of each species is the mean of the 10 log-transformed ecomorphological variables of the species. The shape vector for each species is calculated by subtracting the size of the species from each variable (Mosimann 1970; Mosimann and James 1979). Because values of size and shape for any given taxon do not depend on inferences based on phylogenetic relatedness and values for other taxa, one of the fundamental advantages of this method is that size and shape quantification does not require accounting for phylogenetic independence (Claramunt 2010); quantification per se only depends on the observed variation among morphometric traits across taxa (Mosimann 1970; Mosimann and James 1979) regardless of phylogenetic relatedness. Further use in comparative analyses of the multispecies shape matrix (i.e., all of the species' shape vectors) and the size vector (i.e., all of the species' size values), does require explicit incorporation for phylogeny. On the other hand, other methods to estimate size and shape variation using regressions and principal components require accounting for phylogenetic relatedness because phylogenetic structure determines obtained size and shape values (reviewed by Revell 2009).

To estimate the relative contribution of body size and shape in both groups, we then estimated the shape/size variance ratio, based on computation of the total variance, a multivariate phenotypic diversity measurement that can be partitioned into size and shape components (Darroch and Mosimann 1985; Claramunt 2010). Because here we compare the volume occupied by size and shape variation of ecomorphological space regardless of phylogenetic relatedness, the size vector and the shape matrix do not have to be corrected for phylogeny. To assess whether the obtained shape/size variance ratio for the family and the *Myrmotherula* complex represented significant deviations from null expectations (i.e., Brownian motion), we compared the observed values against null distributions of expected ratios created by performing the same calculations on 999 permutations of the log-corrected morphological matrix with a significance threshold of 0.05.

Ecomorphological evolution over time

To evaluate the rate of morphological evolution in relation to lineage diversification, we conducted disparity-through-time analyses (Harmon et al. 2003), as implemented in the Geiger package v.1.3 (Harmon et al. 2008) in R. We conducted these analyses for the size vector and for the size-corrected phylogenetic principal components of shape variation using the complete phylogeny,

and using a trimmed phylogeny depicting only the history of the core *Myrmotherula* group (32 species; i.e., tribe Formicivorini [sensu Moyle et al. 2009]). Disparity-through-time analysis compares observed average phenotypic disparity among subclades relative to total disparity contained in the phylogeny with average phenotypic disparity simulated under Brownian motion. Then, it computes the morphological disparity index (MDI), which quantifies the overall difference in relative disparity compared with Brownian motion expectations, and describes whether disparity was accumulated during the early or recent history of the phylogeny. Negative MDI values indicate lower subclade disparity than expected under Brownian motion and generally describe clades that accumulated disparity during their early history (i.e., disparity distributed primarily among subclades). Positive MDI values represent clades that accumulated disparity during their recent history (i.e., disparity distributed primarily within subclades). We compared observed relative disparity with the mean expectation of 1000 simulations under Brownian motion.

To test whether mechanisms consistent with adaptive evolution have produced phenotypic divergence over time, we followed a model-based approach (Anderson 2008) that assessed which models of phenotypic evolution provides a better fit to the size and shape data given the phylogeny. For the size vector and for the size-corrected phylogenetic principal components of shape variation, we evaluated four models that have different implications for understanding the mechanisms generating phenotypic diversity: Brownian motion—BM (i.e., diffusive drift), Ornstein–Uhlenbeck—OU (i.e., bounded evolution around a single phenotypic optimum), early burst—EB (i.e., exponential variable rates), and white-noise—WN (i.e., moving optimum) models. Brownian motion represents diffusive drift with gradual phenotypic change at a constant rate (Felsenstein 1985) that can result from genetic drift or randomly fluctuating directional selection (Felsenstein 1988). OU is a modified Brownian motion model that describes phenotypic change with a tendency toward a central value (Hansen 1997; Butler and King 2004). OU is often associated either with a process of stabilizing selection in which variation of phenotypic traits revolves around stationary optimal values or adaptive peaks (Hansen 1997; Butler and King 2004), or with neutral evolution bounded within a small portion of phenotypic space (Harmon et al. 2010). EB describes a process in which evolutionary rates of phenotypic change increase or decrease exponentially through time (Harmon et al. 2010). We specifically assessed a scenario of exponentially decreasing rates of phenotypic evolution (rate parameter < 0) that is analogous with a model of adaptive radiation: phenotypic change occurs rapidly after lineages enter available niches, and decreases as niches are filled (Simpson 1944). WN represents a process in which variation of phenotypic traits revolves constantly around moving optima, which generates evolutionary phenotypic change that is

independent from phylogenetic relationships, and is sometimes associated to neutral evolution (Hunt 2006; Estes and Arnold 2007). Therefore, assessing these four models allows opportunities for finding patterns that are consistent with a role of adaptive processes in driving ecomorphological evolution.

Testing for true convergent evolution

To test whether ecomorphological similarities within the *Myrmotherula* complex might be the result of convergent evolution, we used the SURFACE package (Ingram and Mahler 2013) implemented in R. SURFACE allows one to explicitly model the macroevolutionary convergence of independent lineages in phenotypic space by fitting OU models that vary in the number of adaptive regimes allowed to evolve. The model selection procedure starts with a model in which there is only one adaptive regime in the phenotypic surface and then increases the number of peaks in a step-wise fashion. Then, to identify convergent adaptive peaks SURFACE tests whether corrected AIC (AICc) values improve as it allows to collapse compatible adaptive regimes found in different branches. Therefore, SURFACE assumes that all clades of the tree can be evolving around different optima (i.e., adaptive regimes) under an OU process, and allows the identification of those clades that are convergent. We ran SURFACE using a dataset containing the size vector for all species calculated following Mosimann (1970) and the two first phylogenetic principal components of size-corrected ecomorphological variation. To assess whether observed patterns of true convergence differ from those expected by Brownian motion, we compared the true convergence parameter (Δk) from our observed data to those of 500 datasets simulated under a Brownian motion mode of evolution.

Ecological correlates of phenotypic evolution

We investigated the role of habitat, foraging strata, and flocking behavior in driving morphological evolution in the *Myrmotherula* complex. These ecological factors have been shown to correlate with behavioral and ecomorphological variation in birds (Miles and Ricklefs 1984; Fitzpatrick 1985; Winkler and Preleuthner 2001), including various antwrens and other species in the Thamnophilidae (Pearson 1977; Schulenberg 1983; Stotz 1990). To minimize potential effects of missing taxa in the phylogeny, we focused these analyses exclusively on the Formicivorini. Habitats and foraging strata were coded as categorical variables, based on previous descriptions (e.g., Pearson 1971; Wiley 1980; Stotz 1990; Whitney 1994; Stotz et al. 1996; Whitney and Pacheco 1997; Zimmer and Isler 2003) and recent updates based on our own field experience (Table S5). Habitats were coded into five categorical states, using the main habitat where each species is known to occur (tropical lowland evergreen forests, seasonally flooded evergreen/gallery forests, montane evergreen

forests, tropical dry/white sand forests, open habitats). Foraging strata were coded into three categorical states that describe the height above ground in which each species primarily forages (understory, midstory, canopy). Quantitative estimates of mixed-species flocking behavior (MSF) for 17 of the 33 species were obtained from the literature (Oniki 1971; Pearson 1977; Powell 1979; Gradwohl and Greenberg 1980; Munn 1985; Stotz 1990; Whitney and Pacheco 1997; Develey and Peres 2000; Develey and Stouffer 2001; Thiollay 2003) and then converted into three categorical states (no MSF 0–25%, occasional–common MSF 25–75%, obligate MSF 75–100%; Table S5). For the remaining species, MSF was coded based on previous qualitative descriptions (Zimmer and Isler 2003) and our own field experience.

We first performed an ML estimation of ancestral character states for the three discrete ecological variables using the APE library (Paradis et al. 2004) in R. Following a model-based approach, we evaluated a model of equal rates (ER), a model of symmetrical rates (SYM), and a model that allows all rates to be different (ARD). We tested whether habitat, foraging strata, and MSF groups are more different morphologically than would be expected from random differentiation given the phylogeny, by performing phylogenetic multivariate analyses of variance (MANOVAs) as implemented in the Geiger package in R. To assess evolutionary associations among ecological groups and specific ecomorphological features, we performed phylogenetic analyses of variance (ANOVAs) and post hoc tests for the size vector and each of the 10 size-corrected ecomorphological traits using phytools in R language.

Results

PHYLOGENY

The phylogenetic analyses based on ML and Bayesian methods yielded identical, highly supported topologies (Fig. S1). This topology corroborates previous results that *Myrmotherula* is not monophyletic (Hackett and Rosenberg 1990; Isler et al. 2006; Belmonte-Lopes et al. 2012; Bravo et al. 2012a), with members of the genus placed in four distantly related clades (*Myrmotherula sensu stricto*, *Epinecrophylla*, *Isleria*, and *Rhopias*; Fig. 2). *Myrmotherula sensu stricto* itself is also paraphyletic with respect to the genera *Terenura*, *Formicivora*, *Stymphalornis*, and *Myrmochanes*. Taxonomic implications within *Myrmotherula sensu stricto* will be discussed and published elsewhere (Bravo et al., unpubl. ms.).

BODY SIZE AND SHAPE DIVERSITY

The distribution of the *Myrmotherula* complex in size-uncorrected morphological space was predominantly associated with

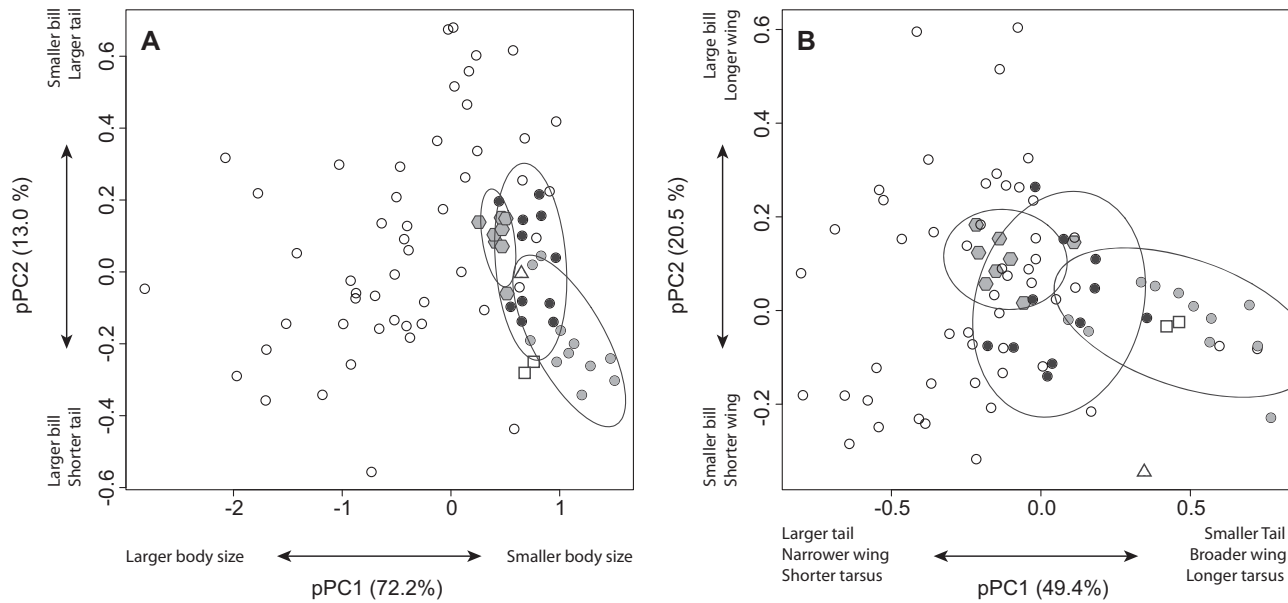


Figure 2. Size-uncorrected (A) and size-corrected (B) morphospace of the family Thamnophilidae showing that shape variation is greater than size variation among *Myrmotherula* complex plumage groups. Gray dots—streaked assemblage. Black dots—gray assemblage. Gray hexagons—stipple-throated assemblage. Hollow squares—*Iseria guttata* and *I. hauxwelli*. Hollow triangle—*Rhopias gularis*. Ellipses represent 95% confidence intervals.

Table 1. Factor loadings of ecomorphological variables in size-corrected and uncorrected phylogenetic principal component analyses.

| Morphological Trait | Size-Uncorrected Loadings | | | | Size-Corrected Loadings | | | |
|--|---------------------------|-------|-------|-------|-------------------------|-------|-------|-------|
| | pPC1 | pPC2 | pPC3 | pPC4 | pPC1 | pPC2 | pPC3 | pPC4 |
| Wing length to longest primary feather | -0.91 | -0.22 | -0.17 | 0.05 | -0.25 | 0.22 | -0.03 | -0.2 |
| Wing length to 10th primary feather | -0.86 | -0.33 | -0.2 | 0.03 | 0.06 | 0.27 | -0.1 | -0.13 |
| Wing length to first secondary feather | -0.93 | -0.17 | -0.17 | 0.01 | -0.42 | 0.19 | -0.1 | -0.07 |
| Tail maximum length | -0.82 | 0.51 | 0.19 | -0.15 | -0.96 | -0.01 | 0.21 | 0.14 |
| Central rectrix maximum width | -0.9 | 0.3 | -0.07 | 0.27 | -0.88 | -0.09 | -0.27 | -0.36 |
| Bill length | -0.77 | -0.42 | 0.13 | 0.19 | -0.04 | 0.7 | -0.32 | -0.21 |
| Bill width | -0.69 | -0.48 | 0.46 | -0.01 | -0.05 | 0.94 | 0.02 | 0.02 |
| Bill depth | -0.87 | -0.35 | 0.17 | -0.08 | -0.17 | 0.8 | 0.11 | 0.13 |
| Tarsus length | -0.87 | -0.02 | -0.3 | -0.23 | -0.44 | -0.11 | -0.51 | 0.55 |
| Hallux length | -0.84 | -0.17 | -0.36 | -0.2 | -0.2 | -0.03 | -0.69 | 0.55 |

The distribution of the *Myrmotherula* complex in size-uncorrected morphological space was predominantly associated with variation in body size, whereas its distribution after size-correction was explained primarily by variation in tail length, rectrix width, tarsus, and wing breadth.

variation in body size (pPC1 = 72.2%), whereas shape differences in tail and bill account for variation explained by pPC2 (13.0%; Fig. 2A; see Table 1 for variable loadings). pPC1 showed a significant inverse correlation with log-transformed body weight ($F_{1,81} = 941$, adjusted $R^2 = 0.92$, $P < 2.2 \times 10^{-16}$; Fig. S2). After ecomorphological space was size-corrected, the distribution was explained primarily by variation in tail length, rectrix width,

tarsus, and wing breadth (pPC1 = 49.4%; Fig. 2B; see Table 1 for variable loadings) and variation of bill dimensions was mainly associated with pPC2 (20.5%). Differences in ecomorphospace between size-corrected and size-uncorrected datasets suggest greater variation in body shape than in size, relative to other members of the Thamnophilidae (Fig. 2). The shape/size variance ratio for all thamnophilids in the analysis was 0.24, but the same

ratio for members of the *Myrmotherula* complex was 1.25. A permutation analysis showed that the former ratio is much lower than expected by chance alone ($P < 0.00001$, $\bar{x} = 1.25$, $SE = 0.001$), and that the latter ratio is higher than expected by chance alone ($P < 0.00001$, $\bar{x} = 1.22$, $SE = 0.002$).

ECOMORPHOLOGICAL DIVERSIFICATION OVER TIME

Body size disparity was primarily accumulated early in the history of the group among subclades (Fig. 3A; $MDI_{SIZE} = -0.19$), and the model that provided the best fit to the observed data was EB ($\alpha = -0.06$, $\omega_i = 0.97$, $\ln L = 48.01$, $AIC = -90.03$, ΔAIC of other models > 4). When models of body size evolution were tested exclusively on the Formicivorini, body size disparity was also concentrated primarily among subclades (Fig. 3B; $MDI_{SIZE} = -0.10$). OU ($\alpha = 0.05$, $\ln L = 33.45$, $AIC = -60.90$, $\omega_i = 0.83$), followed by BM ($\sigma^2 = 6.4 \times 10^{-4}$, $\ln L = 30.56$, $AIC = -57.12$, $\Delta AIC = 3.77$, $\omega_i = 0.13$) that provided the best fit for the observed pattern of body size evolution in the Formicivorini. Body shape disparity was also concentrated mainly among subclades both in the entire *Myrmotherula* complex and in the Formicivorini (Tables 2 and 3; Fig. 3B and 3D). However, a single model does not uniquely explain body shape evolution neither for the entire complex nor for the Formicivorini. All models were similarly informative to explain shape variation (Tables 2 and 3).

CONVERGENT EVOLUTION

SURFACE analyses support a scenario in which both body size and shape evolve around adaptive peaks at the family level. Sixteen shifts of regime were identified to occur. The most informative model included 10 independent adaptive regimes (k'), three of which appear after multiple shifts in independent branches (k'_{conv}) and are thus considered to exhibit true convergence ($\loglik_{size} = 94.75$, $\loglik_{pPC1} = 39.37$, $\loglik_{pPC2} = 66.04$, $\alpha_{size} = 3.62 \times 10^{-3}$, $\alpha_{pPC1} = 6.02 \times 10^{-2}$, $\alpha_{pPC2} = 1.2 \times 10^{-1}$, $\sigma^2_{size} = 3.42 \times 10^{-4}$, $\sigma^2_{pPC1} = 3.29 \times 10^{-3}$, $\sigma^2_{pPC2} = 3.09 \times 10^{-3}$, $AICc = -268.19$, $\omega_i = 0.91$). Information on other informative models can be found in Table 4. The three regimes exhibiting true convergence include all members of the *Myrmotherula* complex, as well as the genera *Formicivora*, *Terenura*, *Stymphalornis*, *Myrmochanes*, *Drymophila*, and *Herpsilochmus* (Fig. 4A). Inferred adaptive peaks of body size for the three convergent regimes are below observed values for all species, which suggests that, contrary to other members of the family, lineages in these clades are evolving toward smaller body sizes (Fig. 4B). These three regimes seem to be evolving toward diverging adaptive peaks in body shape, which suggest that members of the complex are drifting apart in tail, wing, and tarsus morphology (Fig. 4C). Although the fitted OU model might not reflect the biological reality in terms

of the magnitude of optimal phenotypes, especially for body size, it captures the tendency of different adaptive regimes to evolve in different directions. Observed true convergence, measured as the reduced number of regimes after accounting for convergence ($\Delta k = 6$), is significantly higher than the mean value resulting from the distribution of Δk from 500 datasets simulated under Brownian motion ($t = -34.34$, $P < 0.00001$, $\bar{x} = 3.54$, $SE = 0.07$). However, its value coincides with the 95% percentile of the distribution of Δk from the 500 simulated datasets (Fig. 4D). In other words, the degree of observed convergence was lower than random convergence approximately 5% of the times, but was significantly higher than the mean convergence level across Brownian motion simulated datasets.

ECOLOGICAL CORRELATES OF PHENOTYPIC EVOLUTION

Reconstruction of ancestral character states of habitat and foraging strata was most informative under a model of ERs, whereas a symmetrical model was most informative for MSF behavior (Fig. S3; Table S6). The ML ancestral state for habitat was tropical lowland evergreen forest (scaled likelihood = 94.1%), for foraging strata was understory (scaled likelihood = 79.3%), and for MSF behavior was occasional–common (scaled likelihood = 64.2%).

Results from phylogenetic MANOVAs on the phylogenetic size-corrected principal components of the ecomorphological variation showed associations between morphological characters and habitat (Fig. 5; $F_{4,27} = 3.79$, Wilks' $\lambda = 0.25$, $P < 0.001$), forest strata ($F_{2,29} = 7.14$, Wilks' $\lambda = 0.31$, $P < 0.0001$), and MSF behavior ($F_{2,29} = 14.34$, Wilks' $\lambda = 0.15$, $P < 0.0001$). Ecological variables predicted variation in body size. Species of open habitats were significantly larger than those of tropical lowland evergreen forests and seasonally flooded forests (Fig. 5; $F = 7.07$, $P = 0.012$). Likewise, species of tropical dry/white sand forests were significantly larger than those of seasonally flooded forests. Also, two body size groups were recovered based on foraging strata (Fig. 5; $F = 15.08$, $P = 0.02$): larger species forage in the understory, whereas species of the canopy are smaller. Midstory birds do not differ significantly from either canopy or understory birds. Species that do not join mixed-species flocks are significantly larger than those that are obligate mixed-flock members and those that join them occasionally ($F = 26.98$, $P = 0.002$). Regarding shape variation, species of open habitats and tropical dry/white sand forests have longer ($F = 6.26$, $P = 0.010$) and wider tails ($F = 6.98$, $P = 0.007$), longer tarsi ($F = 8.85$, $P = 0.003$), and longer halluces ($F = 8.59$, $P = 0.003$). Likewise, species that do not join mixed-species flocks have longer ($F = 13.62$, $P = 0.02$) and wider tails ($F = 13.31$, $P = 0.03$), longer tarsi ($F = 82.02$, $P = 0.001$), and longer halluces ($F = 21.92$,

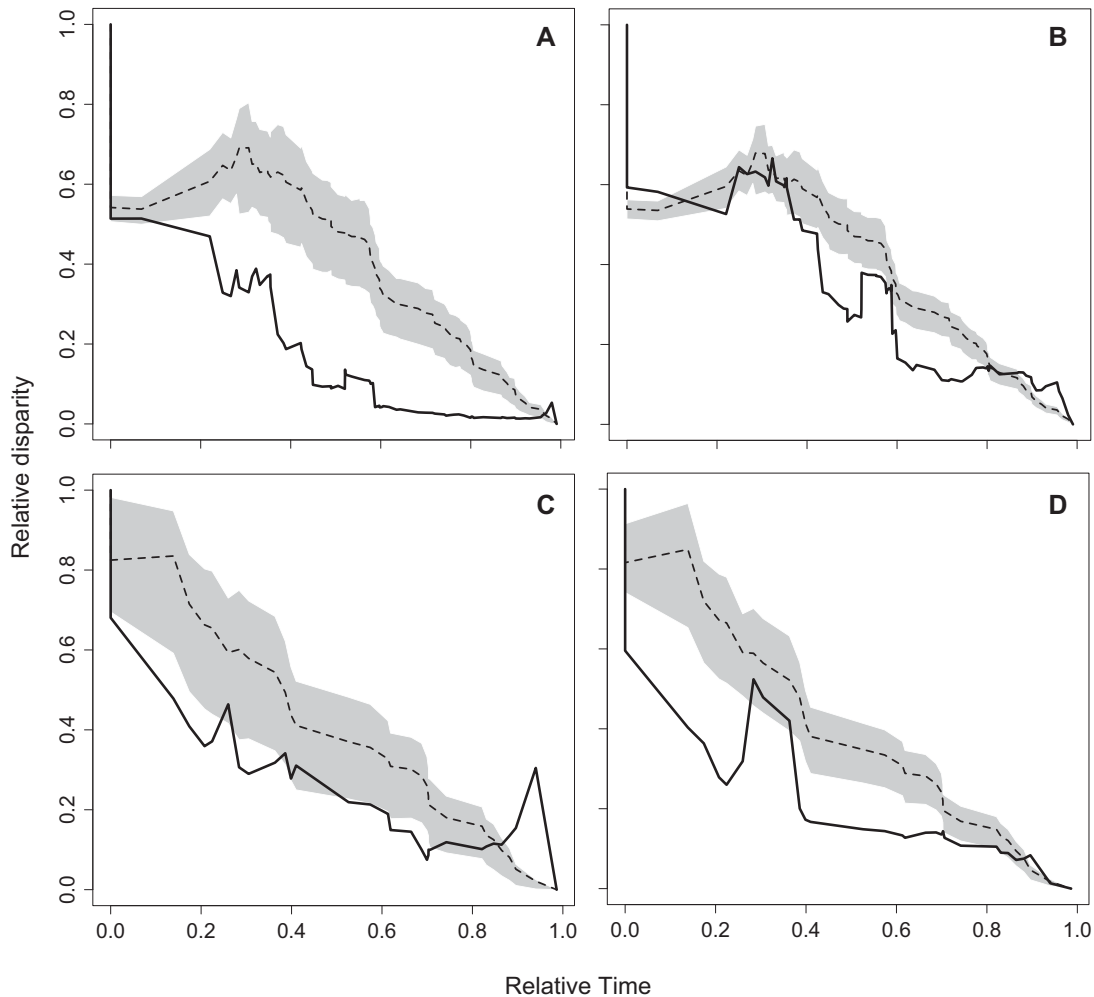


Figure 3. Disparity-through-time plots for size (A and C) and shape (B and D) for the complete *Myrmotherula* complex (top) and the Formicivorini (bottom). Relative to expectations under Brownian motion, size disparity was accumulated at a slower pace than shape disparity. Solid line represents observed disparity. Dashed line represents the mean of 999 Brownian motion simulations and gray area denotes distribution of simulations between 25 and 75% quartiles.

$P = 0.01$). Species that forage in the canopy have relatively shorter wings ($F = 19.26$, $P = 0.008$) and shorter secondary feathers ($F = 18.79$, $P = 0.01$) than do those species that forage in other forest strata.

Discussion

ECOMORPHOLOGICAL CONVERGENT EVOLUTION IN THE MYRMOTHERULA COMPLEX

The *Myrmotherula* complex consists of different distantly related clades that underwent ecomorphological convergent evolution. Relative to the ecomorphological variation observed in the Thamnophilidae, these clades are similar in body size, but different in body shape. Within clades, the evolution of body shape and size is bounded around phenotypic optima (i.e., PNC) that

are associated with habitat and microhabitat components. Phenotypic optima observed for different clades tend toward lower values of body size, but diverge in tail, tarsus, and wing shape. This is consistent with the idea that stabilizing selection within each clade might be responsible for generating divergent morphotypes among clades, but relatively cohesive morphotypes within clades. Also, it suggests that high levels of syntopy among members of different clades (e.g., Amazonia) are possible, despite their similar size, because they are excluding each other ecologically by using different resources (e.g., prey items, microhabitat). Therefore, this diverse complex of insectivorous birds has likely undergone adaptive processes similar to other ecologically diverse and species-rich groups (e.g., MacArthur and Levins 1967).

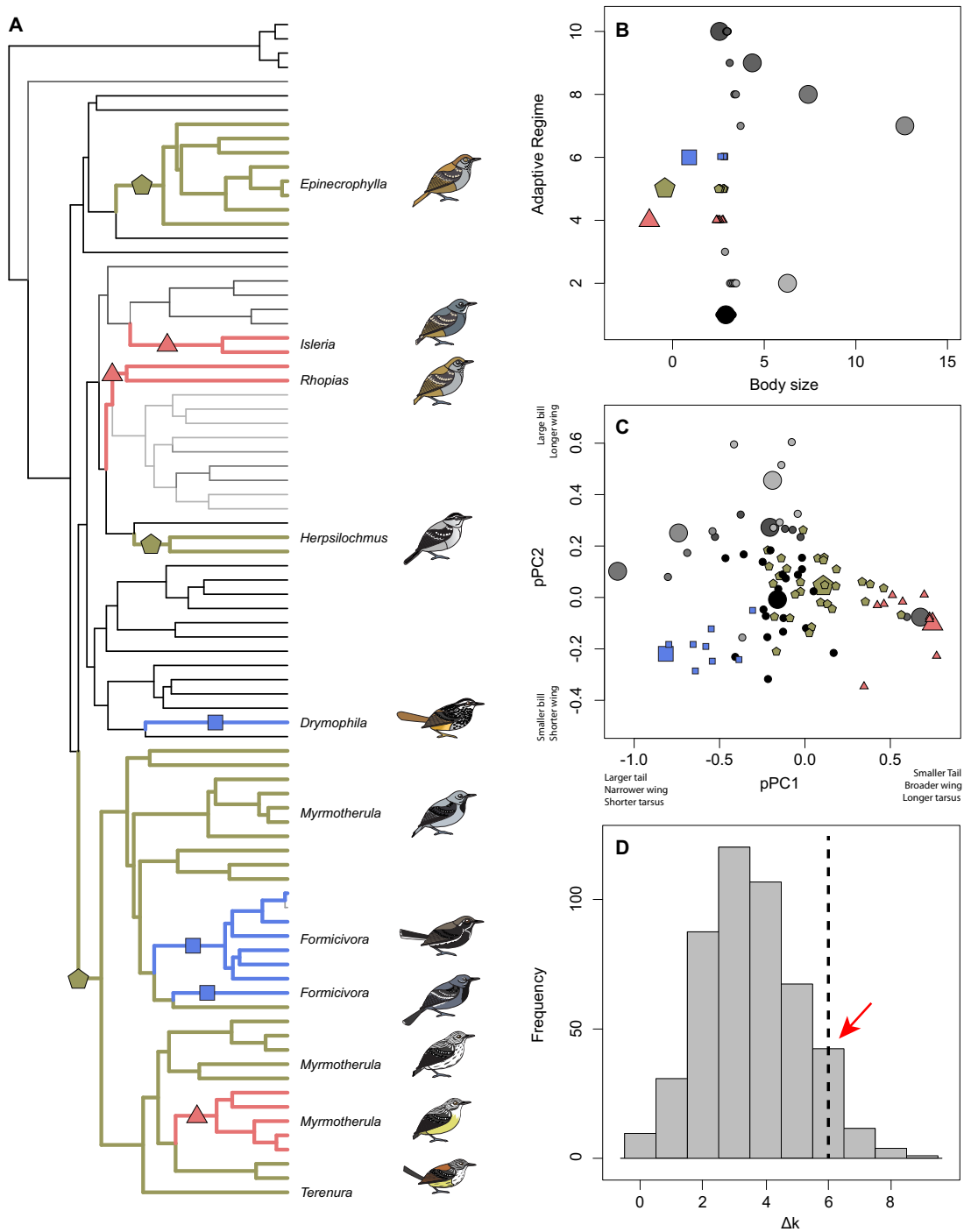


Figure 4. Convergent adaptive regimes of the *Myrmotherula* antwrens. (A) Relative time-measured phylogeny of the Thamnophilidae with adaptive regimes identified by SURFACE. Colored branches represent convergent adaptive regimes and gray or black branches denote nonconvergent regimes. Symbols on branches label the three convergent adaptive regimes that involve all members of the *Myrmotherula* complex and other morphologically similar antwrens (adaptive regime 4: red triangle; 5: green pentagon; 6: blue square). (B) Representation of how extant members of adaptive regimes (small symbols) tend toward adaptive optima of body size (large symbols). Convergent regimes tend toward small values of body size, whereas nonconvergent regimes tend toward larger body sizes (adaptive regime 4: red triangles; 5: green pentagons; 6: blue squares). (C) Size-corrected morphospace of the family Thamnophilidae showing that adaptive optima involving members of the *Myrmotherula* complex and other antwrens tend to diverge in tail, wing, and tarsus morphology. (D) Frequency distribution of levels of true convergence (Δk) resulting from 500 Brownian motion simulations. The observed pattern of convergence is greater than average expectations by chance alone. The black dashed line represents the 95% quantile and the red arrow represents the observed value of true convergence.

Table 2. Information theoretic statistics and ranking for each of the five models of character evolution evaluated for the five principal components of body shape for the entire phylogeny.

| Shape Trait | Model | Rank | lnL | ΔAIC | ω_i |
|--------------------|--|------|--------|-------|------------|
| pPC1 (MDI = -0.09) | BM ($\sigma^2 = 3.3 \times 10^{-3}$) | 1 | -0.82 | 0 | 0.55 |
| | EB ($r = -0.02$) | 2 | -0.60 | 1.55 | 0.25 |
| | OU ($\alpha = 1.4 \times 10^{-13}$) | 3 | -0.82 | 2.00 | 0.20 |
| | WN ($\sigma^2 = 0.13$) | 4 | -31.96 | 62.28 | 0 |
| pPC2 (MDI = 0.06) | OU ($\alpha = 0.02$) | 1 | 37.02 | 0 | 0.50 |
| | BM ($\sigma^2 = 1.3 \times 10^{-3}$) | 2 | 35.68 | 0.67 | 0.36 |
| | EB ($r = -1.3 \times 10^{-10}$) | 3 | 36.68 | 2.67 | 0.13 |
| | WN ($\sigma^2 = 0.04$) | 4 | 20.90 | 30.24 | 0 |
| pPC3 (MDI = -0.02) | OU ($\alpha = 7.9 \times 10^{-17}$) | 1 | 75.76 | 0 | 0.53 |
| | BM ($\sigma^2 = 5.3 \times 10^{-4}$) | 2 | 74.33 | 0.86 | 0.34 |
| | EB ($r = -3.0 \times 10^{-13}$) | 3 | 74.33 | 2.86 | 0.13 |
| | WN ($\sigma^2 = 0.01$) | 4 | 59.27 | 31.00 | 0 |
| pPC4 (MDI = 0.05) | OU ($\alpha = 0.03$) | 1 | 81.91 | 0 | 0.92 |
| | BM ($\sigma^2 = 4.9 \times 10^{-4}$) | 2 | 78.09 | 5.64 | 0.06 |
| | EB ($r = -8.6 \times 10^{-12}$) | 3 | 78.09 | 7.64 | 0.02 |
| | WN ($\sigma^2 = 0.01$) | 4 | 72.81 | 16.20 | 0 |

BM, Brownian motion; OU, Ornstein-Uhlenbeck; EB, early burst; WN, white noise. Statistics provided are ΔAIC value, and Akaike weight (ω_i). Morphological disparity index (MDI) is also provided for each component.

Table 3. Information theoretic statistics and ranking for each of the five models of character evolution evaluated for the three principal components of body shape in the formicivorini.

| Shape Trait | Model | Rank | lnL | ΔAIC | ω_i |
|--------------------|--|------|--------|-------|------------|
| pPC1 (MDI = -0.20) | BM ($\sigma^2 = 3.6 \times 10^{-3}$) | 1 | 2.80 | 0 | 0.44 |
| | EB ($r = -0.06$) | 2 | 3.68 | 0.26 | 0.39 |
| | OU ($\alpha = 1.9 \times 10^{-12}$) | 3 | 2.80 | 2.00 | 0.16 |
| | WN ($\sigma^2 = 0.19$) | 4 | -18.75 | 43.11 | 0.0 |
| pPC2 (MDI = 0.23) | WN ($\sigma^2 = 0.01$) | 1 | 25.14 | 0 | 0.57 |
| | OU ($\alpha = 0.58$) | 2 | 25.85 | 0.57 | 0.43 |
| | BM ($\sigma^2 = 1.3 \times 10^{-3}$) | 3 | 18.85 | 12.58 | 0.00 |
| | EB ($r = -1.4 \times 10^{-10}$) | 4 | 18.85 | 14.58 | 0.00 |
| pPC3 (MDI = -0.08) | BM ($\sigma^2 = 5.6 \times 10^{-4}$) | 1 | 32.62 | 0 | 0.46 |
| | OU ($\alpha = 2.3 \times 10^{-17}$) | 2 | 33.37 | 0.49 | 0.36 |
| | EB ($r = -9.7 \times 10^{-12}$) | 3 | 32.62 | 2.00 | 0.17 |
| | WN ($\sigma^2 = 0.01$) | 4 | 22.12 | 21.00 | 0.00 |

BM, Brownian motion; OU, Ornstein-Uhlenbeck; EB, early burst; WN, white noise. Statistics provided are ΔAIC value, and Akaike weight (ω_i). Morphological disparity index (MDI) is also provided for each component.

EVOLUTION OF BODY SIZE VERSUS EVOLUTION OF BODY SHAPE IN THE MYRMOTHERULA COMPLEX

The relative contribution of body size variation in the *Myrmotherula* complex is considerably lower than that of shape variation (Fig. 2). That the shape/size variation ratio is greater within the *Myrmotherula* complex than across a larger sample of species encompassing the entire ecomorphospace occupied by the family Thamnophilidae suggests either that phenotypic similarities among the disparate *Myrmotherula* clades reflect evolutionary constraints on body size, but not shape, or that body size

variation is greater than body shape variation when quantified for all Thamnophilidae (Claramunt 2010). Despite methodological differences between our calculations for the *Myrmotherula* complex and those for the entire family (Claramunt 2010), these contrasting but complementary patterns likely reflect scale-dependent processes that operate differentially across stages of the diversification process. The pattern described for the entire family results in greater variance in body size because it represents the outcome of several evolutionary processes acting on more lineages at various phylogenetic, spatial, and temporal scales, whereas the pattern

Table 4. Information theoretic statistics and ranking for each of the “backward” phase SURFACE models evaluating the number of shifts and adaptive regimes in the thamnophilidae.

| Rank | k' | Δk | k'_{conv} | AICc | ΔAICc | ω_i |
|------|------|------------|--------------------|---------|---------------------|------------|
| 1 | 10 | 6 | 3 | -268.19 | 0 | 0.91 |
| 2 | 12 | 4 | 3 | -263.52 | 4.67 | 0.09 |
| 3 | 13 | 3 | 2 | -255.79 | 12.40 | 0 |
| 4 | 16 | 0 | 0 | -227.74 | 40.45 | 0 |

Statistics provided are number of distinct regimes (k'), reduced number of regimes after accounting for convergence (Δk), number of convergent regimes reached by multiple shifts (k'_{conv}), corrected AIC (AICc), ΔAICc value, and Akaike weight (ω_i).

described for the *Myrmotherula* complex reflects the outcome of evolutionary processes acting on more constrained scales and on a relatively similar group ecologically and behaviorally.

EVOLUTION OF BODY SIZE IN THE MYRMOTHERULA COMPLEX

Body size evolution in the *Myrmotherula* complex is inconsistent with a heterogeneous Brownian motion process (i.e., diffusive drift), and has not evolved under a constant rate over time. Observed patterns of body size evolution are consistent with a time-dependent model of fluctuating selection of decreased fluctuation rates among adaptive peaks over time (Revell et al. 2008). In other words, body size evolution in the *Myrmotherula* complex fits a model in which a highly variable environment in space and time offers multiple adaptive peaks that cause fluctuations in the intensity and directionality of selection over time, ultimately leading to changes in body size (Estes and Arnold 2007; Labra et al. 2009; Bell 2010; Uyeda et al. 2011) and phenotypic convergence among distantly related groups. Under this scenario, higher rates of accumulation of body size disparity followed by a decrease in the rate of size evolution are consistent with a decrease in the rate of change among adaptive peaks (i.e., ecological opportunities hypothesis; Ricklefs 2006; Harmon et al. 2010; Mahler et al. 2010) that results in bounded evolution around optimal values (Simpson 1944).

Whether the observed adaptive pattern leading to convergence is the result of selective processes acting directly on body size remains to be explored further. Convergence is not necessarily the result of adaptation (Revell et al. 2007b). As reviewed by Losos (2011), it can be the result of coincidence, adaptation, exaptation, or a correlated response to selection on another character. In some terrestrial vertebrate groups, it has been suggested that convergent evolution is primarily observed in body shape as a result of adaptation in allopatry mediated by ecological factors such as energetics, locomotion, perch location and structure, and food item size (e.g., Grant et al. 2004; Harmon et al. 2005; Wiens

et al. 2006). However, if body size strongly influences resource use, strong stabilizing selection around optimal values of size might have resulted in all coexisting and potentially competing members of the *Myrmotherula* complex to have a similar size (i.e., phenotypic clustering; Gómez et al. 2010), but to differ in other phenotypic traits. This has been proposed as a potential mechanism to explain phenotypic similarity in species-rich communities (Scheffer and van Ness 2006), and it has been described in a group of broadly sympatric North American salamanders (Kozak et al. 2009), cichlid fishes in Africa (Muschik et al. 2012), aquatic beetles, and prairie birds (reviewed by Scheffer and van Ness 2006). If distantly related groups of the complex originated in allopatry and selection acts directly on body size, convergent evolution in body size would be the result of adaptation (e.g., Harmon et al. 2005; Aliabadian et al. 2012; McGee and Wainwright 2013). In contrast, if those clades originated in the same geographic areas exhibiting similar high levels of sympatry and syntopy as they do today, then it would be likely that body size is not the main subject of natural selection and that convergence would be the result of exaptation or correlated response to selection on other phenotypic traits (e.g., Poe et al. 2007).

ECOLOGICAL CORRELATES OF BODY SIZE EVOLUTION IN THE MYRMOTHERULA COMPLEX

Associations among some ecomorphological and ecological traits of the Formicivorini provide further evidence that body size evolution revolves around adaptive peaks. Although our analyses lack power to detect causation between ecological attributes and variation of body size or to pinpoint specific ecological attributes triggering variations in body size, they showed that larger species are associated with tropical dry forests and open habitats, and with lower foraging strata. Reconstruction of ancestral states showed that habitat and foraging strata diverged among clades early in history, supporting the idea that changes in body size coincided with changes in habitat and foraging strata. In reality, a combination of various ecological and environmental factors not directly assessed in our analyses is likely to influence these evolutionary associations between body size and habitat attributes. Differential effects of these factors along with stochastic processes would partially explain the observed variation in body size among species in those adaptive regimes converging toward smaller body sizes. For instance, higher seasonality (e.g., Murphy 1985) and aridity (e.g., Hamilton 1958) might favor increased body size, and higher humidity favors smaller body size (e.g., Hamilton 1958). Differences in vegetation density and microhabitat structure might provide an explanation for differences correlated with foraging strata. A correlation between vertical vegetation density and the intensity of foraging activity causes smaller species to forage in denser vegetation located in higher strata, whereas larger species make use of less dense vegetation of lower strata (e.g., Pearson 1971;

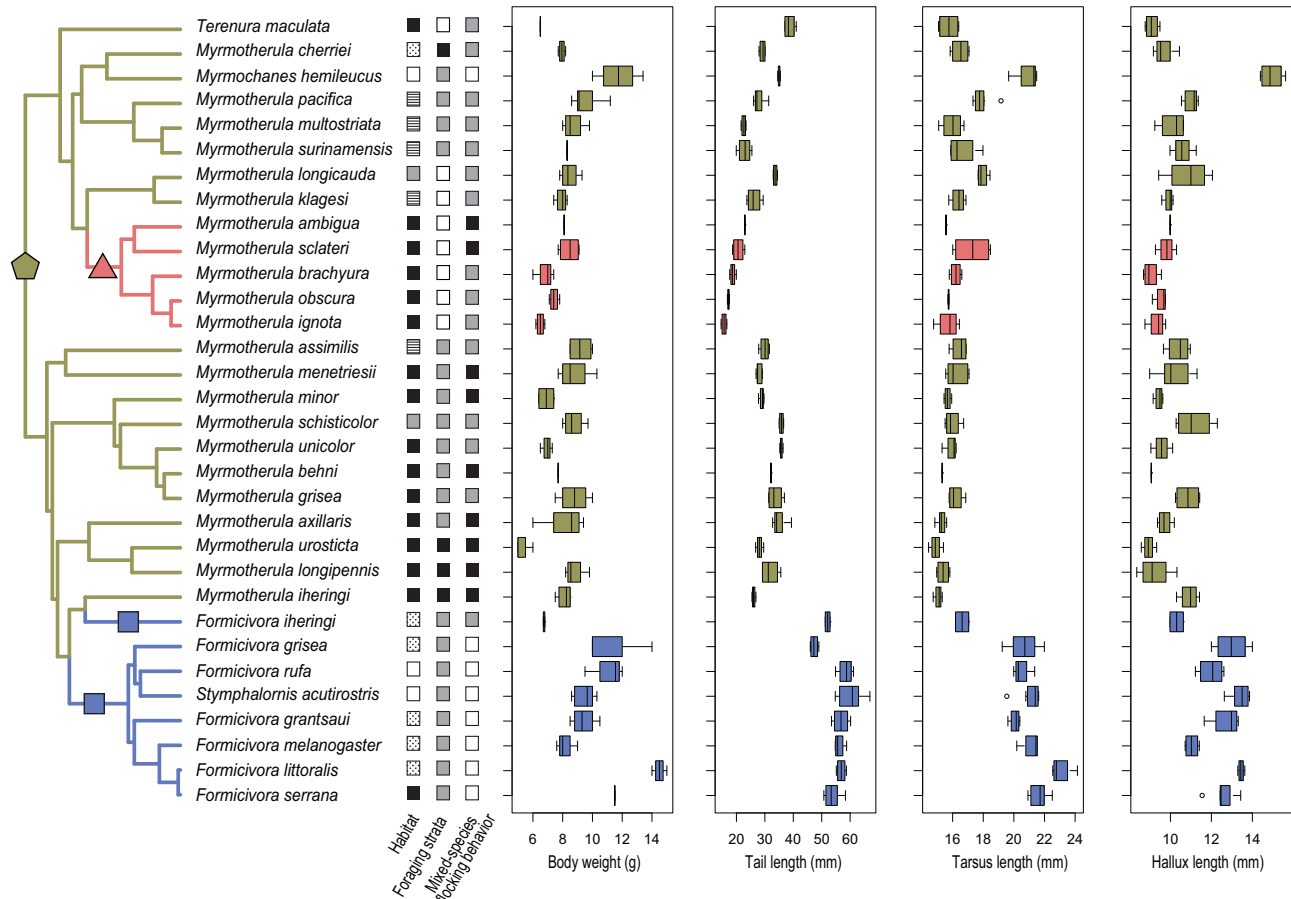


Figure 5. Mapping of ecological and morphological character states onto the relative time-measured phylogeny of the Formicivorini. Colors and symbols on branches denote the three convergent adaptive regimes identified in the tribe (adaptive regime 4: red triangles; 5: green pentagons; 6: blue squares). (1) Habitat: tropical lowland evergreen forest (black), seasonally flooded forest/gallery forest (horizontal lines), montane evergreen forest (gray), tropical dry/white sand forest (dots), open habitats (white). (2) Foraging strata: understory (black), midstory (gray), canopy (white). (3) MSF behavior: no MSF (white), occasional MSF (gray), obligate MSF (black).

Greenberg 1979; Stotz 1990). Physical constraints conferred by larger size impede the movement in restricted spaces and the use of smaller branches (Greenberg 1979). However, other potential correlates, such as productivity, microhabitat structure, and interspecific competition might also provide mechanistic explanations of these associations (e.g., Pearson 1977; Stotz 1990; Greve et al. 2008; Olson et al. 2009) and should be further explored, especially in tropical birds.

EVOLUTION OF BODY SHAPE IN THE MYRMOTHERULA COMPLEX

Shape evolution is not responding solely to any single mechanism, but represents a mosaic of different adaptive and nonadaptive processes acting differently on various components of ecomorphospace. Because the intensity of selective pressures differs across ecomorphospace (e.g., Losos 1990; Kozak et al. 2005), and some traits are known to evolve as a consequence of selec-

tive pressures on other traits (e.g., Grant and Grant 2002; Irschick et al. 2008), such a noisy pattern was expected. Differences in tail, tarsus, and the first secondary feather were accumulated earlier in history, whereas differences in other traits were concentrated in the recent history of the group.

In the Formicivorini, high rates of disparity accumulation early in history, high phylogenetic signal with phenotypic change concentrated toward the base of the tree, make the evolution of tail and tarsus consistent with a process of adaptive radiation. Moreover, simulations of two time-dependent models (genetic drift and decreased fluctuation rates among adaptive peaks Revell et al. 2008) are in accordance with the information obtained for the evolution of tail and tarsus. Bill evolution was best explained by models in which character evolution revolves around near constant well-differentiated adaptive peaks that carry low phylogenetic signal, suggesting that bill shape might be highly tied to specific ecological conditions and that the amount of change

in bill shape is almost equally distributed throughout the clade (i.e., functional constraints; Revell et al. 2008). This represents an expected pattern because bill morphology in passerine birds has been regarded as highly labile with low phylogenetic signal (Remsen 2003). Wing and hallux evolution is consistent with true Brownian motion evolution or constant stabilizing selection with weak selective pressures (Revell et al. 2008).

ECOLOGICAL CORRELATES OF BODY SHAPE EVOLUTION IN THE *MYRMOTHERULA* COMPLEX

Evolution of shape in the *Myrmotherula* complex can be partially explained by habitat, foraging strata, and mixed-flocking behavior associations. Differentiation of habitat and foraging strata occurred early in history in concert with changes in the principal components of ecomorphological variation, and a statistical association was found between tail, tarsus, and hallux and specific ecological traits. Such ecological associations have been shown not only to drive phenotypic diversification, but also to explain convergent patterns of morphological evolution in other groups (Losos 1990; Blackledge and Gillespie 2004; Aliabadian et al. 2012; Edwards et al. 2012; Lindgren et al. 2012; Muschick et al. 2012; Nyakatura 2012; Schelumpberger and Renner 2012). Previous work based on quantitative characterization of ecology and foraging behavior found that associations between tail, feet, and tarsal morphology can be explained by mechanical and physiological adaptations in specific conditions (e.g., Pearson 1977; Fitzpatrick 1985; Stotz 1990; Price 1991; Rosenberg 1993). If such constraints on performance ultimately affect individuals' fitness, then these associations likely have evolved as a consequence of varying selective pressures toward specific adaptive peaks combined with other processes such as drift.

Here, we have shown that examination of size and shape evolution in the *Myrmotherula* complex is consistent with adaptive processes. Body size in the group represents a convergent trait among distantly related clades in the *Thamnophilidae* that biased previous taxonomic and ecological work into recognizing *Myrmotherula* as a natural and taxonomic unit. Optimum body size values are associated with specific habitats and foraging forest strata that have likely contributed to a convergent evolution pattern among these clades. Shape variation in the complex is greater than previously acknowledged and is far from showing high levels of phenotypic similarity. For some specific traits, such as tail, tarsus, and hallux, it is likely that selective pressures have contributed to distinct morphologies suitable for different environmental conditions, therefore enabling co-existence and high levels of syntopy at local spatial scales (Gómez et al. 2010). Further, quantitative data on habitat use and foraging behavior (sensu Remsen and Robinson 1990; Stotz 1990) will allow a clearer understanding of the adaptive basis of ecomorphological traits.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Taxa and sequences used in this study with tissue collection voucher number.

Table S2. Partitioning strategies evaluated to construct the phylogenetic hypotheses of the *Myrmotherula* complex.

Table S3. Substitution model selected by mrmmodeltest for each of the 16 partitions included in the most informative partition strategy.

Table S4. List of voucher study specimens examined and measured for ecomorphological analyses of the *Myrmotherula* complex.

Table S5. Foraging strata, habitat, and mixed-flocking behavior categorization of the species in the formicivorini.

Table S6. Information theoretic statistics and ranking for each of the three models of habitats, foraging strata, and mixed-flocking behavior change evaluated in the formicivorini clade.

Figure S1. Fifty percent majority-rule Bayesian topology of a subset of the Thamnophilidae showing phylogenetic relationships of the *Myrmotherula* complex.

Figure S2. Correlations between pPCs and log-transformed body weight.

Figure S3. Ancestral reconstruction of habitat (top left), foraging strata (top right), and mixed-species foraging behavior (bottom).