

**Foraging niche structure and coexistence in a highly diverse community of
Amazonian antbirds (Thamnophilidae: Aves)**

by

SANTIAGO DAVID

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Abstract

The high species richness of antbirds (Thamnophilidae) in Amazonian lowlands, where as many as 40 species may coexist at local scales, represents a major challenge for ecologists to explain patterns of coexistence and niche evolution. I studied the foraging ecology of a local community of antbirds in a 2-Km² area of lowland forest in SE Peru to examine how co-occurring antbird species differ in their use of foraging resources, and whether these differences result in niche partitioning at the community level. I also examined whether resource use similarity was related to phylogenetic similarity in this local assemblage. Forty-four species of antbirds were detected in the study plot in a four-year period, with 30 species categorized as the local assemblage of common resident breeders. Multivariate analysis of foraging parameters showed that segregation at two height layers in two types of forest was more important than foraging substrates and maneuvers in explaining the differences observed in foraging behavior. However, a null model analysis revealed that at the community level, antbirds exhibited high foraging niche overlap, with average observed overlap significantly larger than expected by chance, indicating that antbirds prefer, rather than avoid, resources used by other species. No general relationship exists between phylogenetic similarity and niche overlap. Closely related species consistently exhibit high values of niche overlap, but some distantly related species also exhibit high niche similarity. Taken together, these results suggest that foraging niche similarity is the predominant pattern among co-occurring antbirds, and that positive interactions might explain the stable coexistence of species that use similar resources and habitats at a local scale.

Preface

Research questions and project design were carried out collaboratively between my supervisor, Dr. Jill Jankowski, and me. I carried out the fieldwork for collecting foraging information. Dr. Gustavo Londoño and Dr. Jill Jankowski provided data on mist-netting captures, point counts and nest surveys to define the species assemblage, from the Manu Bird Project. Phylogenetic data was obtained from published literature. I conducted all analyses and writing of this thesis. Dr. Jankowski provided helpful feedback on interpretation of results and thesis preparation.

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A Paulina, Kelly y Sofia, los pilares de mi vida

Chapter 1: Introduction

1.1 Species diversity in tropical bird communities

Bird species richness reaches its peak in tropical South America with the highest richness found anywhere in the world occurring in the Amazon basin and the eastern Andes (Hawkins et al. 2007). This region possesses an exceptional diversity of birds both in terms of species in the region as a whole and species coexisting in any given point (Pearson 1977, Terborgh et al. 1984). Extensive field observations in Manu National Park, SE Peru revealed that 245 species are resident territory holders on a 97-ha forest plot, with single point (alpha) diversity exceeding 160 species with overlapping territories in portions of the plot (Terborgh et al. 1990). These numbers attest to the extraordinary diversity of Amazonian lowland bird communities at local scales.

Diversification and coexistence in tropical birds is influenced by historical and geographical circumstances as well as by contemporary and local ecological factors (Ricklefs and Schluter 1993). Recent work has shown that both neutral and tradeoff-based processes contribute to community assembly in plants (e.g. Tilman 2004, Weiher et al. 2011); however, in some animal systems, it is clear that deterministic factors, such as competition and niche partitioning, structure species assemblages (e.g. Pimm et al. 1985, Graves and Gotelli 1993, Jankowski et al. 2010). In particular, tropical bird communities can be shaped by interspecific competition, facilitated by factors such as low dispersal, narrow and specialized niches, and large number of co-occurring congeners at local scales (Robinson and Terborgh 1995, Tobias and Seddon 2009, Jankowski et al. 2012). However, the extent to which interspecific competition and

species-level differences in ecological strategy influence the structure of highly diverse tropical bird communities remains controversial.

In comparison with temperate regions, higher species-packing and finer niche-partitioning in resources and habitat in the tropics are proposed as explanations for the high alpha diversity observed (MacArthur 1969, Marra and Remsen 1997). Within tropical assemblages, alpha diversity is heavily influenced by year-round availability of resources such as fruits (Orians 1969), or large insects (Schoener 1971), and also by other resources and habitats particularly common in the tropics, including river-generated habitats (Remsen and Parker 1983), bamboo thickets (Cockle and Areta 2013), and foraging substrates such as suspended dead leaves (Rosenberg 1997) or army ants (Willis and Oniki 1978, Willson 2004). Thus, detailed ecological data on resource and habitat partitioning is required to understand the organization and high alpha diversity observed in tropical bird communities; however, basic natural history information of species niches is virtually unavailable for many tropical birds.

1.2 Species coexistence and evolution of ecological traits

The alpha (α) niche refers to the region of the realized niche of a species corresponding to species diversity at the local community (or alpha diversity) scale at which interactions among species occur (Silvertown 2004). According to most theories of coexistence, species must differ in their ecological niches for coexistence to be possible, with a high degree of niche overlap leading to competitive exclusion (Chesson 2000, Silvertown 2004). Furthermore, ecological traits associated with alpha (α) niches are generally susceptible to the processes of evolution, and

are hypothesized to be evolutionary labile to promote stable coexistence (Silvertown et al. 2006). Co-occurring closely related species should be more ecologically similar than distantly related ones, if these ecological traits change slowly through evolutionary time (Wiens et al. 2010). Alternatively, there should be no or very little correlation between ecological similarity and phylogenetic distance if niches are highly labile through evolutionary time (Fowler et al. 2014). Thus, incorporation of phylogenetic approaches allows a better understanding of the evolution of ecological traits that determine species coexistence.

1.3 Antbirds (Thamnophilidae) as a complex case of coexistence

Among tropical bird groups, one of the most diverse and distinctive families within lowland bird communities is the Antbird (Thamnophilidae) family. This Neotropical radiation comprises ~ 230 species occurring mostly in the Amazonian lowlands. Antbirds are insectivorous birds that vary substantially in body size, plumage, vocalization, social system, habitat use, and nesting and foraging behavior (Terborgh et al. 1990, Zimmer and Isler 2003). Nevertheless, antbirds share a common tendency to maintain territories year-round, most species are sexually dimorphic and socially monogamous and they reside in forest rather than open areas (Zimmer and Isler 2003, Stutchbury et al. 2005, Tobias et al. 2011).

One of the most intriguing features of this Neotropical family is its high species richness in Amazonian lowlands, where as many as 40 species may co-occur (Terborgh et al. 1990, Zimmer and Isler 2003, Blake 2007). Such a high degree of sympatry of bird species within the same family represents a challenge to explain patterns of coexistence and niche evolution.

Although some of the earliest studies on foraging behavior in sympatric antbirds showed evidence of segregation and resource partitioning among closely related species in α niche traits, such as foraging height (Pearson 1977, Powell 1989), use of foraging maneuver (Schulenberg 1983, Rosenberg 1997) and foraging substrate (Remsen and Parker 1984, Rosenberg 1993), there is no comprehensive analysis addressing the coexistence of so many species of antbirds in a local community. In part this is due to a lack of detailed ecological and behavioral information about foraging and resource use for most species. Rather, previous analysis of resource partitioning within this family compared species using a traditional classification based on plumage and morphological features (Cory and Hellmayr 1924, Peters 1951). Recent acoustic and molecular phylogenetic analyses have provided new insights into the evolutionary relationships and diversification within *Thamnophilidae*, with numerous taxonomic consequences (Irestedt et al. 2004, Moyle et al. 2009, Bravo et al. 2012). This provides an opportunity to integrate new detailed ecological data and phylogenetic information to reappraise the assembly of these highly diverse communities.

1.4 Study goals and questions

In this study I explore how antbird species differ in their use of foraging resources within a local community, how these differences potentially contribute to species coexistence and whether the amount of niche overlap within a local community is related to phylogenetic similarity among species. First, I use an extensive survey dataset that includes mist netting, point counts, and nest searches collected from 2011 to 2014 to define the community of antbirds in the study area and identify the assemblage of potentially interacting species. Second, using

ecological data collected from 30 resident species of antbirds in this local assemblage, I quantify foraging patterns among co-occurring antbirds and apply multivariate analysis to identify the principal axes of differentiation in foraging ecology. I also calculate the amount of niche overlap in resource use among coexisting antbirds to detect whether niche partitioning resulting from competition pressure is a predominant pattern in the local assemblage. I build a resource utilization matrix to calculate the average observed niche overlap and use a null model approach to determine whether such observed niche overlap is in fact the result of interspecific interactions or random expectation in the absence of species interactions. I conclude by testing whether the resource utilization niche and amount of niche overlap among species pairs is related to phylogenetic similarity among species.

Chapter 2: Foraging patterns and resource partitioning in a community of antbirds

2.1 Introduction

A major challenge to community ecologists is understanding the factors that maintain the high alpha diversity, or the number of species observed, in some communities at small spatial scales. Several lines of evidence have shown that niche differentiation is necessary for ecologically similar species to coexist in a habitat (MacArthur and Levins 1964, Levine and HilleRisLambers 2009), with differences in microhabitat, diet and temporal activity among the most important resource axes involved in reducing niche overlap (Schoener 1974). In birds, foraging specialization has been associated with coexistence of ecologically similar species in diverse tropical families such as flycatchers (Tyrannidae, Sherry 1984, Botero-Delgado 2011), tanagers (Thraupidae, Naoki 2007), hummingbirds (Trochilidae, Feinsinger 1976), and swifts (Apodidae, Collins 2015). Detailed observations of habitat use and foraging behavior have been useful to quantify the degree of niche overlap among co-occurring species, which in turn allows us to ask whether niches overlap more or less than expected in the absence of competition (Naoki 2007, Gotelli et al. 2010).

With the rapidly increasing number of phylogenetic studies and recent advances in comparative phylogenetic methods, it is possible to explore not only patterns of niche partitioning, but also, the role of evolution in structuring local communities. For example, one

might ask whether traits related to within-community niche differences (α niche) evolve conservatively. In other words, it is possible to estimate the degree of phylogenetic signal in the niche structure of local communities (Ackerly et al. 2006, Silvertown et al. 2006). Several studies have explored the extent to which niche similarity is a function of phylogenetic similarity by focusing on environmental (climatic) species' niches (Knouft et al. 2006, Warren et al. 2008, Kozak and Wiens 2010), however these traits are most likely influencing species assemblages at regional rather than local scales. At the more local scale, spatial foraging niches have been useful to investigate the correlation of ecological and phylogenetic similarity, with evidence for both conservatism and lability in different niche axes (Richman and Price 1992, Losos et al. 2003, Lovette and Hochachka 2006). Similarly, field experiments have been conducted by quantifying niche use and strength of species' interactions in communities of ants and plants (Burns and Strauss 2011, Fowler et al. 2014), in both cases by testing the assumptions that closely related species are more ecologically similar, but these experimental approaches are hard to implement in other animal systems, such as birds.

Among tropical birds, one of the most distinctive examples of high alpha diversity within local communities is the Antbird family (Thamnophilidae) in Amazonian lowland rainforest, where as many as 40 species can be found coexisting in areas of relatively small size (~ 100 ha; Terborgh et al. 1990, Zimmer and Isler 2003, Blake 2007). In these plots, some antbirds can attain high densities, and groups of ecologically similar species are frequently found interacting in the same habitat (Stotz 1990, Zimmer and Isler 2003). Gómez and collaborators (2010) used morphological, vocal and macroecological traits to explore the phylogenetic and phenotypic structure (i.e. similarity in songs, ecology and morphology among coexisting species) of antbird assemblages at different spatial scales. At the smallest scale (i.e. mixed species flocks), antbird

assemblages were composed of closely related species that did not exhibit significant phenotypic structure, whereas at intermediate scales (~100 ha plots), no significant phylogenetic or phenotypic structure was detected, suggesting that competitive interactions might not play a role in structuring antbird assemblages at local scales. Co-occurring antbirds usually vary in traits that include foraging height, foraging substrate, foraging maneuver and microhabitat (Schulenberg 1983, Powell 1989, Rosenberg 1993, 1997, Marra and Remsen 1997), and there is strong evidence of aggressive interactions between closely related antbirds with contiguous, non-overlapping territories (Robinson and Terborgh 1995), advocating a pattern of within-community niche partitioning on foraging traits. Despite being a signature bird family of Amazonian forests, only a few antbird species have been studied intensively and the basic natural history of many species is poorly known (Zimmer and Isler 2003).

In this chapter, I explore foraging patterns to determine how microhabitat and resource use may differ among antbirds at a local scale, and whether these differences potentially contribute to species coexistence. I then incorporate the results of these analyses with information on phylogenetic relationships within *Thamnophilidae* to examine patterns of niche evolution within antbird communities. First, I identify a local assemblage of potentially interacting species by combining detections with multiple survey methods. I describe major foraging differences of species within this assemblage and ask if these differences result in niche partitioning at the community level. I build a resource utilization matrix to calculate the average observed niche overlap and use a null model approach to determine whether such observed niche overlap is the result of interspecific interactions or random expectation in the absence of species interaction. I expect that if niche partitioning resulting from competition pressure is a predominant pattern in local assemblages, then overall niche overlap observed in the community

should be less than expected if species use resources randomly. I also examine the evolution of foraging niches in this local assemblage to ask whether the amount of niche overlap among species pairs was related to the phylogenetic similarity among species. If foraging niches are evolutionarily conserved, then I expect niche overlap (similarity) to be negatively related to phylogenetic relatedness. If, on the other hand, foraging niches are evolutionarily labile, then there should be no correlation between ecological similarity and phylogenetic distance among species.

2.2 Methods

2.2.1 Study Site

I conducted fieldwork in August to October of 2013 and 2014 in a 2 km² area of lowland forest (350-400 m asl) at Pantiacolla Lodge, Madre de Dios, Peru (12° 38' 31.3'' S, 71° 14' 21.2'' W). The station is located in Amazonian lowland rainforest in the buffer zone of Manu National Park. Vegetation in the area consists of a mosaic of contiguous Amazonian habitats including *terra firme* forest, which transitions into seasonal flood plain forest with areas of successional forest dominated by *Cecropia* trees, small patches of bamboo (*Guadua spp.*) and *Tessaria* scrub. Monthly average temperature is 23.1 ± 2.5 °C (min-max = 13.6 to 39.1 °C) with a rainy season from October to April and a dry season from May to August (Rapp 2010).

2.2.2 Local community of antbirds

Data collected from 2011 to 2014 in the study plot, using three complementary methods, were compiled to identify all antbird species present. These included mist-netting, point counts and nest surveys and were supplemented with foraging observations collected between 2013 and 2014. Mist-netting was conducted from 2011 to 2014 using ten nets (12 x 3 m, 34 mm mesh) per site. Twelve mist-netting sites were placed in the plot during the breeding season (August–November) for three consecutive days from approximately 0600–1600 hrs during suitable weather conditions. These 12 sites were visited twice each year for a total of six days of mist-netting per site. Point counts were conducted in 2011 and 2012 and consisted of 10-minute surveys, along 20-point transects in two separate transects (10 points per transect), following two principal foot trails in the plot. Each point count was separated by > 130 m and were conducted from 0500-0800 during the beginning of the breeding season (August-September) when the majority of antbirds are most easily detected by song (Jankowski et al. 2013). Nest surveys were conducted daily from 2011 to 2014 during the breeding season (August-December). Nests were monitored and identified using a motion camera trap (Reconyx PC-800; <http://www.reconyx.com>) focused on each nest at a distance of at least 1.0 m. The camera was programmed to take one photo every minute and ten photos when any movement occurred at the nest.

Although each of these methods has its own detection biases (e.g. mist-netting data, *see* Remsen and Good 1996), combining all information collected over the four year period should provide a more comprehensive view of the antbirds species present in the plot, their relative rarity and their potential to interact with other species.

2.2.3 Foraging data

I collected information on ecological traits related to important resources that are generally partitioned among sympatric antbirds. These included foraging height, foraging substrate, foraging maneuver and habitat (Robinson and Terborgh 1995, Marra and Remsen 1997). Foraging observations were made throughout the day, but mostly between 0530-1130 and 1600-1730 hrs between August and October of 2013 and 2014. I located birds by sight and sound and observed individuals using 10-40x binoculars. I quantified the behavior of adult birds that were actively foraging and not involved in other activities that might affect foraging estimates, such as territory defense or mating (Robinson and Holmes 1982). Birds were observed as long as they could be kept in sight, but only the first (independent) foraging attack was recorded to avoid problems with non-independent data and sequential observations in statistical analysis (Hejl et al. 1990). However, only some birds were banded, and I was not able to identify individuals in most cases.

For each foraging observation, I recorded the following parameters: foraging height, attack maneuver, substrate type and habitat. Foraging height was estimated using a laser rangefinder (Nikon, Tokyo, Japan) as a continuous variable. To allow multivariate analysis of foraging height along with other categorical variables, I defined six foraging height categories (strata): ground (0 m), sapling layer (0-2 m), shrub layer (2-4 m), mid-story (4-8 m), sub-canopy (8-12 m), and canopy (>12 m). Attack maneuver describes how the food items are taken by the birds and were defined as: (FC) flutter-chase, (GL) glean, (HG) hang-glean, (LG) leap-glean, (PR) probe, (RE) reach, (SH) sally-hover, and (SS) sally-strike, following Remsen and Robinson (1990). Substrate type is the material (microhabitat) from which food items are taken and was

defined as: (AIR) air, (BGL) bamboo green leaves, (DSS) dead stems or branches, (GRL) green live leaves, (HDL) hanging dead leaves, (LLT) leaf litter, and (LST) live stems or branches, following Remsen and Robinson (1990) and Marra and Remsen (1997). Habitat was categorized as (1) terra firme forest, (2) Bamboo (*Guadua* spp.) patches, (3) transitional (floodplain) forest, and (4) river-edge forest dominated by *Cecropia*, following Remsen and Parker (1983).

2.2.4 Foraging data analysis

Multivariate analyses were performed on data to extract foraging patterns. Each category was expressed as a proportion of total foraging observations for that species. Principal component analysis (PCA) and correspondence analysis (CA) are the two most commonly used multivariate tests when analyzing foraging data (Miles 1990). I used the arcsine-square root transformation before performing the PCA and raw proportions for CA (Miles 1990). Although CA was considered a better method for analyzing foraging data after Miles (1990), both CA and PCA are widely used to analyze and compare foraging variables at the community level, with similar results (Miles 1990, Naoki 2007, Botero-Delgado 2011, Mansor and Mohd Sah 2012). In this study, PCA was more effective in explaining the amount of variation in my dataset, both in terms of variation per axis and interpreting the continuum of foraging behavior.

2.2.5 Null model analysis

I used null model analyses (EcoSimR 1.00, Gotelli and Ellison 2013) to test the hypothesis that antbird species partition foraging niches. I created a matrix in which each column

represented a resource niche category, each row was a different species in the assemblage and each entry was the observed proportion of the resource used by each species. A zero value represents a niche category that was not utilized by a particular species. A graphical representation of this matrix is included in the appendix (Fig. A1). With this resource utilization matrix, I tested the hypothesis that average niche overlap over all unique species pairs in the observed matrix was different than expected at random, in which antbird species use resources without influence of interspecific interactions. In such an analysis, a niche overlap value significantly lower than expected by chance indicates that antbirds tend to avoid resources used by other species, whereas a niche overlap value higher than expected by chance indicates that antbirds prefer the resources used by other species. Niche overlap was estimated using Pianka's overlap index (Pianka 1973) for each unique species pairs in the assemblage, and then an average niche overlap was calculated for the observed utilization matrix. Pianka's index is a symmetrical overlap index that ranges from 0 to 1, where the species being compared have no resources in common to complete overlap in resource use, respectively (Krebs 1989). The resource utilization matrix was reshuffled using randomization algorithm 4 (RA4) in EcosimR 1.00 (Gotelli and Ellison 2013), which is the most constrained niche overlap algorithm, and generates null matrices that are more similar in structure to the original data. Analysis with less constrained randomization algorithm, such as RA3, produced similar results. RA4 randomizes the resource utilization matrix by reshuffling the non-zero elements for each species (rows) among the different resource categories (columns), thus retaining zero values and the observed niche breadth per species (i.e. degree of specialization). In this scenario if the species never uses the resource in nature, it also does not use it in the null matrix and the number of utilized resource categories in nature is preserved in the null matrix. A graphical representation of one simulated

matrix is included in the appendix (Fig. A1). This procedure was repeated 1000 times to create a distribution of random average niche overlap values for the community. The same analysis was repeated for each group of foraging categories separately and results are summarized in the appendix (Fig. B1). All analyses were performed in R (R Development Core Team 2015).

2.2.6 Niche overlap and phylogenetic distance

I tested whether niche overlap was greater for close relatives compared to distantly related species. I used a published phylogeny for 142 species of antbirds (Gómez et al. 2010) to estimate phylogenetic similarity among all species pairs in my local assemblage. This species-level phylogeny is based on a maximum-likelihood analysis of one nuclear intron and three mitochondrial genes. Using this published ML ultrametric tree, I derived patristic distances from branch lengths among all pairwise taxonomic comparisons using the package APE (Paradis et al. 2004) in R (R Development Core Team 2015). This published phylogeny (Gómez et al. 2010) included all but four antbird species that occurred in my local assemblage; these four species were substituted in the community dataset by closely related species present in the phylogeny based on the most recent phylogenetic and taxonomic information available (Isler et al. 2012, 2013, Bravo et al. 2014). These species were *Drymophyla devillei* by *D. genei*, *Hypocnemis subflava* by *H. peruviana*, *Myrmoborus leucophrys* by *M. myotherinus* and *Myrmotherula iheringi* by *Formicivora grisea*.

If the evolution of foraging niches in antbirds is slow and conservative within a local assemblage, then the similarity of their niches should increase with decreasing phylogenetic distance. In other words, species that are close relatives should have higher resource niche

overlap. Because neither the pairwise phylogenetic distances nor the niche overlaps are mutually independent, traditional methods for assessing the significance of a correlation are inappropriate here. Therefore, I used a Mantel test to test the significance of a correlation between niche overlap and phylogenetic distance (Knouft et al. 2006, Warren et al. 2008, Fowler et al. 2014). A significant negative correlation would indicate some degree of phylogenetic signal in foraging niches.

2.3 Results

2.3.1 Local community of antbirds

In total, 44 antbird species were detected in the plot during the breeding season over four years (Appendix C). This is the most diverse assemblage of antbirds documented so far to the best of my knowledge. Of these, 30 species were recorded by at least two methods, including 22 with nesting information, in at least three years. As such, these species were considered as the local assemblage of resident breeders in the study plot and are the focus of foraging and community analyses. The remaining 14 species were recorded only occasionally and fall into two categories, described here, based on their relative rarity and habitat specificity: resident breeders with presumably very low densities and non-resident species.

Residents with low densities: Seven species were categorized as residents in the study plot, but with presumably very low densities (< 1 pair/km²) based on consistent detections of individuals or pairs in the same territory over different years (Appendix C). These species were *Cymbilaimus sanctaemariae*, *Dichrozona cincta*, *Frederickena unduliger*, *Myrmeciza*

atrothorax, *Neotantes niger*, *Schistocichla brunneiceps* and *Taraba major*. Three species, *D. cincta*, *F. unduliger*, and *N. niger*, were recorded in one single territory in the plot in two different years. They are generally considered widespread but uncommon in western Amazonia and described as secretive and elusive birds with little published information on their natural histories (Hilty and Brown 1986, Zimmer and Isler 2003, Schulenberg et al. 2007). *C. sanctaemariae*, *M. atrothorax* and *T. major* were recorded only as pairs in their specific habitats, which comprise a small portion of the study plot: bamboo patches for *C. sanctaemariae* and river-edge thickets for the other two species. These are also poorly known species that prefer dense vegetation in their respective habitats (Zimmer and Isler 2003, Schulenberg et al. 2007). *S. brunneiceps* was detected only by location of active nests every year, presumably of two different pairs along one stream in the study plot. This is a virtually unknown antbird that was recently split from a group of related species, referred to as the “*Schistocichla* complex” (Isler et al. 2007, Remsen et al. 2015).

Non-resident species: Seven species were categorized as non-resident species given that they were recorded only occasionally in the study plot (Appendix C). Four species were detected only once, and three only twice in the four year period. Although some of these species are common in other areas of the Amazonian region, they were rare and occasional visitors in this study. These species were *Cercomacra nigrescens*, *Hypocnemoides maculicauda*, *Microrhophias quixensis*, *Myrmeciza hyperythra*, *Myrmotherula sclateri*, *Rhegmatorhina melanosticta*, and *Thamnophilus doliatus*. These species are more common either at a different elevation or in a different habitat than in my study plot. *M. quixensis* and *R. melanosticta* are more abundant in foothill forest (> 600 m) upslope from the plot (unpublished data), and *M. hyperythra* and *M. sclateri* are more common at elevations below 400 m (Terborgh et al. 1990). All four species

were detected only once in the study area. One pair of *C. nigrescens*, *H. maculicauda*, and *T. doliatus* was recorded twice during the study period. These species are habitat specialists of dense undergrowth of *Cecropia* forest, oxbow lake edges and sandbar scrub, respectively (Zimmer and Isler 2003), small areas of habitat present in the surroundings of the plot.

2.3.2 Foraging behavior

A total of 871 independent foraging observations were made on 30 antbird species defined as the local assemblage of resident breeders (Table 1). Seventeen additional observations were obtained for the low-density species, *M. atrothorax* (n = 5), *C. sanctaemariae* (n = 3), *T. major* (n = 4) and *F. unduliger* (n = 2) and the non-resident *M. quixensis* (n = 3); these species were excluded from foraging analyses.

Antbirds used all foraging heights available, with the most frequently strata used by birds being the understory layers (0, 0-2 m, 2-4 m). Just over half of the birds, 54.3%, foraged within these strata, followed by mid-story layer (4-8 m) with 23.4%, sub-canopy (8-12 m) with 12.2% and canopy (>12 m) with 10.1% of observations. Nearly 50% of the species consistently foraged within four meters of the ground. Species that foraged higher also tended to use a broader range of forest strata (Fig. 1). Overall, gleaning was the most frequently used maneuver by antbirds, with approximately one-third (34.1%) of all observations, followed by reaching (23.2%) and sally-striking (14.7%). None of the species used one maneuver exclusively, but gleaning was the maneuver most frequently used (> 60%) by *M. goeldii* and *H. subflava*, whereas sally-strike was the primary maneuver of *T. ardesiacus* and *T. schystogynus* (>65%) (Fig. 2). Green leaves were the most frequently used substrate by most species with 52% of total observations, followed by

hanging dead leaves (17.1%), and live stems (10%). Green leaves was the predominant foraging substrate (> 70%) of *T. ardesiacus*, *M. axillaris*, *M. brachyura*, *I. hauxwelli*, *M. longipennis*, *M. menetriesii*, and *T. schistaceus* (Fig. 3). *E. erythrura* and *E. leucophthalma* used predominantly hanging dead leaves (> 75%), and *D. devillei* and *C. manu* foraged mostly on bamboo leaves (> 65%). Dead stems were used by fewer than 1% of birds.

Two principal component axes cumulatively accounted for 57.7% of total variance in foraging parameters. The first PC axis, PC1 (31.1%), was predominantly associated with foraging height and described variation in foraging at the sapling layer (0-2 m, loading = 0.62) and mid-story level (4-8 m, loading = - 0.35), and the use of leaf litter as a foraging substrate (loading = 0.35). The second PC axis, PC2 (26.7%), was associated with habitat type with the highest loadings on *terra firme* forest (loading = 0.64) and bamboo patches (loading = - 0.53), as well as the use of bamboo leaves as a foraging substrate (loading = - 0.36). Ordination of antbirds in the first two principal components described a gradient of species in their use of two main forest layers within bamboo and *terra firme* forest, and the use of bamboo green leaves and leaf litter as foraging substrates (Fig. 4). Differences in other foraging variables accounted for variation explained by PC axes 3, 4 and 5, which together with PC1 and PC2 explained 81% of the total variance in foraging parameters (Table 2). Specifically, use of different foraging maneuvers was important in variance explained by PC3 and use of specific substrates such as hanging dry leaves and green leaves accounted for variation explained by PC4 and PC5 (Table 2).

2.3.3 Niche overlap and phylogenetic distance

At the community level, species exhibited high foraging niche overlap, with average observed overlap significantly larger than expected by chance (Fig. 5; Appendix Fig. B1, Pianka's index observed = 0.579, mean Pianka's index random = 0.394, $P < 0.001$).

No significant relationship was found between niche overlap and phylogenetic similarity, indicating no consistent pattern in the evolution of foraging niche in the local assemblage (Fig. 6, $r = -0.04$, $P = 0.68$). Niche overlap was consistently high (>0.6) for the most closely related species, but distantly related species pairs also exhibited high values of niche overlap. Overall, niche overlap was negatively related to the degree of phylogenetic relatedness, but this relationship was weak and not statistically significant.

2.4 Discussion

The high species richness of antbirds in Amazonian lowland rainforests represents a complex case of coexistence of members of the same family at local scales. A lack of quantitative information of microhabitat and resource use of antbirds have prevented any thorough analysis of community assembly (Gómez et al. 2010), although several studies have indicated a role for segregation along these niche axes to allow coexistence of closely related antbirds (Powell 1989, Robinson and Terborgh 1995). This study provides the first quantification of habitat and resource use of co-occurring antbirds in a local assemblage, to determine its role in species coexistence and explore the evolution of these traits.

Foraging information in antbirds is, for most species, limited to qualitative descriptions of general habitat, foraging height and anecdotal observations of prey captured in different substrates (Zimmer and Isler 2003). Quantitative information on foraging height, substrate, maneuvers and habitat use have been described for some antbirds in SE Peru from localities in close proximity to my study plot; these species include the Bluish-slate Antshrike (*Thamnomanes schistogynus*), Dusky-throated Antskrike (*T. ardesiacus*), Plain-winged Antshrike (*Thamnophilus schistaceus*), Chestnut-tailed Antbird (*Myrmeciza hemimelaena*), White-browed Antbird (*Myrmoborus leucophrys*), Black-faced Antbird (*M. myotherinus*), Spot-winged Antshrike (*Pygiptila stellaris*) and White-eye Antwren (*Epinecrophylla leucophthalma*) (Schulenberg 1983, Remsen and Parker 1984, Marra and Remsen 1997, Rosenberg 1997). Although with a slightly different classification scheme of foraging variables, all major foraging patterns described for these species were also observed in the present study. For example, species considered dead-leaf foraging specialists, such as the White-eye Antwren or the Rufous-tailed Antwren (*E. erythrura*) (Remsen and Parker 1984, Zimmer and Isler 2003), were also observed foraging more than 75% of the time in hanging dead leaves in my study plot. More generalist understory antbirds, such as the Chestnut-tailed Antbird or the White-browed Antbird (Marra and Remsen 1997), were also observed using a broader range of foraging maneuvers and substrates. These patterns of foraging and habitat use could potentially be applied to the species, rather than only to the populations being studied, but the lack of quantitative behavioural information for most Amazonian antbirds prevents such a broader comparison.

Most variation in foraging traits among antbirds in the local assemblage is explained by the combination of few parameters, specifically by the proportion of use of two layers of forest strata in two habitats, and preference of two substrate types. These results were congruent with

previous studies focused on pairs or groups of closely related antbirds co-occurring at local scales, where differences in resource use were observed. Segregation in foraging height was described for co-occurring antshrikes (*Thamnomanes* spp.) (Schulenberg 1983) and antwrens (*Myrmotherula* spp.) (Powell 1989), and segregation in substrate and microhabitat use has been noted in sympatric antwrens (Rosenberg 1993) and other Amazonian antbirds (Robinson and Terborgh 1995).

I began the community analyses with the expectation that these major differences in foraging behaviour among closely related co-occurring antbirds would result in an overall pattern of low niche overlap at the community level. However, I found the opposite pattern – observed average niche overlap was significantly higher than expected by chance – indicating that antbirds in a local assemblage prefer, rather than avoid, habitat and resources used by other species in the area. This result contrasts with the common resource-partitioning pattern observed among sympatric insectivorous birds (MacArthur 1958, Naoki 2007, Mansor and Mohd Sah 2012, Collins 2015, Lara et al. 2015), which is suggested as a mechanism to allow coexistence.

My expectation of low resource overlap among co-occurring species relies on the assumption that the resource is a limiting factor for coexistence. If resources are not a limiting factor, then species are expected to use them randomly, or even frequently in the same area without severe competition. Antbirds are largely insectivorous birds, and thus, arthropods are their primary food resource (Zimmer and Isler 2003). Unlike fruits or flowers that tend to exhibit a patchy distribution with seasonal high abundance (Feinsinger 1976, Naoki 2007), arthropods are often cryptic and limited in quantity, and insectivorous birds usually specialize on substrates or searching methods to capture them (Robinson and Holmes 1982, Rosenberg 1993). Thus, there is substantial evidence to suggest that arthropods are a limiting resource for antbirds. In this

study, however, it is unclear if the estimates of niche overlap are heavily affected by differences in distribution and abundance of specific prey items or resource categories. The null model analysis assumes that all resource categories are equally abundant (Gotelli and Ellison 2013), which might not be the case for some categories at the scale of the present study. Incorporation of quantitative independent data on resource abundance will be necessary to detect an effect of very abundant or very scarce resources categories in the estimates of niche overlap.

High niche overlap among co-occurring species could also result from niche filtering, if the use of different resources is strongly limited by habitat or environmental factors. This idea is partially supported in an experimental study with ant communities. Fowler et al. (2014) proposed that niche filtering, instead of niche partitioning, explained the use of similar micro-habitats and resources by co-occurring ant species in temperate forests. I found that segregation in *terra firme* forest and bamboo patches was important in explaining variation in foraging behavior among co-occurring antbirds (PCA), but these differences were not large enough to differentiate subunits of the assemblage, and in fact, most species used more than one habitat type; thus, at the scale of this study, it is unlikely that habitat filtering is constraining species' resource use. Also, habitat filtering is suggested to play a more important role at regional rather than local scales, in tropical bird communities (Graham et al. 2009, Gómez et al. 2010).

Another explanation for this unexpected pattern of niche overlap is that positive (i.e. facilitation), rather than negative (i.e. competition), interactions are more predominant in determining niche structure in antbirds communities. Recent evidence has shown that positive plant-plant interactions are important in shaping communities, especially in resource-limited environments (Bruno et al. 2003, Fajardo and McIntire 2011, Martorell and Freckleton 2014), but evidence of these effects in birds communities is largely unexplored. Using 55 datasets on

mixed-species birds flocks composition from multiple continents, Sridhar et al. (2012) identified a strong positive correlation between association strength of species in flocks and phenotypic and foraging behavior similarity, which suggests a strong effect of positive interactions on mixed-species flocks assembly. Furthermore, it has been shown that mixed-species bird flocks in the tropics are stable in space and composition over long periods of time (Martínez and Gomez 2013). Antbirds are well known participants of these mixed-species flocks in Amazonian lowlands, and substantial evidence supports an important role of some species in the cohesion and stability of mixed-species flocks (Munn and Terborgh 1979, Jullien and Thiollay 1998, Martínez et al. 2016). In my local assemblage, 19 (64%) species participate in mixed-species flocks at some level, and at least seven species can be considered as “nuclear” or obligate flock participants (J. Muñoz unpubl. data). Such strong positive associations in antbirds assemblages might be responsible for the high niche overlap observed in resource use.

A second foraging specialization in antbirds that could influence the overall pattern of niche overlap at the community level is the behaviour of army-ant-following. Many species of birds opportunistically use army ants as a foraging resource and some antbirds are considered army ant following specialists that rely on this resource most of the time (Willson 2004, Brumfield et al. 2007). Several species might forage in the same army ant swarm, and although dominance and spatial segregation within ant swarms has been described (Willson 2004), it is likely that the foraging categories used in this study did not capture this fine segregation among species. As a result, niche overlap would be significantly larger than expected for these species. At least eight (27%) species in my local assemblage utilized in army ants swarms in foraging at some level.

I examined the role of evolution in the niche structure of antbird assemblages, and the degree to which phylogenetic similarity explained patterns of niche overlap among co-occurring antbirds. If foraging niches have evolved conservatively and exhibit a strong phylogenetic signal, niche similarity should be strongly correlated to phylogenetic distance, with more closely related species being more ecologically similar. I found no evidence of phylogenetic signal in foraging niches among antbirds in a local assemblage, which indicates that antbird foraging niches are evolutionarily labile. A similar pattern of evolutionary lability in resource use niches was found in communities of plants (Silvertown et al. 2006), lizards (Losos et al. 2003) and ants (Fowler et al. 2014) coexisting at local scales. These results are congruent with the idea that traits associated with resource use and coexistence within assemblages evolve rapidly and communities become structured by evolutionary labile traits (Silvertown et al. 2006). However, it is important to note that the approach used in this study does not assess the degree of phylogenetic signal on specific niche axes alone, because the metric used is the overall niche overlap for each pair of species in the local assemblage. A more conservative approach would be to analyze the use of particular niche categories in the phylogeny by incorporating different models of trait evolution. We might expect that variables, such as foraging height, can exhibit a stronger phylogenetic signal compared to the use of different foraging substrates. This area warrants further analysis on a finer scale.

Table 1. Foraging information of members of the antbirds assemblage in the study plot at Pantiacolla Lodge, SE Peru.

Species	Body mass (g)*	Foraging height (m) (mean \pm SD)	General foraging pattern §	General habitat ¶	Sample size (n)
<i>Cercomacra cinerascens</i>	14.3	19.3 \pm 5.6	C/Gl-Re	TF	22
<i>Cercomacra manu</i>	19.7	7.0 \pm 3.8	SC/Gl-Re	BP	15
<i>Cercomacroides serva</i>	17	1.8 \pm 0.4	U/Gl	TF	20
<i>Cymbilaimus lineatus</i>	35.8	8.2 \pm 3.1	M/Gl	TF	16
<i>Drymophila devillei</i>	10.2	7.8 \pm 3.2	SC/Gl-Re	BP	21
<i>Epinecrophylla erythrura</i>	11.4	5.4 \pm 3.7	M/Hg-Re-Pr	TF	41
<i>Epinecrophylla leucophthalma</i>	9.4	4.8 \pm 2.8	M/Hg-Re	TF	40
<i>Gymnopithys salvini</i>	25.9	0.4 \pm 0.4	U/Gl	TF	32
<i>Hylophylax naevius</i>	14.2	0.8 \pm 0.7	U/Lg-Ss	TF	24
<i>Hypocnemis subflava</i>	12.6	3.2 \pm 1.2	M/Gl	BP	26
<i>Isleria hauxwelli</i>	10.7	0.6 \pm 0.5	U/Gl	TF-FF	32
<i>Myrmeciza fortis</i>	46.5	0.5 \pm 0.4	U/Gl	TF-FF	15
<i>Myrmeciza goeldii</i>	42	1.5 \pm 1.2	U/Gl	BP-RE	18
<i>Myrmeciza hemimelaena</i>	16	0.4 \pm 0.5	U/Gl	TF	35
<i>Myrmoborus leucophrys</i>	21.5	0.5 \pm 0.3	U/Gl-Re	RE-FF	17
<i>Myrmoborus myotherinus</i>	18.8	0.5 \pm 0.3	U/Gl-Lg	TF	23
<i>Myrmotherula axillaris</i>	8.4	3.0 \pm 1.9	U/Gl-Lg	TF	73
<i>Myrmotherula brachyura</i>	6.4	12.1 \pm 5.5	C/Gl-Re	TF	38
<i>Myrmotherula iheringi</i>	8	5.0 \pm 2.5	M/Gl-Hg-Re	TF-BP	18
<i>Myrmotherula longipennis</i>	9.4	6.4 \pm 2.6	M/Gl-Re	TF	63
<i>Myrmotherula menetriesii</i>	8.6	8.2 \pm 3.3	M/Gl-Re	TF	53
<i>Percnostola lophotes</i>	28	0.9 \pm 0.6	U/Gl	BP-RE	21
<i>Phlegopsis nigromaculata</i>	44.5	0.6 \pm 0.3	U/Gl-Ss	RE	16
<i>Pygiptila stellaris</i>	24.1	10.0 \pm 4.4	SC/Gl-Re	TF	37
<i>Sclateria naevia</i>	24.6	0.2 \pm 0.2	U/Gl-Re	TF	21
<i>Thamnomanes ardesiacus</i>	17.7	3.4 \pm 1.9	U/Ss	TF	31
<i>Thamnomanes schistogynus</i>	17.2	5.5 \pm 2.6	M/Ss	TF-FF	46
<i>Thamnophilus aethiops</i>	25.7	2.3 \pm 1.0	U/Re	TF	10
<i>Thamnophilus schistaceus</i>	20.3	9.2 \pm 4.0	SC/Gl	TF-FF	31
<i>Willisornis poecilonotus</i>	18.4	0.3 \pm 0.3	U/Re-Ss	TF	16

* Mean adult body masses obtained from Dunning (2008) from closest location to our study area.

§ General foraging pattern: strata (U = Understory, M = Midstory, SC = subcanopy, C = Canopy); foraging method (Gl = Glean, Re = Reach, Hg = Hang-glean, Pr = Probe, Lg = Leap-glean, Ss = Sally-strike) ¶ General habitat (TF = Terra firme, BP = Bamboo patches, RE = River-edge, FF = Transitional (foodplain) forest).

Table 2. Principal component analysis of foraging data from members of the antbirds assemblage at Pantiacolla Lodge, SE Peru.

Component loadings		Principal component axes				
Foraging parameter	Variables	1	2	3	4	5
Foraging height	ground (0 m)	0.20	0.09	-0.03	0.01	-0.30
	sapling layer (0-2 m)	0.62	0.05	-0.08	-0.23	0.13
	shrub layer (2-4 m)	-0.16	-0.14	-0.35	-0.28	0.37
	midstory (4-8 m)	-0.35	-0.12	-0.20	0.15	0.08
	subcanopy (8-12 m)	-0.29	-0.07	0.12	0.25	-0.11
	canopy (>12 m)	-0.25	0.12	0.38	0.17	-0.10
Foraging maneuver	flutter-chase	-0.07	0.00	-0.07	0.01	0.08
	glean	0.04	-0.11	0.40	-0.08	-0.01
	hang-glean	-0.11	-0.03	-0.05	-0.35	0.07
	leap-glean	0.07	0.08	0.18	0.12	0.27
	probe	-0.01	0.05	0.04	-0.14	-0.15
	reach	0.00	-0.01	0.20	-0.10	-0.08
	sally-hover	-0.08	-0.01	-0.18	0.10	0.13
	sally-strike	0.02	0.06	-0.47	0.30	-0.08
Foraging substrate	air	0.03	0.07	-0.35	0.17	-0.17
	bamboo green leaves	-0.05	-0.36	0.01	0.05	-0.22
	dead stems	-0.01	-0.06	-0.01	-0.08	-0.01
	green leaves	-0.04	0.17	0.11	0.16	0.45
	hanging dead leaves	-0.19	0.01	0.05	-0.51	0.12
	leaf litter	0.35	0.06	0.03	0.09	-0.22
	live stems	0.00	0.01	0.12	0.17	0.06
	Habitat	bamboo patches	-0.04	-0.54	-0.06	-0.13
river-edge forest	0.17	-0.19	0.13	0.22	0.34	
terra firme forest	-0.21	0.64	-0.07	-0.18	-0.19	
transitional forest	0.11	0.04	-0.06	0.17	0.22	
% of total variance explained		31.10	26.70	9.50	8.50	5.40
% Cumulative variance		31.10	57.80	67.30	75.80	81.20

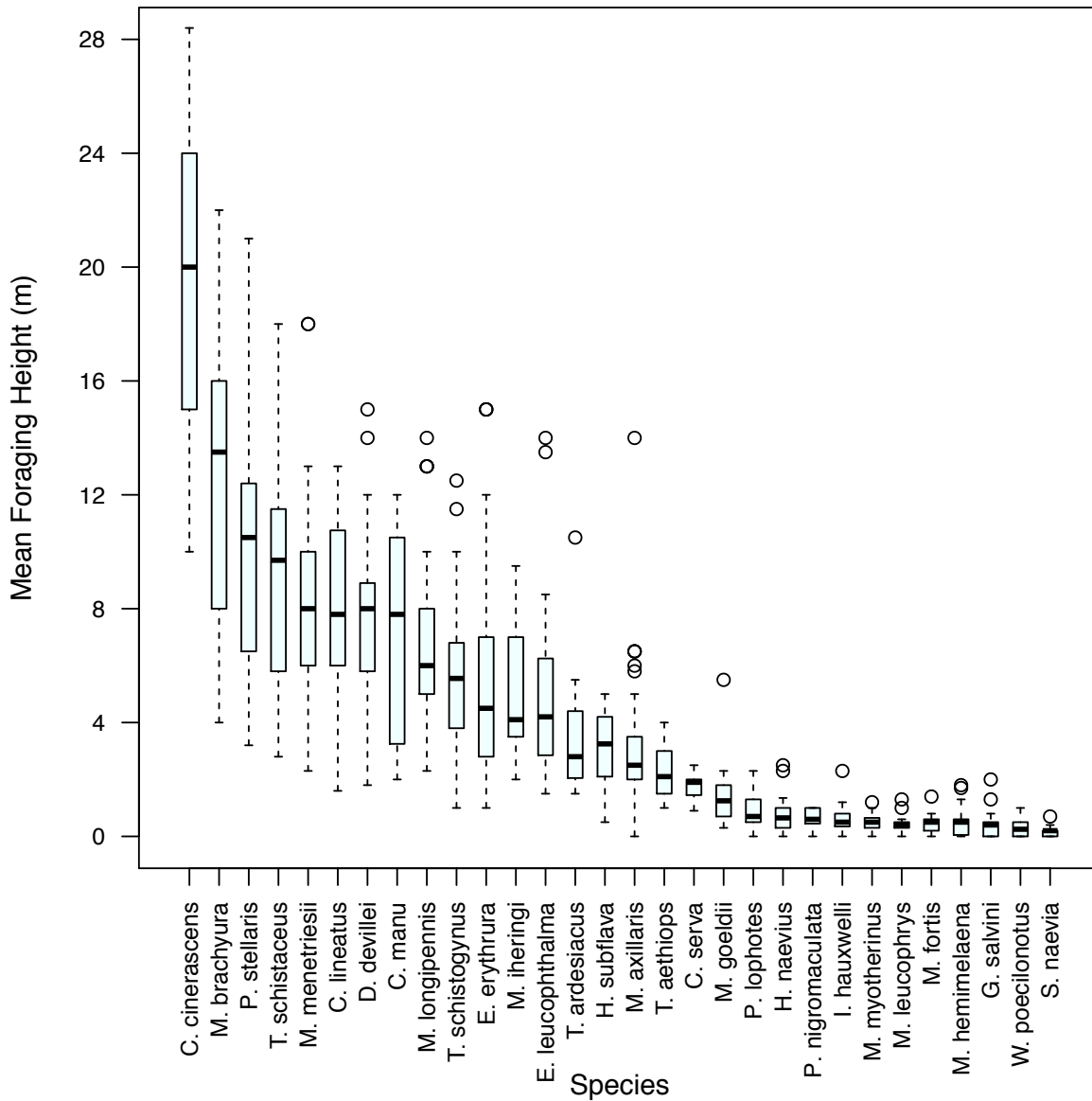


Figure 1. Boxplot of foraging height of the antbird assemblage at Pantiacolla Lodge, Peru. Sample sizes for each species are provided in Table 1. Black horizontal lines represent the median, and the boxes represent the first and third quartile of the distribution of data per species. Circles represent extreme values of foraging height.

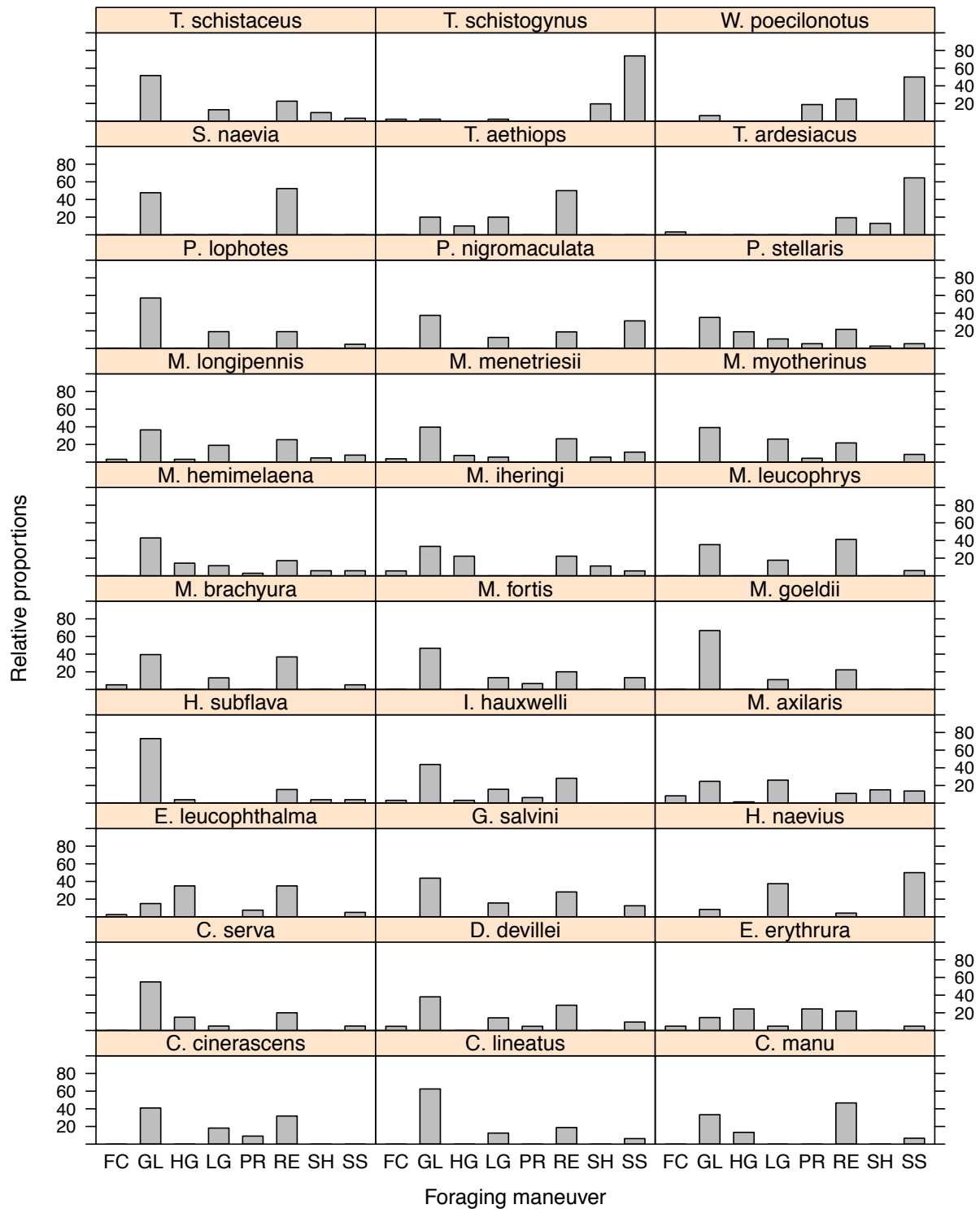


Figure 2. Frequency (% of observations) of use of foraging maneuvers by members of the antbird assemblage at Pantiacolla Lodge, Peru. FC = flutter-chase, GL = glean, HG = hang-glean, LG = leap-glean, PR = probe, RE = reach, SH = sally-hover, SS = sally-strike.

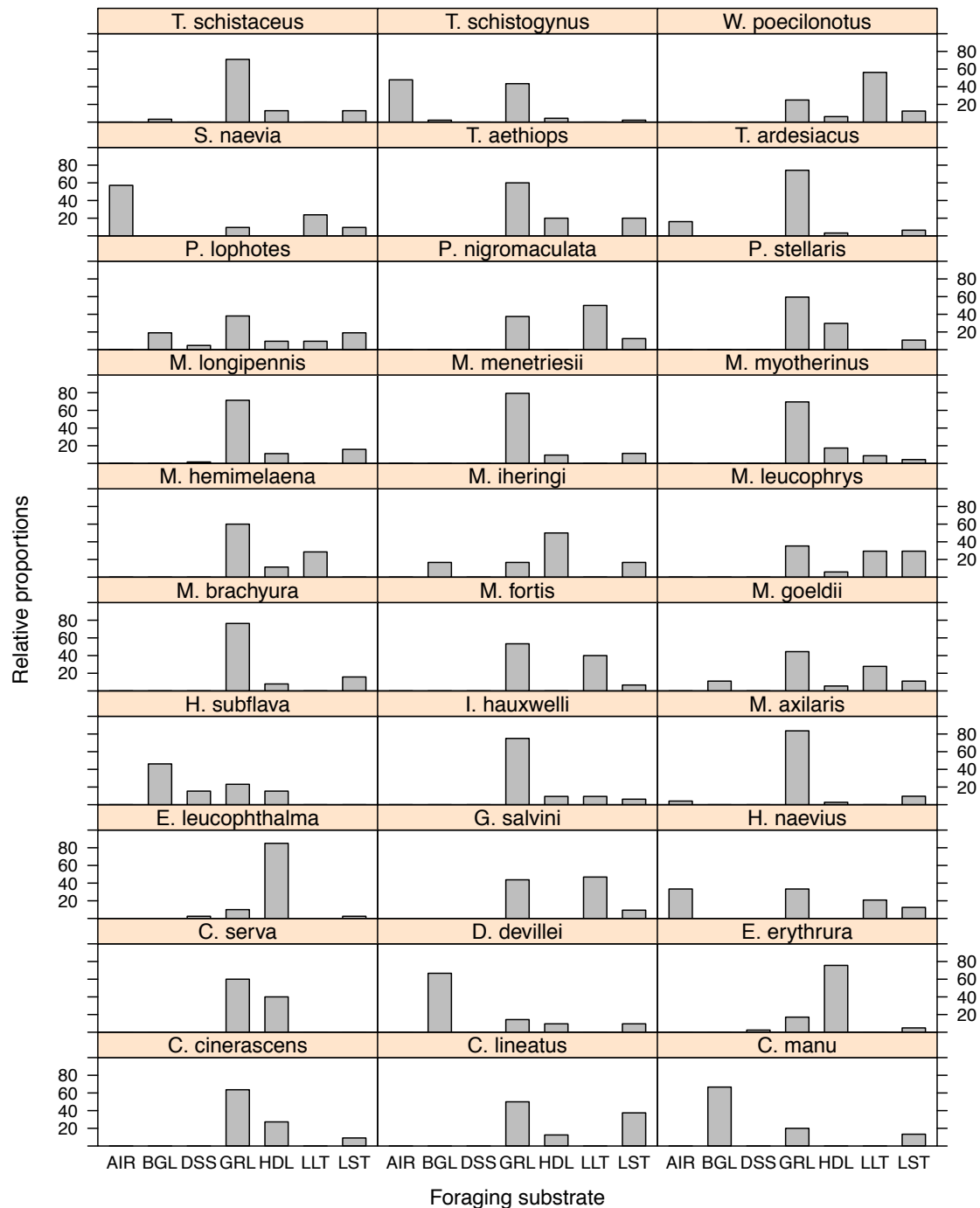


Figure 3. Frequency (% of observations) of use of foraging substrates by members of the antbird assemblage at Pantiacolla Lodge, Peru. AIR = air, BGL = bamboo green leaves, DSS = dead stems or branches, GRL = green live leaves, HDL = hanging dead leaves, LLT = leaf litter, and LST = live stems or branches.

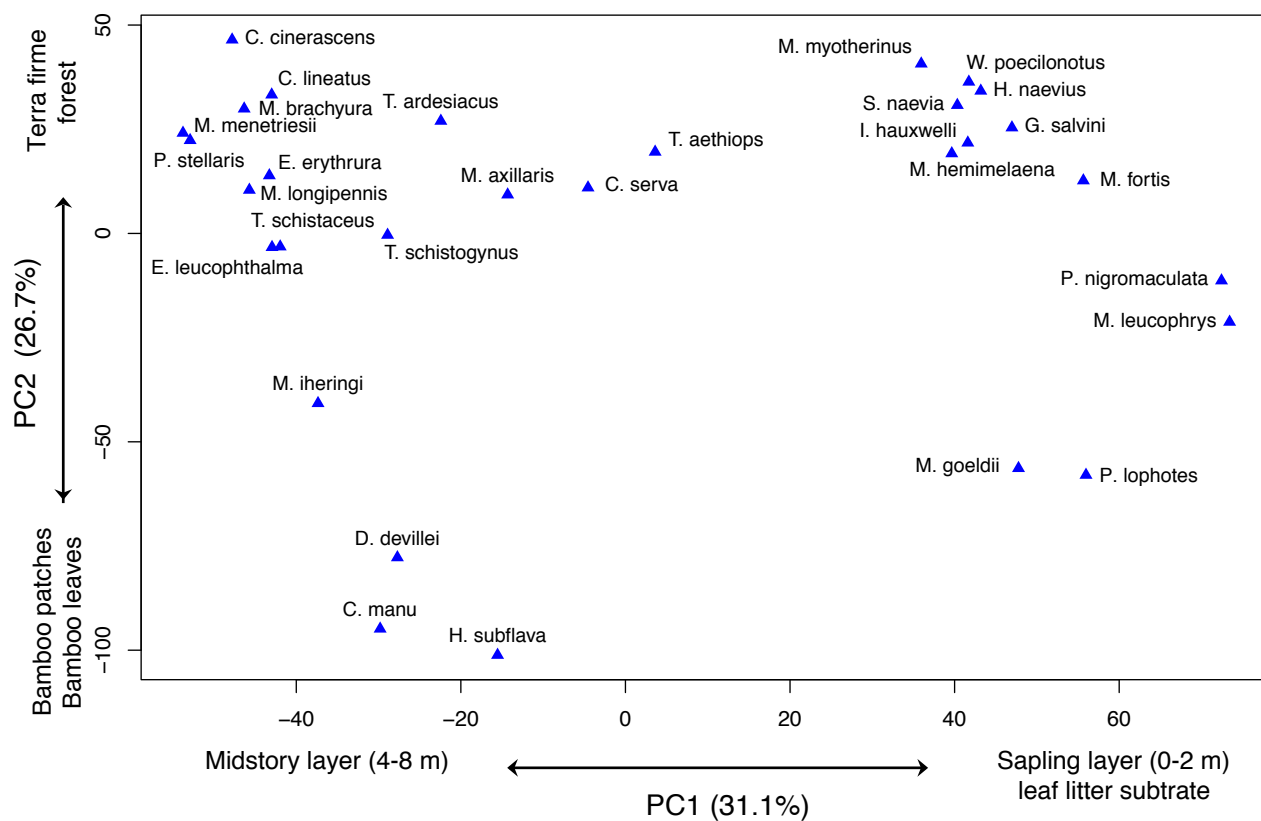


Figure 4. Ordination of the antbirds assemblage of Pantiacolla Lodge from principal component analysis based on foraging data.

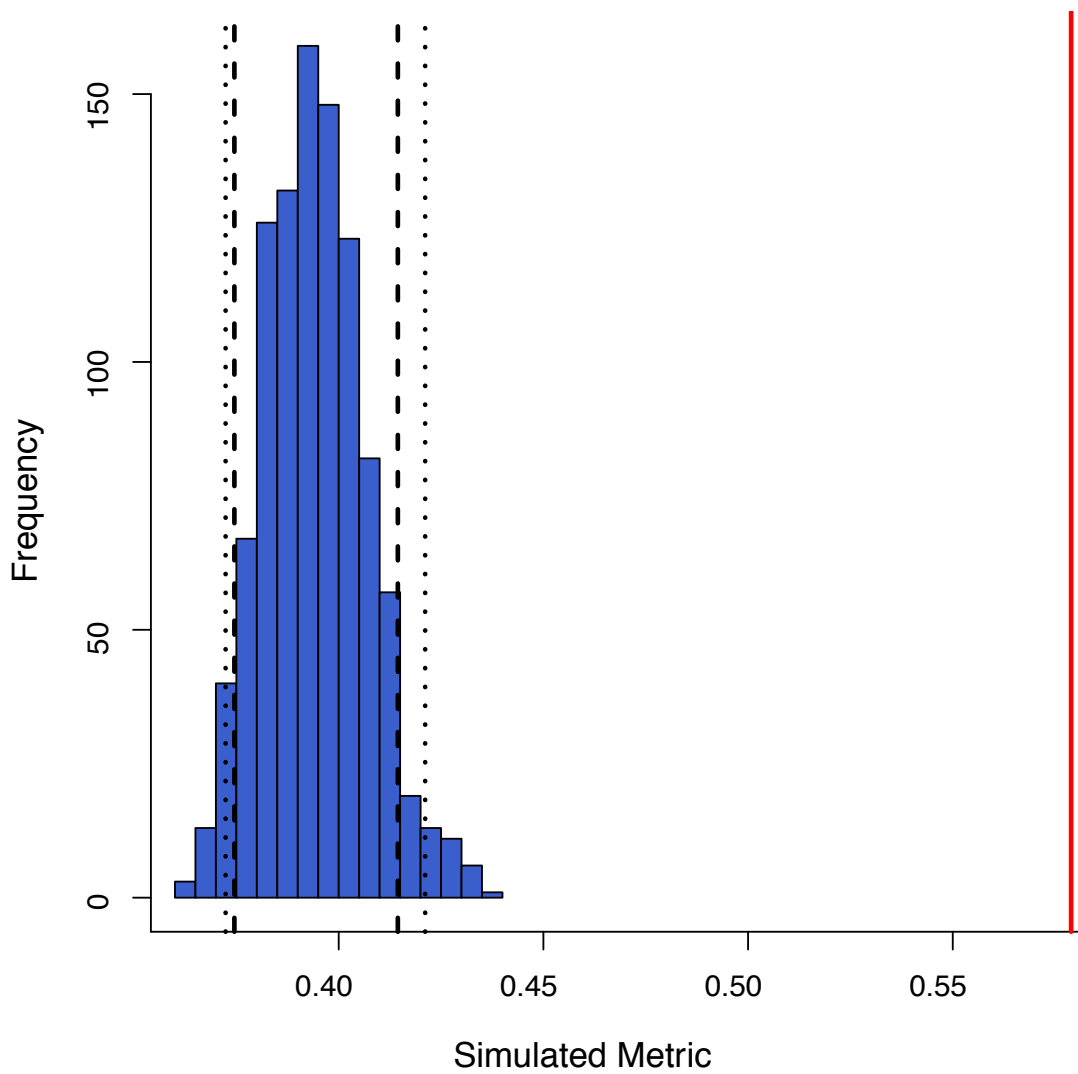


Figure 5. Frequency distribution of random niche overlap values relative to average niche overlap observed (red line) for antbird assemblage. Dotted lines represent the 95% CI for the estimate.

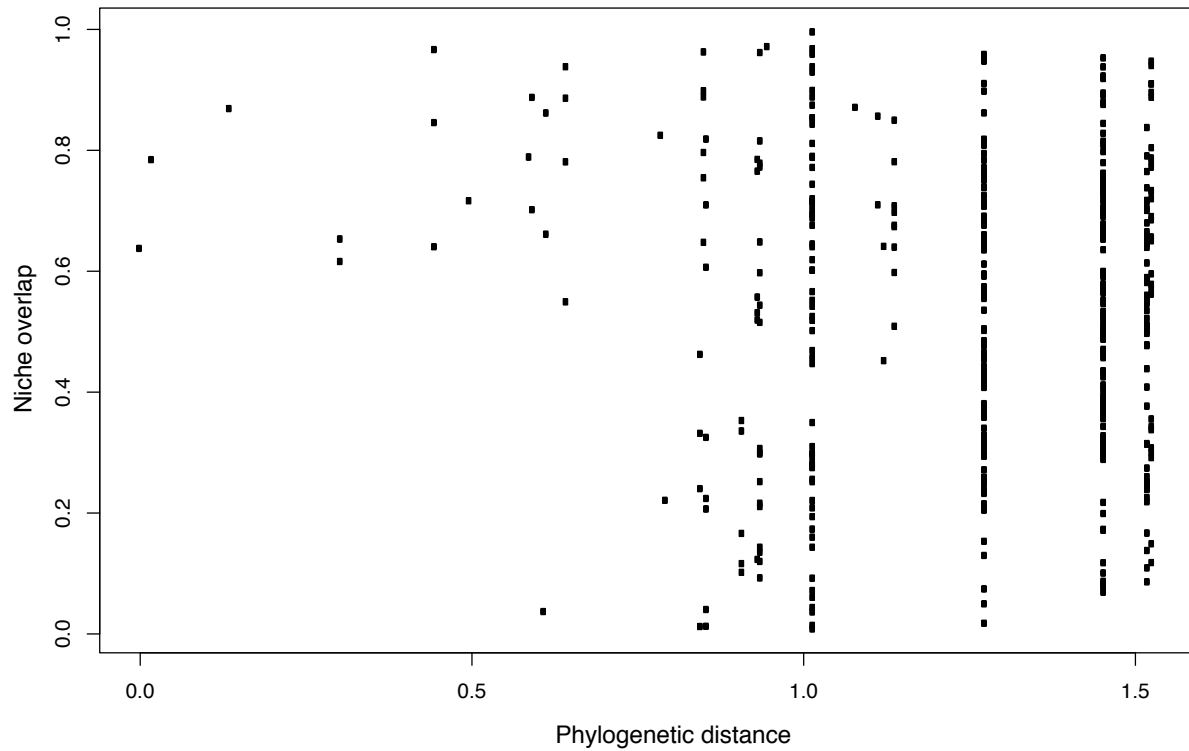


Figure 6. Relationship between pairwise species niche overlap (Pianka's index) and pairwise phylogenetic distance (branch lengths from ML ultrametric tree) among species in a local assemblage, SE Peru. A niche overlap index of 0 indicates species that share no resources, whereas 1 indicates species with complete overlap in resource use.

Chapter 3: Conclusions

3.1 General conclusions

Numerous studies of avian communities have argued that differences in resource use among co-occurring species is a primary way to achieve coexistence of similar or closely related species (MacArthur 1958, Feinsinger 1976, Sherry 1984, Naoki 2007, Collins 2015), but most studies have focused on species pairs or small groups, rather than all potential competitors in a community. Furthermore, few studies have incorporated phylogenetic relationships into analyses of resource partitioning. The goal of this study was to determine whether co-occurring antbirds in Amazonian lowland rainforest exhibited low niche overlap in foraging resources, as a mechanism to reduce competition pressure and promote coexistence. Also, I explored the evolution of foraging niches by incorporating ecological and phylogenetic similarity of each unique pair of species in a local assemblage.

An extraordinary diversity of 44 antbird species was detected during four years in a plot of 2 km² in SE, Peru. This is one of the richest antbird communities studied in Amazonian lowlands, where a total of 30 to 40 species are usually recorded in areas of similar size (Terborgh et al. 1990, Zimmer and Isler 2003). From this pool of species, 30 can be considered as common resident breeders in the plot, which potentially hold territories year-round and reproduce every season.

I found that co-occurring antbirds exhibited striking differences in foraging strategy, with most of the variation explained by segregation between two height layers in two types of forest. Some species can be considered foraging specialists that use one specific substrate or one

foraging stratum more than 90% of the time. Similar patterns have been described in several locations in Amazonian lowlands, where foraging ecology has been studied for pairs or groups of sympatric antbirds (Schulenberg 1983, Powell 1989, Marra and Remsen 1997, Rosenberg 1997). Such foraging specialization has been suggested as a mechanism to avoid resource competition and contribute to the high species coexistence observed in antbird communities (Zimmer and Isler 2003).

Despite these expected foraging niche differences among species, I found that overall niche overlap was high among species pairs, with average niche overlap significantly larger than expected by chance, and indicating that antbirds prefer, rather than avoid, habitats and resources used by other species. This result contrast with the general idea that, in the face of interspecific competition, species must differ in their use of resources to achieve coexistence (Schoener 1974). This pattern also suggests that in Amazonian lowlands, antbirds do not coexist within local assemblages by partitioning foraging niches. Instead, niches overlap more than expected, suggesting that antbirds (even closely related species) share similar resources and habitats.

Antbirds participate in two different positive interactions in Amazonian lowlands and some species are specialists or obligate species of these interactions. These are mixed-species flocking and army-ant following (Zimmer and Isler 2003). Thus, it is possible that participation in these associations would lead to an overall pattern of high niche overlap, if species that participate more frequently, also shared similar resources and habitats to obtain more benefits of this interaction. My research offers little evidence to explore these effects, because I did not quantify participation on mixed-species flocks or foraging behaviour on army ant swarms. But, given that 64% of the species in my local assemblage participate in flocks and 27% foraged in

army ant swarms, it is likely that this participation influences the overall pattern of resource use overlap observed.

I examined the degree to which phylogenetic distances explained among-species difference in resource use. Overall, no relationship was found between phylogenetic and niche similarity, indicating that antbird foraging niches are evolutionarily labile. Qualitative information on habitat and foraging behavior has been incorporated in recent analysis of body size and shape evolution in antbirds (Bravo et al. 2014), and has been useful to evaluate complicated taxonomic groups within Thamnophilidae (Isler et al. 2006, 2013). However, given the lack of quantitative assessments of habitat use and foraging behavior in Neotropical birds, its incorporation in evolutionary analysis of trait evolution or phylogenetic community structure is limited.

3.2 Recommendations for future research

Here, I have shown that antbirds in a local assemblage use foraging space differently with segregation along foraging strata and habitat type. However, at the community level antbirds exhibit high niche overlap, with average observed overlap significantly larger than expected by chance. More quantitative information on foraging behavior of antbirds in multiple assemblages across different geographic regions is necessary to corroborate the patterns observed in my local community. Also, I was not able to quantify resource abundance and distribution of specific arthropods, or differences in specific diet and microhabitat use among species. Additional research should incorporate quantitative comparable information on these traits to detect subtle important ecological differences that may allow coexistence in these highly diverse assemblages.

The effect of positive interaction in the assembly and maintenance of highly diverse avian communities is largely unexplored. Recent evidence suggests that there is a strong positive correlation between association strength and phenotypic and behavioral similarity in mixed-species flocks (Sridhar et al. 2012). Therefore, incorporation of information on the strength of both positive and negative interactions should be considered when interpreting community patterns.

I found no relationship between phylogenetic and niche similarity, but this analysis only offered a general picture of this relationship. Subsequent research on the evolution of foraging niches should also consider a more rigorous test of phylogenetic signal in the use of particular foraging niche categories, such as the K statistics (Blomberg et al. 2003), which incorporates different models of trait evolution.

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Appendices

Appendix A Null model analysis

To test whether antbird species partition foraging niches, I created a matrix in which each column represented a resource niche category, each row was a different species in the assemblage and each entry was the observed proportion of the resource used by each species. This matrix was reshuffled using the randomization algorithm 4 (RA4) in EcosimR 1.00 (Gotelli and Ellison 2013).

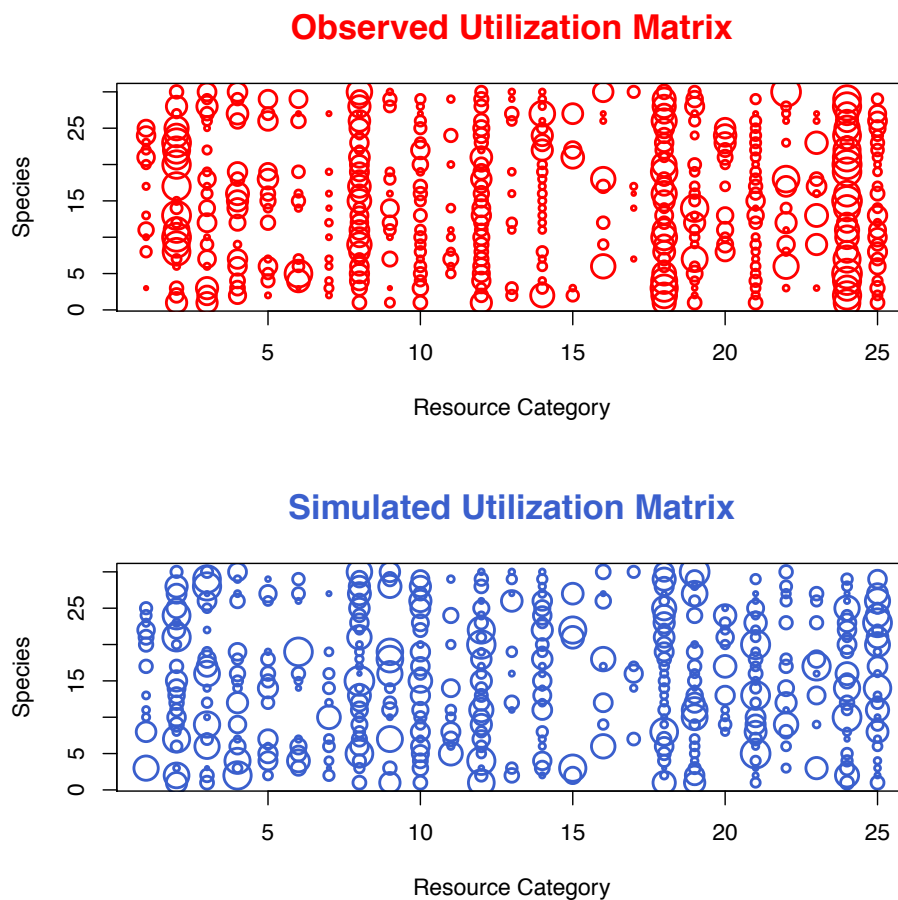


Figure A1. Graphical representation of observed resource utilization matrix (above) and one of the simulated resource matrices (below). For each matrix, the rows are species, the columns are utilization categories, and the symbols are circles, with the area of the circle proportional to the utilization of a particular resource by a species.

Appendix B Null model analysis by group of foraging categories

To test whether niche partitioning or similarity in each group of foraging categories occur among antbirds, I repeated the same null model analysis, but using a separate matrix for each group of categories. Higher than expected foraging niche overlap was also observed in all cases. Average observed niche overlap was significantly larger than expected by chance for foraging height (Pianka's index observed = 0.451, mean Pianka's index random = 0.377, $P = 0.003$), foraging substrates (Pianka's index observed = 0.601, mean Pianka's index random = 0.453, $P < 0.001$), foraging maneuvers (Pianka's index observed = 0.707, mean Pianka's index random = 0.478, $P < 0.001$), and habitat type (Pianka's index observed = 0.621, mean Pianka's index random = 0.399, $P < 0.001$).

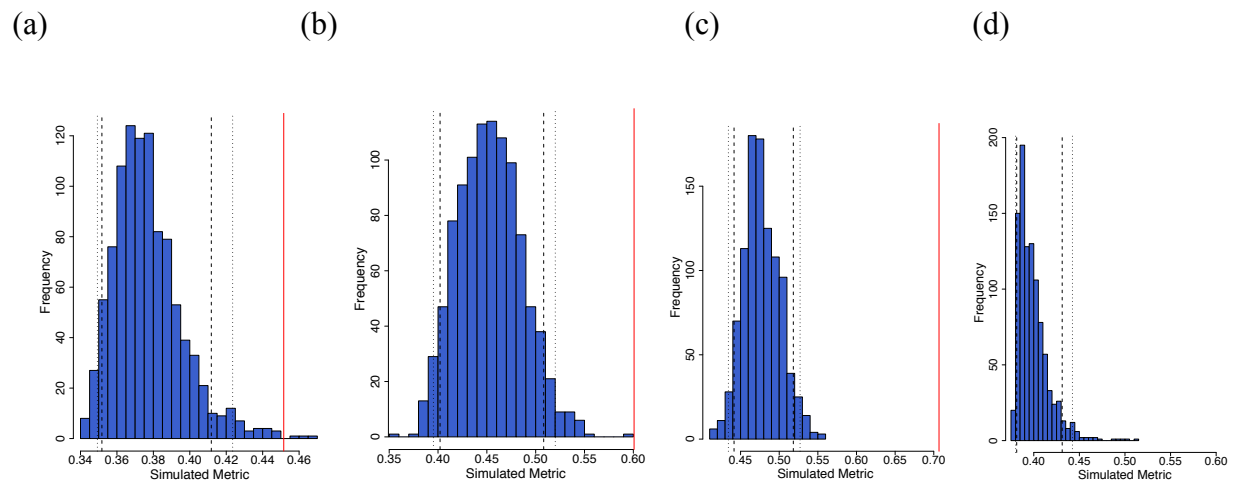


Figure B1. Frequency distribution of random niche overlap values relative to average niche overlap observed (red line) for foraging height (a), foraging substrate (b), foraging maneuvers (c) and habitat type (d). Dotted lines represent the 95% CI for the estimate.

Appendix C Summary of antbirds detected in the study plot

Antbird species detected at the Pantiacolla study plot from 2011 to 2014. No. of years indicated the number of years the species was detected in the four year period.

Species	Detected by				No. years detected	Category
	Mist-netting	Point counts	Nest searching	Foraging observations		
<i>Cercomacra cinerascens</i>	x	x		x	4	Resident breeder
<i>Cercomacra manu</i>	x	x		x	4	Resident breeder
<i>Cercomacroides serva</i>	x	x	x	x	4	Resident breeder
<i>Cymbilaimus lineatus</i>		x		x	4	Resident breeder
<i>Drymophila devillei</i>	x	x		x	4	Resident breeder
<i>Epinecrophylla erythrura</i>	x	x	x	x	4	Resident breeder
<i>Epinecrophylla leucophthalma</i>	x	x	x	x	4	Resident breeder
<i>Gymnopithys salvini</i>	x	x	x	x	4	Resident breeder
<i>Hylophylax naevius</i>	x	x	x	x	4	Resident breeder
<i>Hypocnemis subflava</i>	x	x	x	x	4	Resident breeder
<i>Isleria hauxwelli</i>	x	x	x	x	4	Resident breeder
<i>Myrmeciza fortis</i>	x	x	x	x	4	Resident breeder
<i>Myrmeciza goeldii</i>	x	x	x	x	4	Resident breeder
<i>Myrmeciza hemimelaena</i>	x	x	x	x	4	Resident breeder
<i>Myrmoborus leucophrys</i>	x	x	x	x	4	Resident breeder
<i>Myrmoborus myotherinus</i>	x	x	x	x	4	Resident breeder
<i>Myrmotherula axillaris</i>	x	x	x	x	4	Resident breeder
<i>Myrmotherula brachyura</i>		x		x	4	Resident breeder
<i>Myrmotherula iheringi</i>	x			x	3	Resident breeder
<i>Myrmotherula longipennis</i>	x	x		x	4	Resident breeder

<i>Myrmotherula menetriesii</i>	x	x		x	4	Resident breeder
<i>Percnostola lophotes</i>	x	x	x	x	4	Resident breeder
<i>Phlegopsis nigromaculata</i>	x	x	x	x	4	Resident breeder
<i>Pygoptila stellaris</i>	x	x		x	4	Resident breeder
<i>Sclateria naevia</i>	x		x	x	3	Resident breeder
<i>Thamnomanes ardesiacus</i>	x	x	x	x	4	Resident breeder
<i>Thamnomanes schistogynus</i>	x	x	x	x	4	Resident breeder
<i>Thamnophilus aethiops</i>	x	x	x	x	4	Resident breeder
<i>Thamnophilus schistaceus</i>	x	x	x	x	4	Resident breeder
<i>Willisornis poecilonotus</i>	x	x	x	x	4	Resident breeder
<i>Cymbilaimus sanctaemariae</i>		x		x	3	Resident with low density
<i>Frederickena unduliger</i>			x	x	2	Resident with low density
<i>Neotantes niger</i>		x	x		2	Resident with low density
<i>Myrmeciza atrothorax</i>		x		x	3	Resident with low density
<i>Taraba major</i>	x			x	2	Resident with low density
<i>Schistocichla brunneiceps</i>			x		3	Resident with low density
<i>Dichrozona cincta</i>	x	x			3	Resident with low density
<i>Myrmeciza hyperythra</i>				x	1	Non-resident
<i>Hypocnemoides maculicauda</i>			x		1	Non-resident
<i>Rhegmatorhina melanosticta</i>	x				1	Non-resident
<i>Cercomacra nigrescens</i>	x				1	Non-resident
<i>Myrmotherula sclateri</i>		x			1	Non-resident
<i>Microrhopias quixensis</i>	x			x	1	Non-resident
<i>Thamnophilus dolliatus</i>	x				2	Non-resident
