

RESEARCH ARTICLE

Sociality and morphology differentiate niches of 13 sympatric Amazonian woodcreepers (Dendrocolaptinae)

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ABSTRACT

Woodcreepers (Dendrocolaptinae) represent a remarkably uniform group of brownish birds that move by hitching up tree trunks as they forage for arthropod prey. Despite these superficial similarities, we were able to uniquely differentiate the niches of all 13 species north of Manaus by integrating morphological traits (e.g., mass and bill size) with behavioral traits (e.g., sociality, stratum use, and foraging maneuvers). The 5 ant-following (myrmecophilous) species, with their larger bodies and heavier bills, were morphologically distinct from the 7 species that join mixed-species flocks. A combination of vertical stratum, mass, and bill length further distinguished among mixed-flocking species. Two canopy species—the solitary *Dendrexetastes rufigula* and the mixed-flocking *Lepidocolaptes albolineatus*—consistently foraged at higher strata than other species. For the remaining mixed-flocking species, the largest 3 species differed significantly by mass, whereas the smallest 3 species, which overlapped broadly in mass, were uniquely distinguished by bill length. The 5 ant-following species differed in their degree of specialization on ant swarms, from facultative (*Hylexetastes perrotii*) to obligate (*Dendrocincla merula*). The ant-followers also showed nearly discrete mass distributions that essentially differed by Hutchinsonian 1:1.3 ratios, which likely allows them to maintain interspecific dominance hierarchies at the front of raiding army ant swarms. The behaviors we quantified (sociality, vertical strata, and myrmecophily), together with morphology (mass and bill size), separated all 13 species. We speculate that niche partitioning and competitive exclusion allow each woodcreeper to uniquely access invertebrate prey, permitting coexistence and contributing to high alpha diversity at our study site.

Keywords: ant-following birds, interspecific competition, mixed-species flocks, Neotropical birds, niche partitioning, trait divergence

LAY SUMMARY

- A remarkable 13 woodcreeper species coexist in the Amazon Rainforest north of Manaus, Brazil.
- All are small- to medium-sized, uniformly drab brownish birds that hitch up tree trunks.
- Theory states that species cannot coexist if they occupy the same niche, so what distinguishes each of these similar species?
- We used a combination of behavioral (e.g., social structure, foraging style, vertical stratum, and propensity to follow army ants) and physical traits (e.g., mass, bill size) to measure the niches of these species.
- Social structure separated many species, as did their preferred height in the forest.
- Mass and bill length further distinguished among species, with all 13 having a uniquely defined niche.
- We speculate that these differences in behavior and physical traits allow them to coexist in the same patch of Amazon rainforest.

Socialidade e morfologia diferenciam os nichos únicos de 13 arapaçus (Dendrocolaptinae) simpátricos da Amazônia

RESUMO

Arapaçus (Dendrocolaptinae) representam um grupo notavelmente uniforme de pássaros acastanhados que se movem engatando os troncos das árvores enquanto procuram presas artrópodes. Apesar dessas semelhanças superficiais, fomos capazes de diferenciar exclusivamente os nichos de todas as 13 espécies ao norte de Manaus integrando características morfológicas (e.g., massa e tamanho do bico) com características comportamentais (e.g., socialidade, uso de estrato e manobras de forrageamento). As cinco espécies que seguem as formigas (mirmecófilas), com seus corpos maiores e bicos mais pesados, eram morfológicamente distintas das sete espécies que unem bandos de espécies mistas. Uma combinação de altura no dossel, massa e comprimento do bico distinguiu, ainda mais, entre as espécies de bandos mistos. Duas espécies de dossel, a solitária *Dendrocolaptes rufifigula* e a *Lepidocolaptes albolineatus* de bandos mistos - forrageavam consistentemente em estratos mais elevados do que outras espécies. Para as espécies remanescentes de bandos mistos, as três maiores diferiam significativamente em massa, enquanto as três menores, que se sobrepunham amplamente em massa, eram distinguidas exclusivamente pelo comprimento do bico. As cinco espécies que seguem as formigas diferiram em seu grau de especialização em enxames de formigas, de facultativa (*Hylexetastes perrotii*) a obrigatória (*Dendrocincla merula*). As formigas seguidoras também mostraram distribuições de massa quase discretas que diferiam essencialmente pelas proporções Hutchinsonianas de 1: 1,3, o que provavelmente lhes permite manter hierarquias de dominância interespecíficas na frente de enxames de formigas de correição. Os comportamentos que quantificamos (sociabilidade, estratos verticais e mirmecofilia), juntamente com a morfologia (massa e tamanho do bico), separaram todas as 13 espécies. Especulamos que a diferenciação de nicho e a exclusão competitiva permitem que cada arapaçu tenha acesso exclusivo às presas invertibradas, permitindo a coexistência e contribuindo para a alta diversidade alfa em nosso local de estudo.

Palavras-chave: aves seguidoras de correições de formigas, aves Neotropicais, bandos mistos de aves, competição interespecífica, diferenciação de nicho, divergência de características

INTRODUCTION

The concept of defining a species' niche is practically as old as the field of ecology itself (Chase and Leibold 2003, McInerney and Etienne 2012). Hutchinson (1959) described a species' niche as an “*n*-dimensional hypervolume” to describe some number (*n*) of species traits—each representing a different component (i.e. an axis or dimension) of that niche. Together, those traits represent the requirements of a species for existence in a given environment and its impacts on that environment—loosely, its niche (Chase and Leibold 2003). Because organisms select environments in which they can survive and reproduce, interspecific competition will exert pressure on organisms to obtain resources by exhibiting dissimilar foraging strategies and behaviors or by selecting microhabitats where competition is minimized (Hutchinson 1957). Early ecologists realized the importance of competition in unstable systems where species with broadly overlapping niches cannot coexist in equilibrium (Gause 1934, Hardin 1960). As such, species' niches, likely shaped by interspecific interactions, may determine the collection of species that coexist in a local guild (Huston and Huston 1994). Therefore, these patterns of community structure are central to ecology, including ecosystem function and conservation (Dhondt 2012).

There are myriad dimensions that can differentiate species' niches. In a famous early example, MacArthur (1958)

studied 5 sympatric *Setophaga* warblers in the spruce forests of New England, which broadly overlapped in mass, bill shape, and diet. These warblers, however, separated themselves in niche space by foraging in different microhabitats and by using different foraging maneuvers, thereby partitioning the limited resources. Working in the foothills of the Andes, Willis (1983) described a combination of microhabitat, foraging maneuver, and social aspects that differentiated woodcreepers (Furnariidae: Dendrocolaptinae). Larger species moved closer to the ground and often followed swarms of raiding *Eciton* army ants (hereafter “ant-followers”), consuming the arthropods that fled from the ants. Willis and Oniki (1978, in Panama) and Willson (2004, in Peru) also found that obligate ant-followers (woodcreepers and antbirds: Thamnophilidae) exhibited a mass-based dominance hierarchy while attending swarms of army ants.

Mass likely helps to mediate the coexistence of not only ant-followers, but presumably mixed-species flock members as well (hereafter “mixed-flockers”; Powell 1985). Mixed-flockers include a diverse array of species that regularly forage together, roaming across a home range of approximately 10–15 ha. Powell (1989), working at the Biological Dynamics of Forest Fragments Project (BDFFP) in the north-central Amazon, reasoned that 3 similar and tiny (~8 g) *Myrmotherula* antwrens were able to coexist because of their reliance on mixed-species flocks. This requirement meant that they used home ranges much larger than would be expected for birds of their size, thus underutilizing the food resources within that large area.

Consequently, the presence of diverse mixed-species flocks permits more species to pack into the hyper-diverse tropics—diversity begets diversity.

In this study, we used field observations and mist-net capture data from an ensemble of 13 co-occurring woodcreeper species at the BDFFP in the central Amazon to assess overlap and dissimilarities in niche space. Three notable studies previously focused on niche partitioning in Amazonian woodcreepers. Pierpont (1986; 13 species in Peru) and Riegner (2019; 3 species in Brazil) used myriad behavioral observations, but both theses remain unpublished; and Chapman and Rosenberg (1991) morphologically examined stomach contents to explore diet partitioning in 4 sympatric Peruvian woodcreepers.

Previous work at the BDFFP showed that woodcreepers are ubiquitous throughout the study area (Cohn-Haft et al. 1997, Johnson et al. 2011, Rutt et al. 2017). Our study species ranged from the 14-g Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) to the Curve-billed Scythebill (*Campylorhamphus procurvoides*), with a bill nearly as long as its body, to the Red-billed Woodcreeper (*Hylexetastes perrotii*), which at 114 g is dominant over all other woodcreepers (Willis 1982, Marantz et al. 2003; Table 1). All diverged from a common ancestor 16–17 myr (Harvey et al. 2020; Figure 1) and, although most are superficially similar (small- to medium-sized, drab brown, insectivorous birds, which employ stiffened tails to hitch up tree trunks), they may vary in behavioral and morphological adaptations that could contribute to niche differentiation and coexistence. Five of the BDFFP's woodcreepers are common ant-following birds (Willis 1983), whereas 7 are commonly found with mixed-species flocks (Mokross et al. 2018, Rutt et al. 2020).

Our objective was to use species traits to quantify how these 13 woodcreepers separate in niche space. We predicted that by quantifying morphology, social affiliation, vertical stratum, microhabitat, foraging behavior, and propensity to follow army ants (myrmecophily), we could quantitatively describe differences in niche that may facilitate coexistence among these ecologically similar species in a diverse tropical system. We also predicted that, as a group, ant-followers and mixed-flockers would separate from each other in niche space, based upon the unique constraints of their respective social structures.

METHODS

Study Area

We conducted all observations at the BDFFP, including (1) behavioral observations during 3 dry seasons (June–October of 2009–2011), (2) vertical stratum measurements during 3 dry seasons (June–October of 2016–2018), (3) flock-following attendance across 15 months (September 2015 to August 2016; August–October 2017), and (4)

long-term mist-netting data (1979–2017) to calculate mass and quantify myrmecophily. We use the term “vertical stratum” throughout to describe the observed vertical height of the bird off the ground. The BDFFP is located ~80 km north of Manaus, Amazonas, Brazil (2°30'S, 60°W; for site details, see Bierregaard Jr. and Gascon 2001, Laurance et al. 2011). The site is embedded within a vast continuous landscape of primary rainforest to the north, east, and west, with increasing anthropogenic influence to the south (Rutt et al. 2019). The experimental forest component of the BDFFP consists of 11 experimentally isolated 1-, 10-, and 100-ha primary forest fragments within a matrix that was dominated by secondary forest from 11- to 30-years-old at the time of our fieldwork. Primary forest at the BDFFP has a typical canopy height of 25–30 m with emergent trees that regularly ascend to heights of ~40 m (C. L. Rutt, personal observation, Almeida et al. 2019).

Data Collection

While performing fieldwork for other projects in 2009–2018 (Johnson et al. 2011, Mokross et al. 2014, Powell et al. 2015, Rutt et al. 2020), we opportunistically documented woodcreeper behavioral data including foraging maneuver (e.g., sally, chisel, glean; Remsen and Robinson 1990) and microhabitat use (vertical stratum; tree diameter where the bird was spotted, hereafter tree width; substrate: tree, branch, liana, dead tree etc.). We also recorded the social affiliation of the individual (solo/pair, ant-swarm, mixed-species flock), which we then used to calculate individual flocking propensity (i.e. for a given species, the proportion of individual-level observations with a mixed-species flock or at an ant swarm). From 2009 to 2011, we documented 360 observations: 75 in continuous forest, 197 in 100-ha forest fragments, and 88 in 10-ha forest fragments. We excluded observations from 1-ha fragments as the forest structure had been highly modified. We estimated vertical stratum by eye and calibrated with known height of mist nets, so height estimates of birds in the subcanopy and canopy almost certainly became less accurate. To estimate tree width, we first recorded tree width relative to the width of the bird being observed (e.g., tree width = $2.5 \times G. spirurus$ width). For each species, we then measured the width of 3 specimens (at the widest point) from the Louisiana State University Museum of Natural Science (LSUMNS). We then used mean widths of museum specimens for each species to convert relative tree width to absolute tree width for each observation (e.g., 2.5 [the relative tree width] \times 2.73 cm [the mean width of *G. spirurus*] = 6.83 cm = absolute tree width).

During later fieldwork (2016–2018), we added vertical stratum data using a laser rangefinder for heights > 5 m. Readings were registered by observers positioned either directly below the bird (or the bird's prior location) or, for more distant birds, by recording the elevated distance from

the observer to the bird's location, as well as the horizontal distance from the observer to the base of the bird's tree (vertical stratum was then calculated using the geometry of a triangle). To diminish temporal autocorrelation, we only recorded successive vertical stratum estimates for a species after at least 10 min had passed.

For each woodcreeper species, flock attendance rates were summarized from 8 primary forest flocks. In total, CLR followed these flocks for 333 hr (36–45 hr flock⁻¹), recording species composition in 30-min time blocks. Attendance rates were then calculated as the proportion of time blocks that a given species was present. Thus, an attendance rate of 0.75 for a flock would indicate that a species was present in three-quarters of all flock-following time blocks, regardless of how many different individuals may have cycled in and out of the flock during that time.

For morphometrics, we used the BDFFP's long-term banding database (1979–2017), which included 4,846 captures of our focal species (summary data from Johnson and Wolfe 2017). We added bill depth (at the anterior end of the nares) and bill length (nares to tip; for *Lepidocolaptes albolineatus* and *Dendrocolaptes picumnus* only) measurements from 3 ($n = 2$ species), 4 ($n = 2$ species), or 5 specimens ($n = 9$ species) curated at the LSU MNS ($n = 12$ species) and the American Museum of Natural History ($n = 1$ species). Where applicable, we prioritized Guianan subspecies; however, to attain our target sample sizes for some species, we had to supplement with other Amazonian subspecies. Each measured specimen was an adult male, with age based on having fully ossified skulls.

To calculate an index of myrmecophily from the BDFFP capture database, we quantified bird aggregations at army ant swarms based on woodcreeper co-captures with obligate ant-following birds. Three obligate ant-followers occur at the BDFFP: *Pithys albifrons*, *Gymnopithys rufigula*, and the woodcreeper, *Dendrocincla merula* (Harper 1989). We considered an individual woodcreeper to be attending an army ant swarm if it was captured in (1) the same mist net as or within 2 adjacent nets of at least two *Pithys* and/or *Gymnopithys* and (2) within 60 min of those 2 obligate ant-followers. Due to conspecific attraction, we removed *D. merula* from our criteria to avoid biasing the myrmecophily estimate for that species. We then calculated myrmecophily as the proportion of swarms where an individual of a given species was present. Myrmecophily indices were not used to classify birds as obligate or facultative ant-followers, but rather as a relative measure of swarm attendance. Obligate ant-followers were classified based on the literature (Willis and Oniki 1978, Harper 1989).

Statistical Analyses

We first used ordinations to visualize niche differences among species with different social affiliations (mixed-flocking or ant-following) and then ran generalized linear

models (GLMs) and generalized linear mixed models (GLMMs) to determine how traits differed among species. We continued analyzing differences among traits until species were differentiated by at least one niche dimension, or until we ran out of traits. Our approach included both multivariate (ordination) and univariate (GLM, GLMM) analyses because the datasets we drew from were diverse (i.e. captures, observations from flocks, opportunistic observations) and not directly comparable.

Ordination Plots

Because an animal's niche is inherently multivariate (i.e. an n -dimensional hypervolume), we used non-metric multidimensional scaling (NMDS) to quantify and visually describe how this ensemble separates in niche space. Using a series of NMDS ordinations, we first examined all 18 trait variables together and then separately by morphology (3), microhabitat use (6), and foraging maneuvers (9). Because these are dissimilarity and not community data (i.e. a species-by-characteristics matrix), we disabled default data transformations for NMDS ordinations in the package *vegan* (v. 2.5-5, Oksanen et al. 2013). For each ordination, we collapsed dimensionality down to two axes using the Bray-Curtis dissimilarity index. We then evaluated the significance of each environmental variable using 1,000 permutation tests with the function *envfit*. If the observed squared correlation coefficients (r^2) were larger than 95% of random permutations, we considered that variable "significant" ($P < 0.05$) and plotted all such fitted vectors. Finally, because all species except *Dendrexetastes rufigula* regularly join either army ant swarms or mixed-species flocks, we grouped species by sociality (standard error ellipses with 95% confidence limits) and similarly employed *envfit* to evaluate the significance of this grouping. For metric validation of the morphological data, we performed a second ordination, a principal components analysis (PCA), using the same dataset as the NMDS. We categorized the remaining 12 species as ant-followers or mixed-flockers using Cohn-Haft et al. (1997) and our observations. This allowed us to gain further insight about whether species that forage interspecifically share niche space and, if so, which characteristics most differentiate these distinct lifestyles (i.e. morphological, microhabitat, or foraging maneuvers).

Statistical Modeling

To model vertical strata, we ran one normal GLMM to determine if vertical stratum (response variable) varied by species (fixed effect or explanatory variable). We combined data collected using different observational methods (one flock-based, one individual-based; see *Data Collection* above). We used individual woodcreeper or individual flock (the highest available sampling unit depending on the data collection method) as a random effect to control for

TABLE 1. Mean mass and estimates of territory size and density for the 13 woodcreeper species at the Biological Dynamics of Forest Fragments Project. Two-letter species codes are referenced in [Figure 2](#) and in [Supplementary Material Figures S1 and S2](#)

Scientific name ^a	Code	Common name	Mass (g) ^b	Stratum ^c	Sociality ^d	Territory size (ha) ^e	Density per 100 ha ^e
<i>Certhiasomus stictolaemus</i>	CS	Spot-throated Woodcreeper	16.8	understory	mixed-species flock	12.0	7
<i>Sittasomus griseicapillus</i>	SG	Olivaceous Woodcreeper	14.2	midstory	mixed-species flock	36.7	3
<i>Deonychura longicauda</i>	DL	Long-tailed Woodcreeper	29.1	understory	mixed-species flock	15.0	6
<i>Dendrocincla merula</i>	DM	White-chinned Woodcreeper	53.0	understory	army-ant follower	–	12
<i>Dendrocincla fuliginosa</i>	DF	Plain-brown Woodcreeper	40.2	understory	army-ant follower	16.8	9.5
<i>Glyphorhynchus spirurus</i>	GS	Wedge-billed Woodcreeper	13.7	understory	mixed-species flock	5.2	33
<i>Dendrozetastes rufigula</i>	DR	Cinnamon-throated Woodcreeper	70.0 ^b	canopy	solitary	11.0	2
<i>Dendrocolaptes certhia</i>	DC	Amazonian Barred-Woodcreeper	66.6	midstory	army-ant follower	17.1	7
<i>Dendrocolaptes picumnus</i>	DP	Black-banded Woodcreeper	78.5	midstory	army-ant follower	40.0	2
<i>Hylexetastes perrotii</i>	HP	Red-billed Woodcreeper	115.4	midstory	army-ant follower	20.0	5.5
<i>Xiphorhynchus pardalotus</i>	XP	Chestnut-rumped Woodcreeper	37.7	midstory	mixed-species flock	10.6	18
<i>Campylorhamphus procurviroides</i>	CP	Curve-billed Scythebill	34.4	midstory	mixed-species flock	24.0	3
<i>Lepidocolaptes albolineatus</i>	LA	Guianan Woodcreeper	18.6	subcanopy	mixed-species flock	12.0	10

^a Remsen et al. (2021).

^b Means from Johnson and Wolfe (2017) except *D. rufigula* from Bierregaard (1988).

^c Categories derived from fitted means: understory (<10 m), midstory (10–15 m), subcanopy (15–20 m), and canopy (>20 m).

^d Sociality categories were combined from Cohn-Haft et al. (1997) and our data (e.g., [Supplementary Material Figure S4](#)).

^e Estimates from Johnson et al. (2011).

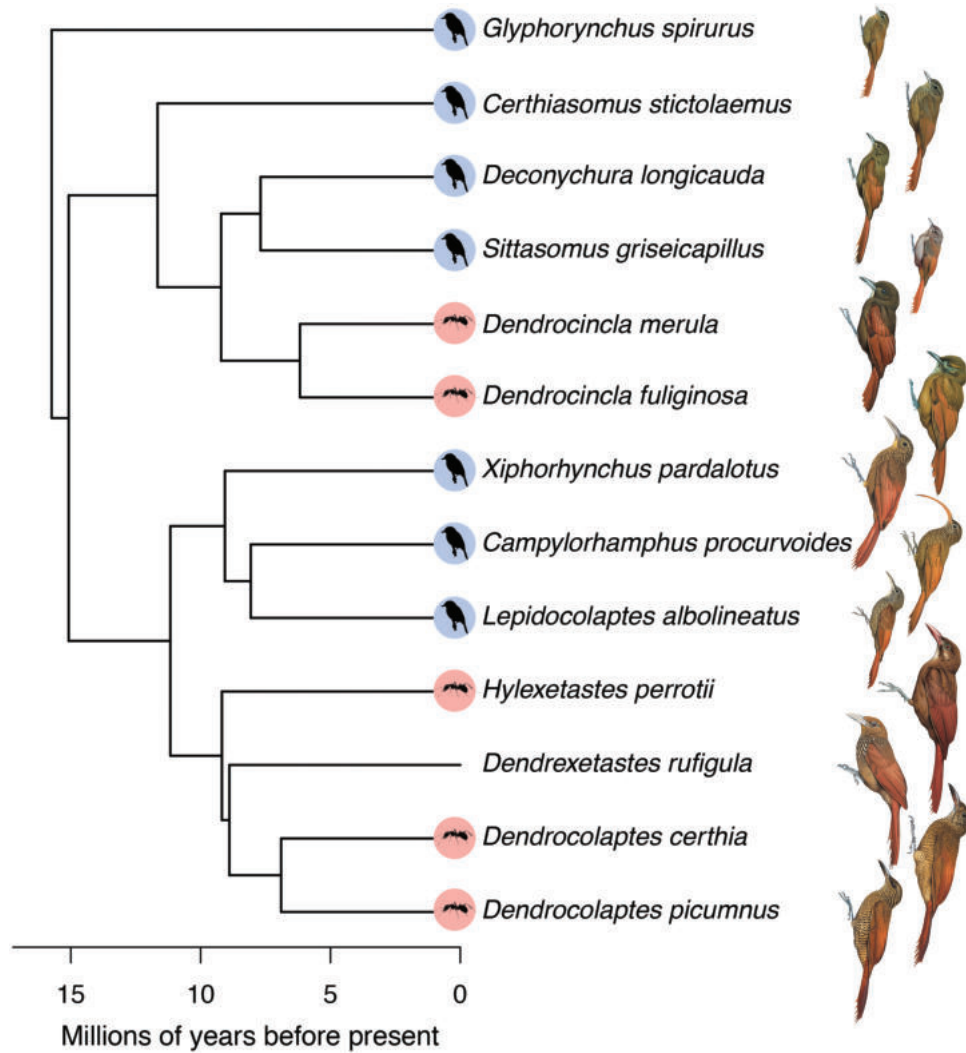


FIGURE 1. Phylogenetic relationships among the 13 woodcreeper species at the BDFFP. Icons represent ant-following birds (red) or mixed-flockers (blue). Bird illustrations reproduced by permission of Lynx Edicions.

repeated observations of individuals or flocks. To model myrmecophily by ant-followers, we ran a negative binomial GLM to determine if the number of captures of an individual at an ant swarm (response variable) varied by species (fixed effect). We then ran normal GLMs to determine if woodcreeper mass (response variable) varied by species (fixed effect or explanatory variable). Because we only used one observation per individual here, we did not include a random effect in this analysis. Finally, we ran a normal GLM to determine if woodcreeper bill length (response variable) varied among the three smallest woodcreepers: *Certhiasomus stictolaemus*, *G. spirurus*, and *Sittasomus griseicapillus* (fixed effect).

For GLMs and GLMMs, we used likelihood ratio tests (LRTs) to confirm that our models explained significantly more variation than null models, which we parameterized as above but excluding the fixed effect of species. We based

conclusions regarding “significant” differences among species using the 95% confidence intervals generated from best-fit models. We performed model diagnostics (Q-Q plots, variance boxplots) on model residuals to confirm that residuals met assumptions. All analyses were performed in Program R (R Core Team 2020).

RESULTS

Mixed-Flocking Species vs. Ant-Following Birds: Ordination

In the full ordination, 3 of the 5 significant trait variables were morphological (mass, bill depth, and bill length; Figure 2A), with r^2 values ranging from 0.92 to 0.81 ($P < 0.01$). Mass and bill depth displayed fitted vectors perpendicular to the axis separating the standard error ellipses between social groups. Fitting contour surfaces to these 2 continuous

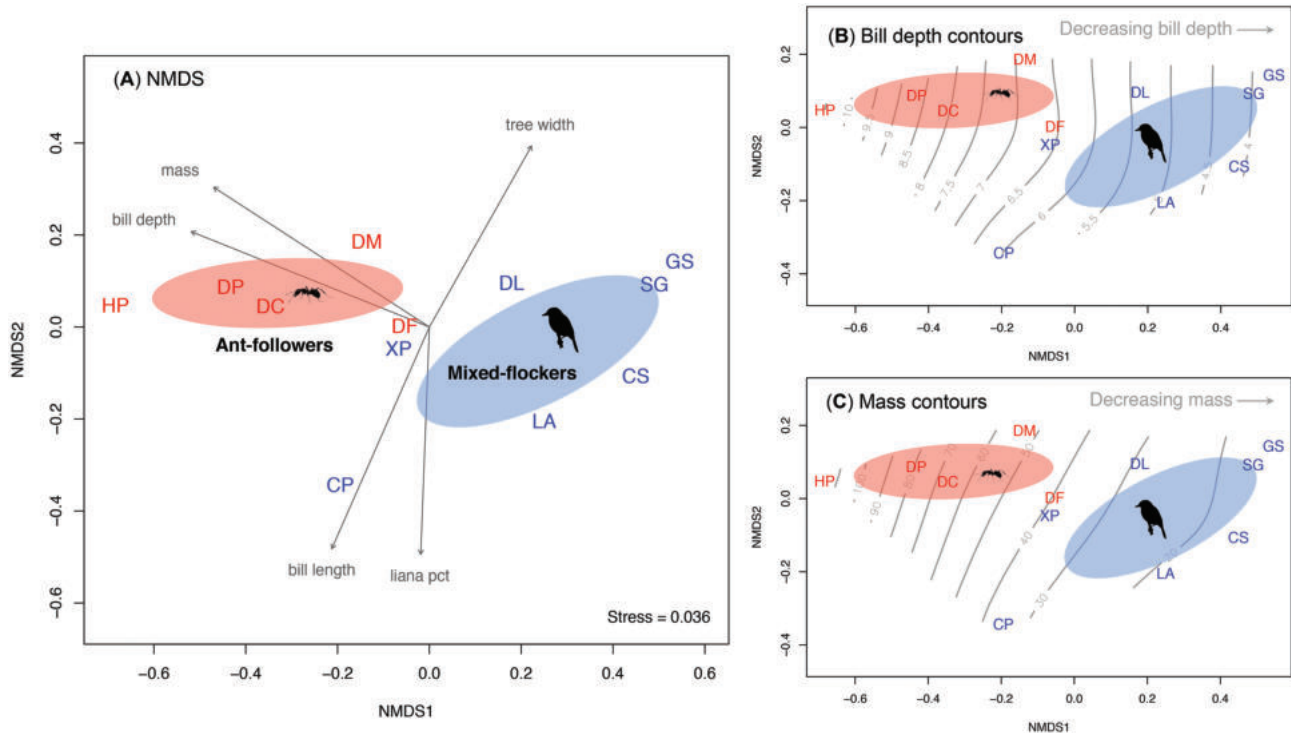


FIGURE 2. Using 18 environmental variables, an NMDS ordination (A) illustrates that ant-following species (red) separate in niche space from those that join mixed-species flocks (blue) at the BDFFP. These differences primarily stem from 2 morphological variables: bill depth (B) and mass (C). Arrows in (A) denote direction of trend. Ordination ellipses in (B) and (C) are identical to ellipses in (A) except (B) provides bill depth contours and (C) provides mass contours. Ellipses represent standard errors. Two-letter abbreviations by species available in Table 1. *Dendrexetastes rufigula* is not shown due to small sample size and solitary sociality.

variables illustrated that both body size (mass = ~40 g) and bill size (depth = ~6.5 mm) neatly delineated the larger ant-followers from the smaller mixed-flockers (Figure 2B–C). In this global NMDS, the ellipses do not overlap, and the two groups differ significantly ($r^2 = 0.51$, $P < 0.01$). Results of the PCA were strikingly similar to those of the NMDS (compare Supplementary Material Figures S1A and S2; essentially mirror images).

However, after splitting the 18 trait variables into separate ordinations by morphology (3), microhabitat use (6), and foraging maneuvers (9), we found that only morphology generated non-overlapping ellipses and significant differences between ant-followers and mixed-flockers ($r^2 = 0.52$, $P < 0.01$; Supplementary Material Figure S1A–C). Neither microhabitat ($r^2 = 0.16$, $P = 0.16$) nor foraging maneuvers ($r^2 = 0.14$, $P = 0.24$) differed significantly between the 2 groups and, in each case, some species were plotted in the “wrong” ellipse (Supplementary Material Figure S1B–C). Nonetheless, the significant variables that most clearly separated the 2 groups were tree width (wider in flock-followers) and 2 foraging maneuvers: sallying (more often in ant-followers) and chiseling (a maneuver almost exclusively employed by *G. spirurus*; Supplementary Material Figures S1 and S3).

Niche Separation Within Mixed-Flocking Species

Mixed-flockers occupied a wide vertical range from the understory to the canopy. Based on 95% CIs, *Ce. stictolaemus* occupied a vertical niche significantly lower than that of *Ca. procurvoides*, *Xiphorhynchus pardalotus*, *S. griseicapillus*, and *L. albolineatus*—it overlapped only with *G. spirurus* and *Deconychura longicauda*. *X. pardalotus*, *D. longicauda*, *S. griseicapillus*, and *Ca. procurvoides* all overlapped with each other, but *L. albolineatus* occupied a vertical niche higher than all other mixed-flockers (LRT: $P < 0.001$, $X^2 = 168$, $df = 12$; Figure 3).

Flocking tendency was difficult to quantify because of stark differences between results at the individual- and flock-level (Supplementary Material Figure S4). For instance, while following mixed-species flocks, at least one *X. pardalotus* and *G. spirurus* were nearly always present with the flock—far more than any other species (Supplementary Material Figure S4A). However, when our observations instead focused on individual birds rather than flocks, individual *Ce. stictolaemus*, *L. albolineatus*, *Ca. procurvoides*, *D. longicauda*, *S. griseicapillus*, and *X. pardalotus* were all, on average, with mixed-species flocks >75% of the time—considerably more than individual *G. spirurus* (Supplementary Material Figure S4B).

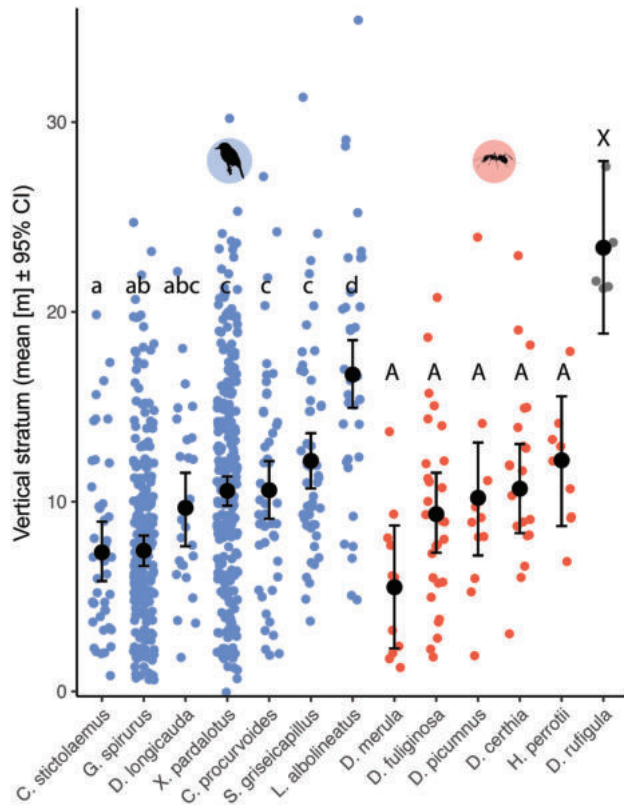


FIGURE 3. Vertical stratum (i.e. height) of 13 woodcreeper species at the BDFFP. Means (black dots) and 95% confidence intervals (error bars) generated from a generalized linear mixed model. Letters above graphs represent significant differences among species within social groups, with identical letters indicating no difference. Lowercase letters and blue dots are for mixed-flockers and uppercase letters and red dots are for ant-followers; *Dendrexetastes rufigula* (gray dots, “X”) is a solitary canopy species.

Because both approaches are potentially biased, we did not include flocking tendency in our quantification of niche.

Overall, mixed-flockers differed significantly by mass (LRT: $P < 0.001$, $X^2 = 12,025$, $df = 5$). The three largest flocking woodcreepers (*X. pardalotus*, *Ca. procurvoides*, and *D. longicauda*) all had significantly different masses; however, we found no significant differences among the three smallest woodcreepers: *G. spirurus*, *S. griseicapillus*, and *Ce. stictolaemus* (Figure 4). Instead, the three smallest flocking species had significantly different bill lengths (LRT: $P < 0.001$, $X^2 = 41.9$, $df = 2$; Figure 5A).

Finally, foraging maneuvers varied widely within and among species, with most species using at least three different foraging techniques. However, two species appeared biased towards particular techniques: 5 of 10 observations for *Ca. procurvoides* were “probe” and 23 of 39 for *G. spirurus* were “chisel.” The only other “chisels” were by *X. pardalotus* ($n = 3$; Supplementary Material Figure S3).

Niche Separation Within Ant-Following Species

Despite considerable variance in vertical stratum among ant-following species, 95% confidence intervals (CIs) overlapped for all five species (Figure 3), indicating no detectable interspecific differentiation. Among ant-followers, vertical stratum means for *Dendrocincla merula* (lowest) and *H. perrotii* (highest) were on opposite ends of the spectrum, although they still overlapped at the extremes.

Our model for myrmecophily (i.e. count of individual captures at ant swarms) found that *D. merula* was captured at ant swarms more often than *Dendrocincla fuliginosa*, *H. perrotii*, and *Dendrocolaptes certhia* (LRT: $P < 0.001$, $\chi^2 = 35.6$, $df = 4$). The latter 3 ant-followers all overlapped one another, whereas *Dendrocolaptes picumnus*, due to its very small sample size, overlapped all other species (only 8 observations of 3 individuals; Figure 5B). In fact, our estimate of myrmecophily for *Dendrocincla merula* was no different from that of *Pithys albifrons* (Thamnophilidae; Figure 5B). Both species are known obligate ant-followers (Willis and Oniki 1978, Willson 2004) and *Pithys* is the most commonly captured species at our site.

Finally, our mixed model indicated that all 5 ant-followers differed from each other in mass (LRT: $P < 0.001$, $\chi^2 = 3109$, $df = 4$; Figure 4), with the 2 *Dendrocincla* and 2 *Dendrocolaptes* increasing in even, stepwise fashion from 40 to 79 g. No individual *H. perrotii* overlapped the mass of any other ant-follower, with this species tipping the scales at a robust 114 g.

Dendrexetastes rufigula: The Solitary Canopy Species

We had just 5 observations of this elusive canopy species, 4 of which were birds with mixed-species flocks. Our model predicted a mean vertical stratum of 23 m, with confidence intervals extending well above those of other species. Our lowest observation of *Dendrexetastes rufigula* was 21 m (72% of local canopy height). This species has never been captured at the BDFFP (in ~70,000 captures), probably because it systematically avoids the lowest 2–3 m of the forest. By contrast, *Dendrocolaptes picumnus*, a bird of similar size, which also occurs at a similar density (Table 1), has been captured 33 times.

DISCUSSION

Using a series of analyses with traits representing both morphological and behavioral aspects of niche space, we were able to separate all 13 species into unique combinations of niche dimensions (Figure 6). The behaviors we quantified highlighted considerable differences among sociality, vertical strata, and myrmecophily, ultimately separating 2 species cleanly into unique niches: *Dendrexetastes rufigula*

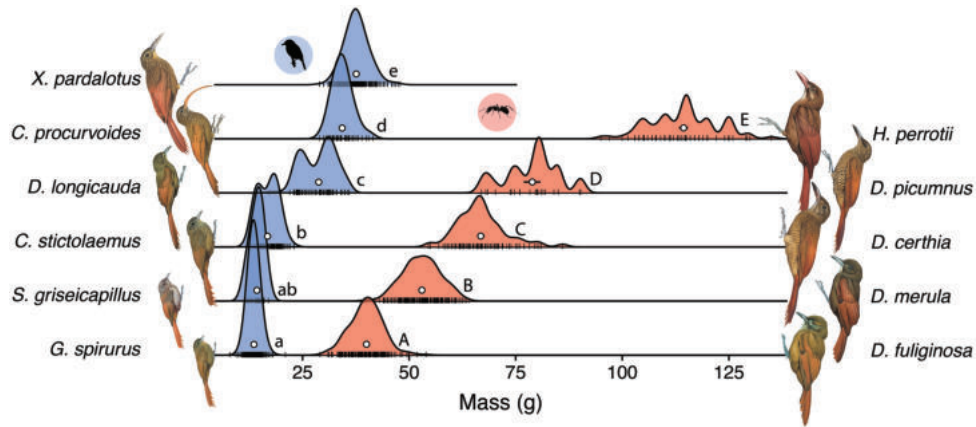


FIGURE 4. Smoothed mass distributions for 11 species of woodcreepers at the BDFFP. Rug plots show individual data points, and white dots and error bars indicate means and 95% confidence intervals, generated from the best-fit model. Most error bars are so narrow that they are concealed by the dot for the mean. Letters next to distributions represent significant differences among species within each social group, with identical letters indicating no difference (lowercase: mixed-flockers; uppercase: ant-following species). In comparison to the ant-followers, mixed-flockers overlap considerably in mass, especially among the 3 smallest woodcreepers. *Lepidocolaptes albolineatus* and *Dendrexetastes rufigula* are excluded from this plot due to insufficient data. Bird illustrations reproduced by permission of Lynx Edicions.

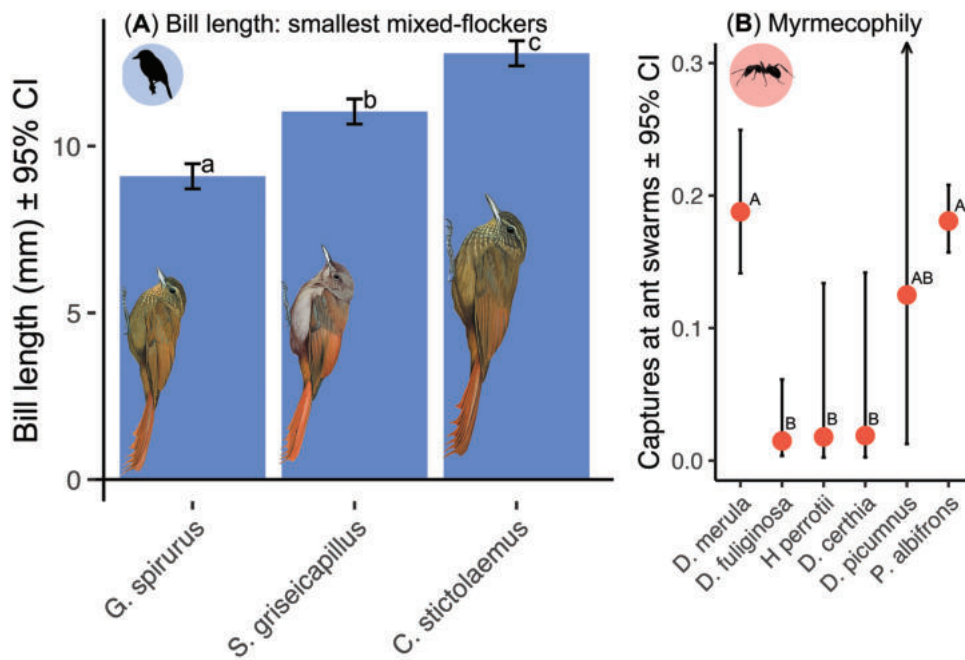


FIGURE 5. (A) Bill length of the 3 smallest woodcreepers and (B) number of captures per individual at ant swarms for ant-following species at the BDFFP. Means and 95% confidence intervals generated from best-fit models. Sample sizes of individual birds in (B) (from left to right) are 396, 29, 17, 6, 3, and 1,449. *Pithys albifrons*, a known obligate ant follower and the most commonly captured species at the project, is included as a reference. Letters next to distributions represent significant differences among species within social groups, with identical letters indicating no difference (lowercase: mixed-flockers; uppercase: ant-followers). Upper confidence intervals for *Dendrocolaptes picumnus* (1.24) truncated to aid visualization. Bird illustrations reproduced by permission of Lynx Edicions.

(solitary, canopy) and *L. albolineatus* (mixed-flocker, subcanopy to canopy). Within each social group, the addition of 2 niche axes (mass and bill size) further distinguished the remaining 11 species. Our ordinations separated the 2 dominant social strategies: the 5 ant-following species,

with their larger bodies and heavier bills, were morphologically distinct from the 7 species that join mixed-species flocks. For the understory and midstory mixed-flockers, the largest 3 species differed significantly by mass, whereas the smallest 3 overlapped broadly in mass, but were

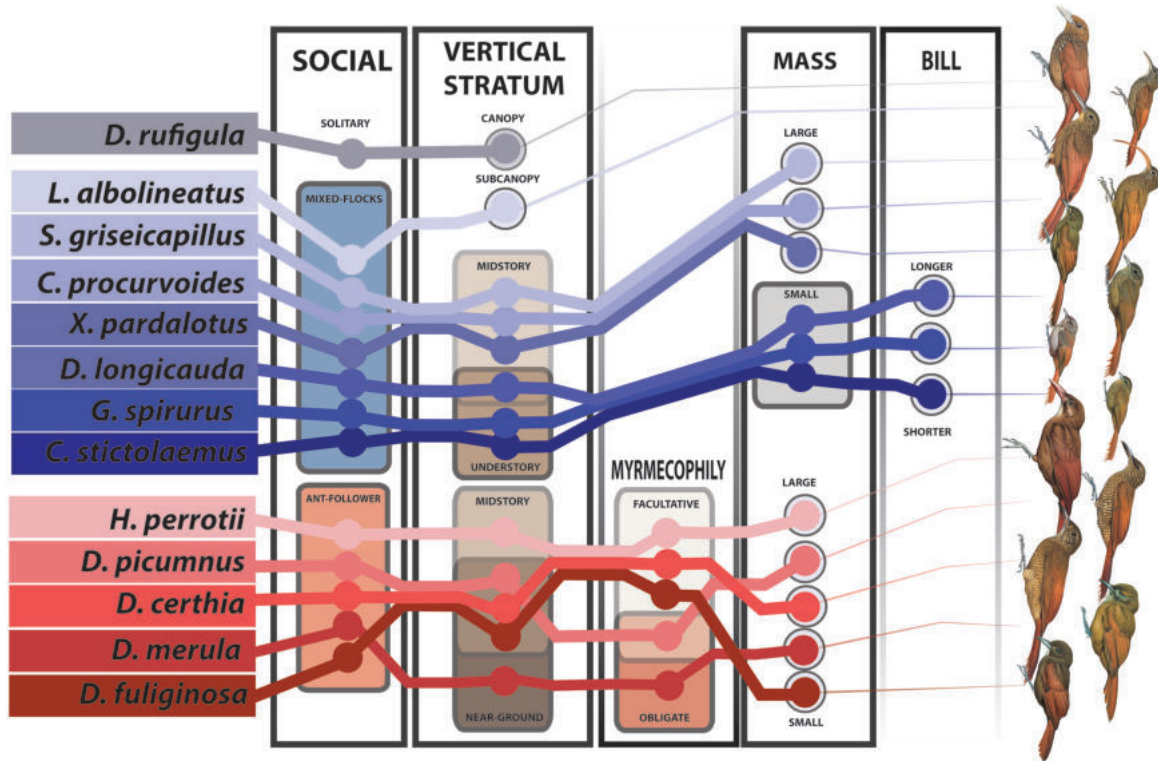


FIGURE 6. Summary demonstrating niche differentiation for the 13 woodcreeper species at the BDFPP. Overlapping circles indicate no detectable difference in a given niche dimension (trait); individual circles indicate that our analyses detected significant differences among species. We used ordination to separate among social groups (mixed-flock vs. ant-follower) and GLMs or GLMMs for all other analyses. Bird illustrations reproduced by permission of Lynx Edicions.

uniquely separated by bill length. The 5 ant-following species had nearly discrete distributions along the mass niche axis, which likely corresponds to their interspecific dominance hierarchies at the front of raiding army ant swarms (Pierpont 1986, Willis and Oniki 1978, Martínez et al. 2021). MacArthur (1958) was able to mostly separate 5 warbler species into unique foraging locations on coniferous trees; however, those species still overlapped considerably in their use of the top and outermost portions of the trees. In the western Amazon, Pierpont (1986), who focused on interspecific aggression, found that woodcreepers were discretely dispersed across mass, vertical strata, and foraging maneuvers, including “pickers” (skinny bills) and “salliers” (wide bills). Larger species were dominant over smaller species, and species with similar microhabitat use were more aggressive towards each other, strongly suggesting a mass-driven interspecific dominance hierarchy that maintained niche partitioning. Both MacArthur and Pierpont speculated, as do we, that behavioral and morphological adaptations driven by competition for arthropod prey promote sympatric coexistence, especially when interspecific competition is high (i.e. among ant-followers). Thus, for our woodcreeper system, one possible evolutionary pathway is that once food-driven behavioral differences had been established to minimize interspecific

competition (ant-followers and mixed-flockers), character displacement within these groups facilitated the evolution of divergent physical traits such as mass and bill length (Anderson and Weir 2021).

Mixed-Flocking Species vs. Ant-Following Birds

Our ordinations illustrate that size is a major determinant of shared niche space for foraging woodcreepers. Ant-following woodcreepers are large-bodied with heavier, more powerful bills than woodcreepers that join mixed-species flocks. For ant-following birds in general, larger size allows a species to dominate smaller birds at ant swarms (Pierpont 1986, Martínez et al. 2021), and we found that ant-following woodcreepers separated neatly by mass (Figure 4), mirroring dominance hierarchies (Martin and Ghalambor 2014). On the other hand, we found substantial overlap in body size for woodcreepers that follow mixed-species flocks (Figure 4). These species have a much wider range of thinner, finer-tipped bills (9.5–54.9 mm), which some species use to probe substrates, an infrequent maneuver for ant-following woodcreepers (Marantz et al. 2003). This then begs the question of whether morphology drove interspecific foraging associations or vice versa. We can imagine plausible scenarios for both hypotheses, whereby a shift in body size opened novel foraging

opportunities (e.g., at ant-swarms) as well as where inter-specific interactions led to the enhancement of advantageous traits (e.g., increasing body size). Regardless of the mechanism, there appears to be a strong phylogenetic signal for ant-following and flock-following; at the BDFFP, each woodcreeper genus includes only one or the other (Figure 1). Further, across the woodcreeper subfamily, all but one genus (*Dendrocincla*) is either entirely ant-following or entirely not ant-following (Supplementary Material Figure S5); only the montane *Dendrocincla tyrannina* is not a regular ant-follower. Therefore, it is especially curious that *Dendrexetastes rufigula* is the only largely asocial woodcreeper at our site, where it often forages alone in the canopy. Despite being embedded within a clade of large-billed and heavy-bodied army ant-followers, it apparently never joins swarms of army ants (Marantz et al. 2003).

Distinguishing Among the Mixed-Flocking Species

Although 7 species of woodcreepers regularly join insectivorous mixed-species flocks, niche overlap among these species is reduced by several factors. First, even though individuals of all species accompany flocks most of the time (>75% for 6 of 7 species; Supplementary Material Figure S4B), these 7 species do not simultaneously participate in the same flock (Supplementary Material Figure S4A). In fact, during 300+ hours of flock observation, we never observed >5 species together with the same flock. Within a given flock, only 2 species were consistently present the majority of the time: *G. spirurus* (71%) and *X. pardalotus* (92%; Supplementary Material Figure S4A). Other woodcreeper species were present less than ~25% of the time, suggesting that realized co-occurrence within flocks is typically limited to just a few species at any given time. The proximal reason for this may be a consequence of 2 non-mutually exclusive factors. First, the territory size for some species (e.g., ~37 ha for *S. griseicapillus*; Johnson et al. 2011) far exceeds that of the flock (~15 ha; Rutt et al. 2020, Rutt and Stouffer 2021), whereas *G. spirurus* is the only woodcreeper with a territory size smaller than that of a primary forest flock (5.2 ha; Johnson et al. 2011). Further, color-banded *D. longicauda* and *Ca. procurvoides* regularly ranged across 2 or 3 flocks in French Guiana (Jullien and Thiollay 1998), thereby limiting opportunities for co-occurrence within any single flock. Second, some species do not saturate the forest with territories and, as a result, are absent from flocks in the lacunae (Johnson et al. 2011). Even when flocking species do co-occur in x - y space, that does not necessarily indicate overlap in three-dimensional space (Figure 3). Although most mixed-flockers hitch upwards from the understory to the midstory, there is a continuum of vertical habitat use from *Ce. stictolaemus*, an understory specialist, to *L. albolineatus*, a subcanopy to canopy specialist. Similarly, although flock-following species exhibit greater overlap in body size than ant-followers

(Figure 4), only the 3 smallest mixed-flockers (14–17 g) were inseparable by mass alone. However, the coexistence of the smallest woodcreepers is probably not dictated by the density of flocks—as was postulated for the smallest antwrens (8–9 g; Powell 1989)—because they are (1) not as diminutive as the antwrens, and should therefore have greater space requirements; and (2) do not adopt territories that perfectly align with those of a single flock. For the smallest mixed-flockers, bill shape, bill length (Figure 5A), and foraging technique (especially for the chisel-foraging *G. spirurus*) were informative, suggesting that differences in diet and prey size are also at play. To test this prediction, recently developed techniques for diet DNA metabarcoding could be applied to our woodcreeper ensemble (Jarrett et al. 2020, Sottas et al. 2020).

Distinguishing Among the Ant-Followers and the Evolution of Ant-Following

The 5 ant-following woodcreepers had discrete masses (Figure 4) but overlapped in vertical strata (Figure 3) and myrmecophily (Figure 5B). We believe that our assessment of niche overlap at swarms is likely reduced by factors that we did not measure, including dominance hierarchies, diet specialization, and microhabitat use. As with the flocking woodcreepers, ant-followers likely vary in their dependence on army ants and may not all simultaneously attend the same swarm. The only obligate ant-following woodcreeper at our site, *Dendrocincla merula* (Harper 1989), forages almost exclusively at swarms, whereas the other woodcreepers are considered facultative species, which regularly follow ants but often forage away from swarms or even, at times, with mixed-species flocks (Supplementary Material Figure S4; Willis 1972, Willis and Oniki 1978). By our measure, *Dendrocincla merula* showed ~10 times higher myrmecophily than *Dendrocincla fuliginosa*, *H. perrotii*, and *Dendrocolaptes certhia*, equivalent to the common antbird *Pithys albifrons*, an obligate ant-follower (Figure 5B; Willis and Oniki 1978). *Dendrocincla merula* only overlapped *D. picumnus* because of the latter's small sample size and correspondingly large confidence intervals. Although our myrmecophily estimates for the four facultative woodcreepers overlapped (Figure 5B), this measure does not reflect realized co-occurrences at swarms. When birds do co-occur at swarms, they adhere to mass-based dominance hierarchies (Willis and Oniki 1978, Pierpont 1986, Martínez et al. 2021). Space at swarms is divided into distinct foraging zones, with the lowest area closest to the swarm front (average width about 9–10 m; Willson 2004) considered to be the most profitable region for prey (Willis and Oniki 1978). Thus, observed overlap in vertical stratum (Figure 3) may be driven by increased pressure to forage near the ground, where most ant raiding takes place. With birds competing for such a small space,

even a few meters difference in foraging height (~4 m between *Dendrocincla merula* and *Dendrocincla fuliginosa*; Figure 3) may disproportionately affect access to food resources. On Barro Colorado Island, for example, 90% of *Dendrocincla fuliginosa* perches were below 5 m compared to only 50% in the presence of a dominant ant-follower (figure 2 in Willis 1966). In this latter scenario, time spent below 1 m dropped by 20% which suggests that foraging height is largely influenced by species composition and mass-mediated dominance at swarms (Willis 1966). The mass ratios of smaller to larger ant-following woodcreepers were remarkably close to the Hutchinsonian ratio of 1:1.3—from smallest to largest: 1.32, 1.26, 1.18, and 1.45 (Hutchinson 1959, Lewin 1983). The consistency of this ratio, which is pervasive in other ecological systems, suggests that interspecific competition was a meaningful force in shaping the BDFFP woodcreeper ensemble. Still, the relationship between mass and dominance may not be clear-cut for woodcreepers. Whereas larger dominant woodcreepers frequently displace smaller species at swarms, being heavy has its downside—larger birds have limited maneuverability in dense undergrowth where smaller woodcreepers have access to lower slender perches. Interestingly, ant-following woodcreepers also sallied more often than mixed-flockers (Supplementary Material Figure S3). Because woodcreepers maneuver by hitching up tree trunks, sallying may often be the only available option for capturing prey at a swarm due to the distance and width of the nearest tree.

Dendrexetastes rufigula

Among woodcreepers at the BDFFP, *Dendrexetastes rufigula* occupies perhaps the most unusual niche. Whereas the other 12 species frequented ant swarms or mixed-species flocks, *Dendrexetastes rufigula* did not, and is typically observed singly or in well-separated pairs throughout Amazonia (Marantz et al. 2003). At our site, it occurs only at the highest levels of the forest—above 21 m in all our observations—and is absent from secondary forest (Cohn-Haft et al. 1997). Curiously, elsewhere in Amazonia, this species occupies edges, flooded forests, and mid-to-late successional growth (Marantz et al. 2003) and is one of the few woodcreepers that occurs on river islands (Rosenberg 1990). Its phylogenetic position, stout bill, and large size (~70 g, compare to Figure 4) all align it with ant-following woodcreepers, just like its two closest relatives at our site (*Dendrocolaptes*; Figure 1). We speculate that, unlike in more depauperate areas such as disturbed forests and river islands, this species is restricted to the canopy of primary *terra firme* forest due to competition with larger, more aggressive woodcreepers, such as those in the genus *Dendrocolaptes* and *Hylexetastes*. Even in depauperate woodcreeper ensembles, however, there appear to be no observations of this species foraging at ant swarms (Marantz et al. 2003).

Caveats and Future Work

Although we provide considerable insight into niche differentiation within the woodcreeper ensemble at the BDFFP, there is much room to build on our findings. Using behavior and sociality alone, we were only able to separate 2 species into unique niches: we required additional morphological traits (mass and bill length) to cleanly separate each of the remaining species. To further characterize niche space, a more universal method of quantifying flocking propensity would be helpful, as would comparing the frequency of interspecific cooccurrences and aggressive interactions within both mixed-species flocks and aggregations of ant-following birds. Given the differences in bill size and shape for the woodcreepers of the BDFFP, we predict that rigorous data on diet and foraging behavior would together separate our species into well-differentiated niches, along with Pierpont's (1986) woodcreepers and MacArthur's (1958) warblers. Unlike migrant species, however, resident birds such as our BDFFP woodcreeper ensemble are permanent fixtures, which means they are much more likely to exist in interspecific equilibrium (Powell et al. 2021) and to partition high-quality resources. Removal (Powell et al. 2021) and natural experiments—for example, on Amazonian islands with different woodcreeper ensembles (Rosenberg 1990, Wolfe et al. 2015)—would provide further insight if they can document release from competition (i.e. a niche shift) in the absence of competing species. Similarly, we would gain further insights about the role of interspecific competition and the constraints of sociality by examining how mixed-flockers and ant-followers shift their niches when they forage away from other woodcreepers (Darrah and Smith 2013).

Woodcreepers at the BDFFP in the Context of Amazonia

The 13 species of woodcreepers at the BDFFP illustrate the high alpha diversity, habitat specificity, and generally widespread distributions of Amazonian woodcreepers. All 13 species overlap at the scale of 100-ha plots within undisturbed forest (e.g., Johnson et al. 2011, L.L. Powell, personal observation). At the same time, *terra firme* forest at the BDFFP and throughout Amazonia excludes woodcreepers associated with riverine forest. At the BDFFP, absent species include *Nasica longirostris*, *Xiphorhynchus obsoletus*, *Dendroplex picus*, and *Dendroplex kiernerii* (Supplementary Material Figure S5), all of which can be found along the Amazon, Negro, and tributaries near Manaus, but have never been recorded at the BDFFP. In some cases, these species occur along tendrils of igapó forest that connect almost imperceptibly with *terra firme* forest, but the birds remain in their appropriate habitat. *Xiphorhynchus guttatus* occurs in mature forest elsewhere in its ample range, but in central Amazonia it also does not appear to penetrate *terra firme* forest. Higher

alpha diversity of woodcreepers reported from western Amazonia includes riverine species accompanying within-plot habitat variation (e.g., Terborgh et al. 1990, Cohn-Haft et al. 1997). Among *terra firme* woodcreepers, the BDFFP species all have broad Amazonian distributions; even the most range-restricted species, *X. pardalotus* and *H. perrotii*, still occur throughout northeastern Amazonia. Only 1 species of *terra firme* woodcreeper that occurs in northeastern Amazonia is absent from the BDFFP: *Xiphocolaptes promeropyrhynchus*, one of the largest woodcreepers, is patchily distributed in lowland rainforest north of the Amazon, although it is more common in southern Amazonia. Thus, any given parcel of *terra firme* forest at the BDFFP, and probably elsewhere across a broad swath of similar forest on the Guianan Shield, will host 13 of the 14 species of woodcreepers possible based on biogeography and habitat specificity. Presumably, this homogeneity across space in woodcreeper species composition reflects the stability of the ensemble, facilitated by the morphological and behavioral differences we describe.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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Author contributions: L.P., C.R., K.M., J.W., E.J., and P.S. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). L.P., C.R., K.M., J.W., E.J., P.R., and P.S. performed the experiments (collected data, conducted the research). L.P., C.R., K.M., J.W., E.J., P.R., and P.S. wrote the paper. L.P., C.R., K.M., E.J., P.R., and P.S. developed or designed the methods. L.P., C.R., and P.R. analyzed the data. P.S. contributed substantial materials, resources, or funding.

Data availability: Analyses reported in this article can be reproduced using the data provided by Powell et al. (2022).

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