



RESEARCH ARTICLE

Connecting Amazonian historical biogeography and local assemblages of understory birds: Recurrent guild proportionality within areas of endemism

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Abstract

Aim: Current diversity patterns in local communities result from historical and contemporary events that operate at distinct spatial and temporal scales. However, the contribution of local and large-scale processes in structuring species diversity remain a contentious topic in ecology. We investigated diversity patterns (species richness, composition and number of captures) of understory bird assemblages in Amazonian unflooded (*terra firme*) forests. We sought to understand whether understory bird assemblages in distinct areas of endemism show distinct patterns of diversity, and whether species replacements among areas of endemism occur while the proportion of species within guilds remains stable.

Location: Amazonia.

Taxon: Understorey birds.

Methods: To investigate diversity patterns, we compiled studies that mist-netted birds at 11 regions across seven Amazonian areas of endemism. We used coverage-based rarefaction curves, non-metric multidimensional scaling (NMDS) and created a heatmap based on the proportion of captures in each area of endemism to access patterns of richness, composition and captures of understory birds, respectively. The relative variance (RVgp index) was calculated to investigate the existence of guild proportionality within each area of endemism.

Results: Bird assemblages diverged across the seven areas of endemism, in terms of species richness, composition and captures. However, the proportion of species and individuals within guilds was similar among areas of endemism, indicating that species replacements across areas of endemism occur while maintaining the same ecological functions. Guild proportionality suggests that interspecific competition and resource availability are more important than environmental heterogeneity in structuring understory bird assemblages.

Main conclusions: The similar proportion of species within guilds suggest that interspecific competition and resource availability are more important than environmental heterogeneity in structuring local assemblages, possibly via a process of limiting

similarity in morphological and functional traits. The observed congruent structure in understorey bird assemblages across areas of endemism shows that coupled historical and ecological processes, operating at local to large scales, have led to current patterns of diversity and composition in Amazonian bird communities.

KEYWORDS

areas of endemism, diversity patterns, guild proportionality, historical biogeography, interspecific competition, understorey birds

1 | INTRODUCTION

Diversity patterns of local communities result from historical and contemporary events that operate at distinct spatial and temporal scales (Hubbell, 1997). At a local scale, habitat characteristics, species idiosyncrasies, resource availability, biotic interactions and niche requirements are fundamentally important in the structure, dynamics and organization of communities in space and time (Ernest et al., 2008; Huston, 1979; Leibold et al., 2004; Wiens, 1989). Current diversity patterns in local communities are also influenced by large-scale historical processes that have unfolded over millions of years, such as the movement of tectonic plates, montane uplifting, long-term climate change and development of modern drainage systems (Hoorn, 2010; Huston, 1994; Levin, 1992). However, the contribution of local and large-scale processes in structuring diversity and its idiosyncrasies between taxa and regions remains a contentious topic in ecology.

Amazonia has undergone important events throughout its history, such as the evolution of major drainages and the establishment of upland (*terra firme*) forests. These large-scale events altered the geomorphological conformation of the biome, directly transforming landscapes and ecosystems and, consequently, the evolution of species (Albert et al., 2018; Aleixo, 2004; Ferreira et al., 2016; Ribas et al., 2012; Schultz et al., 2017). The role of large Amazonian rivers in the evolution of regional biotas, for instance, is a widely discussed and highly controversial subject (Lougheed et al., 1999; Santorelli et al., 2018). Wallace (1854) was the first to notice distinct sets of species on opposite river margins, suggesting that large rivers, such as the Negro River, served as effective physical barriers to dispersal. Recent studies have corroborated this view showing that large rivers often act as effective barriers to dispersal for various taxonomic groups (Hayes & Sewlal, 2004; Maximiano et al., 2020; Moraes et al., 2016; Naka, 2011; Naka & Brumfield, 2018; Pomara et al., 2013), although this is not supported by all studies (Oliveira et al., 2017; Santorelli et al., 2018). It is well documented that the evolution of drainages isolated some populations on opposite banks of large rivers, resulting in allopatric speciation (Ribas et al., 2012). Subsequent recognition of restricted and specific biogeographic patterns in the distribution of some bird species culminated in the delimitation of Amazonian areas of endemism (Cracraft, 1985).

Areas of endemism are characterized by the congruent geographic distribution of endemic species limited by geographic

barriers, thereby disrupting gene flow across adjacent populations (Harold & Mooi, 1994; Hausdorf, 2002; Platnick, 1991). Endemic species include those that, in addition to being spatially restricted by a geographic barrier, have their closest relatives inhabiting adjacent areas of endemism (Harold & Mooi, 1994). Currently, nine areas of endemism based on avian distributions have been described for Amazonia: Belém, Guiana, Imeri, Inambari, Jaú, Napo, Rondônia, Tapajós and Xingu (Borges & Silva, 2012; Cracraft, 1985; Haffer, 1969; Naka, 2011; Silva et al., 2002). These areas are characterized by the restricted distributions of some species, which coincide, at least partially, with major rivers. It has been proposed that the delimitation of areas of endemism is a result of the biogeographic history of Amazonia (Cracraft, 1985; Ribas et al., 2012).

Although several studies have suggested that Amazonian patterns of diversity are related to large rivers (Wallace, 1854; Cracraft, 1985; Ribas et al., 2012; but see Haffer, 1985), decisive factors likely contribute to shape such patterns at local scales. The ways in which species assemblages share available resources is one of the main determinants of the diversity of coexisting species (Pianka, 1974). Hence, the coexistence and structure of local assemblages are based on two main assumptions: (i) Species with a strong overlap in resource use cannot coexist (Hardin, 1960; Simberloff & Connor, 1981); and (ii) coexisting species in syntopy must diverge functionally or morphologically in their ecological requirements to preclude competitive exclusion (Hutchinson, 1959; Pianka, 1974). Thus, both habitat homogeneity and niche convergence can increase the strength of interspecific competition and lead to processes of limiting similarity, enabling coexistence by reducing overlap in resource use (Gómez et al., 2010; MacArthur & Levins, 1967).

The concept of limiting similarity led some authors to propose assembly-rule models that enable species coexistence (Diamond, 1975; Feeley, 2003; Wilson, 1989; Wilson & Whittaker, 1995). Some of these models predict a relevant role of guilds (ie, ecologically similar groups of species that exploit similar resources) in structuring local diversity (Wilson, 1999). Wilson's (1989) model of guild proportionality hypothesizes that if competition plays a strong role in structuring assemblages, the relative proportion of species in each guild should remain stable across assemblages that may diverge in richness and composition (Feeley, 2003). Similar proportionality between assemblages would then result from interactions between co-occurring species. For example, if a new frugivorous species attempts to become established in an assemblage that already includes



other frugivorous that consume similar resources, it can either exclude or be excluded competitively. In both cases, the proportion of species within guilds is maintained (guild proportionality).

Amazonia is the largest and most diverse tropical forest domain on Earth and provides a unique opportunity to explore the interaction between areas of endemism (as a proxy of historical processes) and the structure of biological assemblages. However, few studies have linked historical biogeography and coexistence processes in local assemblages, and most biogeographic studies in tropical forest regions fail to include species abundance data.

If areas of endemism indeed represent biogeographic units useful in understanding diversity patterns of local understorey bird assemblages, we expect that historical processes that culminated in the current Amazonian areas of endemism will also influence widely distributed species, determining similar patterns of diversity between areas for both endemic and non-endemic species. We also predict that species losses or replacements between areas of endemism occur while maintaining the same ecological functions and that interspecific competition can be a decisive factor in structuring local assemblages. Applying this general framework, we investigate the diversity patterns of understorey bird assemblages in *terra firme* forests across seven Amazonian areas of endemism. We examine whether (i) understorey bird assemblages (considering either all species sampled or only widespread species) show distinct diversity patterns (richness, composition and number of captures) across areas of

endemism; (ii) species replacement among areas of endemism occur while the proportion of species within guilds remains stable, resulting in guild proportionality within each area of endemism.

2 | MATERIAL AND METHODS

2.1 | Study area

We used mist-net data of understorey birds from *terra firme* forests in Amazonia (Table 1), encompassing all areas of endemism known for Amazonian birds, except for the Belém and Imeri regions (Figure 1). These landscapes were chosen because they had comprehensive mist-net samples of understorey birds from *terra firme* forests. We focused our analysis on *terra firme* forests because this habitat type represents the dominant portion of Amazonia, and because many species that characterize areas of endemism are specialists of this forest type.

2.2 | Bird data

We compiled data from 11 studies that used mist-nets to sample birds within different areas of endemism across Amazonian *terra firme* forests. Mist-nets are widely used for capturing birds, sampling mainly

TABLE 1 Summary of sampling characteristics of understorey birds in *terra firme* forests in Amazonia used in this study

Area of endemism	Sampling areas ^a	Number of capture sites	Sampling periods	Number of individuals
Napo	Tiputini Biodiversity Station (Harpia) ¹	1	2001–2004	3037
	Tiputini Biodiversity Station (Puma)	1		
Jaú	Jaú National Park (East) ²	5	1994–2007	2917
	Jaú National Park (West)	4		
Guiana	BDFFP ³	1	1985–1989	1391
	Ducke Reserve ⁴	87	2009, 2012–2014	3582
Inambari	Juruá River ⁵	18	1991, 1992, 2010	1370
	BR 319 ⁶	11	2012–2013	843
	Madeira River (left bank) ⁷	4	2010–2011	1500
Rondônia	Madeira River (right bank)	3	2010–2011	1062
	Tapajós River (left bank) ⁸	4	2012–2013	475
Tapajós	Tapajós River (right bank)	7	2012–2013	684
	Tapajós National Forest ⁹	3	1997–2001	1514
	Xingu River (left bank) ¹⁰	6	2007–2008	622
Xingu	Xingu River (right bank)	3	2007–2008	389
	Tocantins River (left bank) ¹¹	10	2005	712
Total	–	–	–	20,098

Abbreviation: BDFFP, Biological Dynamics of Forest Fragments Project.

^a(1) Blake and Loiselle (2009, 2015); (2) Borges et al. (2001); Borges and Carvalhaes (2000); (3) Bierregaard and Lovejoy (1989); Stouffer and Bierregaard (1995); (4) Bueno et al. (2012); Menger et al. (2017); (5) C.A. Peres (unpublished data); (6) Souza (2014); de Abreu et al. (2018); (7) Relatório de pré-enchimento da Usina Hidrelétrica de Santo Antônio (2013); (8) Maximiano et al. (2020); (9) Henriques et al. (2008); (10) Estudo e Relatório de Impacto Ambiental da Usina Hidrelétrica de Belo Monte (2008); (11) Avaliação e Monitoramento da Avifauna na Área do Reservatório de Tucuruí (2008).

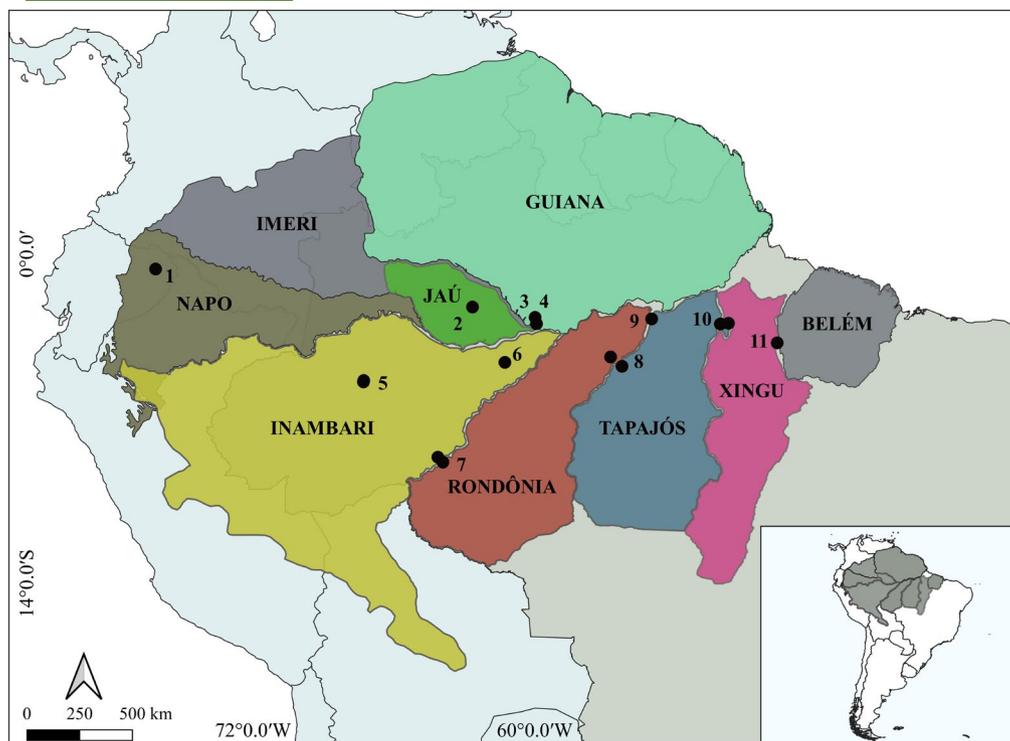


FIGURE 1 Sampling areas within seven areas of endemism throughout Amazonia. Solid circles represent only the central position of the samples, rather than the exact positional location of sample units in each study. The delimitation of areas of endemism follows the boundaries proposed by Haffer (1969); Cracraft (1985); Silva et al. (2002); and Borges and Silva (2012).

those that inhabit the forest understorey. Among the disadvantages of the method, mist-nets capture birds that are largely restricted to within 3 m above ground so that captures are not representative of the total local species diversity (Blake & Loiselle, 2009; Renssen & Good, 1996). However, mist-nets may be efficient in studies on the diversity and abundance of species, because it ensures higher reliability in species identification and facilitates standardization of sample effort, besides allowing quantitative comparisons of species that are difficult to sample through visual or auditory censuses (Karr, 1981; Renssen & Good, 1996).

Mist-net studies used here were implemented with distinct designs, goals and contexts (see Appendix S1), resulting in large variation in the number of captured individuals per landscape (between 389 and 3582 captures for long temporal sampling). Despite this variation, we sought to make the data as comparable as possible. In cases of experimental studies (eg, Biological Dynamics of Forest Fragments Project—BDFFP; Tapajós National Forest), only captures obtained in control areas, representative of undisturbed forest, were used. Moreover, all sites located in seasonally flooded areas (ie, igapó and várzea forests) were removed (see Table S3).

We focused on understorey *terra firme* species and removed species that fit at least one of the following three criteria: (i) Species that are not typically found in the understorey (ie, species that preferably inhabit the midstorey and canopy); (ii) species that inhabit mainly open-habitat areas (eg, *campinas*); (iii) species that inhabit flooded areas but that may occasionally also occur in the understorey of *terra*

firme forest (see Appendix S2). Species selection was based on two databases (Stotz et al., 1997; Wilman et al., 2014) that contain information on habitat use and foraging stratum (understorey, midstorey and canopy). The list was subsequently revised by two ornithologists with extensive field experience in Amazonia. We also excluded recaptures from all analyses as we were interested in the number of individuals per species. With the exception of Xingu and Rondônia, all other areas of endemism were represented by more than 2000 captures, considering all sampling localities within each area of endemism (Table 1).

2.3 | Taxonomic and ecological standardization

The taxonomy of Neotropical birds has gone through intense rearrangement due to the number of published studies involving molecular and acoustic data, which undergo constant revision by the South American Classification Committee (Renssen et al., 2018) and the Brazilian Committee of Ornithological Records (Piacentini et al., 2015), often resulting in splitting previously polytypic species. This required a complete review of the bird taxonomy adopted in each study. First, we integrated the capture data into a single database and updated the species nomenclature based on the Brazilian Committee of Ornithological Records (Piacentini et al., 2015). The taxonomy of all species was assessed using the original or review paper, and those that had been recently split were assigned to the database according to their current geographic distribution. This approach led to renaming



some species that were previously known by the same name in different interfluves. For example, *Hypocnemis cantator* (Boddaert, 1783), which was formerly considered a single species, was split into seven species: *H. cantator*, *H. peruviana*, *H. flavescens*, *H. ochrogyna*, *H. subflava*, *H. rondoni* and *H. striata* (Isler et al., 2007; Whitney et al., 2013). After standardization, we double-checked the geographic distribution of all species using the digital platforms Xeno-canto (2018; <https://www.xeno-canto.org>) and Birds of the World (<https://birdsoftheworld.org/bow/home>; del Hoyo et al., 2018).

A guild is a group of ecologically analogous species that exploit similar resources (Wilson, 1999). In this study, we created two guild classifications: (i) One based on avian diets and body sizes; (ii) and a more refined typology based on diet, body size, sociality and foraging substratum. In both classifications, the feeding guild and body size of each species were retrieved from a global database on bird diets and body mass (Wilman et al., 2014). The diet of each species was based on the most frequently consumed food type (>50%). Based on feeding habitats and body size, we designated the following feeding guilds: small insectivores (≤ 15 g), medium insectivores (16–60 g), large insectivores (>60 g), small frugivores (≤ 20 g), medium frugivores (21–80 g), large frugivores (>80 g), small nectarivores (≤ 5 g), large nectarivores (>5 g), small carnivores (≤ 60 g), large carnivores (>100 g), small omnivores (≤ 40 g), medium omnivores (40–200 g) and large omnivores (>200 g). Omnivores were those species that consume more than three food types, each of which representing <50% of the diet. Diet and body size were combined to avoid grouping species that may share similar food resources but are unlikely direct competitors (ie, a small vs. a large carnivore).

The second guild classification was based on the diet and body size as described above, plus sociality (Cohn-Haft et al., 1997; <https://birdsoftheworld.org/bow/home>; del Hoyo et al., 2018) and foraging substratum (Karr et al., 1990; <https://birdsoftheworld.org/bow/home>; del Hoyo et al., 2018). Sociality criteria resulted in the following groups: solitary or in pairs, army-ant followers, lekking, monospecific flocks, mixed-species flocks and mixed-species assemblages at fruiting or flowering trees rather than flocking. Sociality was considered as a functional trait because it is directly associated with the way resources are used. For example, mixed-species flocks can improve foraging efficiency (Zuluaga, 2013), whilst army-ant followers can take advantage of the activities of ants or other flock members to capture insects flushed by the ant swarm (Willson, 2004). The last criterion was foraging substratum, which resulted in the following groups: ground, live foliage (that include fruits and flowers), dead foliage, army ants, air, water, branches and trunks and twigs.

2.4 | Sampling design and statistical analysis

2.4.1 | Species diversity and composition in local assemblages

We created coverage-based rarefaction curves based on the total number of individuals captured in each area of endemism to

compare species richness of bird assemblages and assess the representativeness of the sampling (Chao & Jost, 2012). The species richness was then extrapolated to total coverage when necessary. This method results in less biased comparisons of richness between communities, as it compares species richness for the same proportion of individuals within each community (Chao & Jost, 2012), but differences between sampling sites may still be masked. Therefore, we also included a coverage-based rarefaction applied to each sampling site (Table 1). We used the package iNEXT (Hsieh et al., 2016) in the R platform (R Core Team, 2020) to estimate species richness and calculate 95% confidence intervals, based on 200 bootstrap permutations (Chao et al., 2014).

To assess species richness, varying patterns of plant diversity and environmental heterogeneity across Amazonia (Steege et al., 2006; Tuomisto et al., 2019), we plotted our sampling points onto the World Wildlife Fund (WWF) map of ecoregions (Olson et al., 2001), which used global plant and animal distribution maps to delineate ecoregions.

We examined dissimilarity in species composition between areas of endemism using non-metric multidimensional scaling (NMDS) adopting four approaches: (a) Number of captures from all species; (b) presence/absence data from all species; (c) number of captures from 51 widely distributed species (ie, species that occur throughout Amazonia, but have not been captured in all areas of endemism); (d) number of captures from 25 widespread species (ie, ubiquitous species captured in all areas of endemism). We compared the available distribution maps of all 224 species captured in this study available on digital platforms Xeno-canto (2018; <https://www.xeno-canto.org>) and Wikiaves (2021; <https://www.wikiaves.com.br>) to provide a more complete picture of the overall widespread species, and those species captured across the seven areas of endemism investigated. We also ran NMDS analyses that excluded all species that are part of Amazonian species complexes (see Figure S1), which can be defined as closely related bird taxa that occur on opposite sides of large rivers throughout Amazonia (Haffer, 1969). This approach is an indirect measure of the degree to which biogeographic history influenced the distribution patterns of non-endemic and widely-distributed species throughout Amazonia.

For NMDS analyses, we generated artificial sampling units using equivalent numbers of individuals captured among sites. In the analysis including all species, samples consisted of 250 individuals, whilst for widely-distributed species samples of 100 individuals were used due to the smaller number of species and captures. Sampling units were generated using bootstrapping, via random draws without replacement, of captured individuals per site within each area of endemism (ie, drawings among all individuals within each area of endemism) and within each sampling area (i.e. within Ducke Reserve, Juruá River, BR 319, etc; see Figure S2). This procedure was adopted because we were unable to use real effort-weighted samples (eg, captures per 100 net-hours). Random samples standardized by number of individuals preserve the intrinsic structure of the assemblages as relative abundance among species while ensuring more reliable comparisons between areas of endemism. The dissimilarity between

samples was based on the Bray-Curtis index considering the abundance (ie, number of captures) matrix and the Jaccard index for the presence/absence matrix (Melo & Hepp, 2008).

To investigate the variation in number of captures of widespread species sampled in all areas of endemism investigated, we created a heatmap based on the proportion of captures in each area of endemism. This analysis creates dendrograms showing clusters of endemic areas (rows) using Euclidean distances to examine which areas are most similar based on species captures. Matrix rows and columns are reordered according to the clustering result with the proportion of captures in endemic areas displayed on a colour scale (Zhao et al., 2014). The heatmap provides a graphical result that facilitates examining differences among areas based on the captures of widespread species.

2.4.2 | Guild proportionality

We calculated the proportion of species and individuals representing each guild for each area of endemism. We also checked the incidence of proportionality in species distribution among different guilds, according to Wilson's (1989) guild-proportionality model. For this analysis, we used real sampling units according to the capture sites, with the exception of long-term sites monitored over several years (Ducke Reserve, BDFFP, Tiputini Biodiversity Station and Tapajós National Forest), for which sampling years were also used in addition to sites. For example, data at Ducke Reserve were collected at several capture sites. Due to the low number of species at each site, sampling units were delimited by year (eg, Ducke Reserve-2009). In Tiputini Biodiversity Station and Tapajós National Forest, samples consisted of two (Harpia and Puma) and three (control areas) sites, respectively, and sampling units were delimited based on both sites and years (eg, Harpia-2001). As sample sizes were highly variable, which may bias results, we only included sampling locations with at least 15 individuals in this analysis. Our used real sampling units restricted by space and time to preserve the inferential power of 'real-world' interaction/competition between individuals as much as possible.

The relative variance of species proportions within guilds (RVgp index) was calculated for three guild classification schemes using (i) only diet and body size for all species; (ii) diet, body size, sociality and foraging substratum for all species; and (iii) diet, body size, sociality and foraging substratum for only insectivores (the most species-rich and abundant feeding guild among understorey birds). This approach was used to test different levels of guild refinement. The observed RVgp was calculated for each guild separately as:

$$D = \sum_{j=1}^J (x_{ij} - \bar{x}_i)^2$$

where D is the deviance (amount of variation); \bar{x}_i is the the mean over the species number of guild i in sample j (out of J samples); x_i is the mean value of species number in guild i over all species in all J samples.

We generated null models by calculating D_{exp} using Monte Carlo simulations (999 randomizations) where overall species richness at a

site and the overall proportion of captures for each species at that site was held constant using the swap algorithm (Gotelli, 2000). D values calculated from observed data (D_{obs}) and mean values calculated for randomized datasets (D_{exp}) were used to compare the observed deviance with that expected under the null model using the standardization:

$$RVgp = 2 \frac{D_{obs}}{D_{obs} + D_{exp}} - 1.$$

A RVgp value was generated for each guild scheme (combination of diet, body size, sociality and foraging substratum), in each area of endemism. The Relative Variance of guild proportionality (RVgp) varies from -1.0 to $+1.0$. $RVgp < 0$ when the observed variance in guild proportions between samples is smaller than expected by the null model (alpha guilds), indicating guild proportionality. When RVgp equals to 0, the observed variance in guild proportions is on average exactly as expected under the null model. $RVgp > 0$ means that variance in guild proportions between samples is higher than expected by the null model (beta guilds), indicating guild disproportionality (Holdaway & Sparrow, 2006; Watkins & Wilson, 2003; Wilson, 1989). We retained all species in the dataset, but discarded monospecific guilds, where it occurred. In the end, RVgp values were calculated for 13 guilds considering diet and body size of all species; 40 guilds considering diet, body size, sociality and foraging substratum of all species; and 28 guilds considering body size, sociality and foraging substratum for only insectivorous species.

Alpha guilds may be generated under the assumptions of limiting similarity and competition, while beta guilds are more common under the strong variation of environmental conditions (Wilson et al., 1987). This analytical framework was originally created to assess individually observed values diverging from random (Wilson, 1988). However, the RVgp metric is standardized by random samples, which are also useful for broader comparisons. Therefore, rather than examining each site separately (ie, test individual hypotheses for each sampling site, generating a large number of inferential tests), we searched for general patterns of RVgp values between areas of endemism. We used a Generalized Linear Model (GLM), where RVgp values generated for each guild and area of endemism were the dependent and independent variables, respectively. We also tested the overall prevalence of one type of guild structure on another (alpha guilds over beta guilds) and the prevalence of one type of guild structure on another within each area of endemism, using a one proportion z-test and a binomial test, respectively.

3 | RESULTS

3.1 | Species diversity and composition of local assemblages

We recorded 224 species from a total of 20,098 individual understorey birds in Amazonian *terra firme* forests, distributed across 7 orders, 30 families and 115 genera. From this total, only 25 species



(11% of the total) were captured in all areas of endemism (ie, considered here as widespread species). A total of 51 species (22.8%) were widely distributed across Amazonia (including the above 25 ubiquitous species), but were not necessarily captured in all areas of endemism.

There was no clear relationship between number of captures and number of species among the areas of endemism. Inambari was represented by most species (123 species; 3713 captures), followed by Rondônia (112; 1537), Napo (107; 3037), Tapajós (105; 2820), Guiana (89; 4973), Jaú (87; 2917) and Xingu (79; 1101). The number of species unique to any given area of endemism ranged from 5 to 19: Xingu (5), Jaú (6), Tapajós (10), Inambari (11), Rondônia (12), Guiana

(17) and Napo (19). These values range between 6.3% and 19.1% of the total number of species recorded in each area.

Coverage-based rarefaction and extrapolation curves suggested that the sample coverage was sufficient for most areas, ranging from 0.982 to 0.989 (Xingu and Rondônia) to 0.998 (Guiana, Inambari, Napo; Figure 2a). Considering the extrapolation to complete sample coverage, the most species-rich area of endemism was Inambari (125 species), followed by Rondônia (124), Napo (109), Tapajós (106), Xingu (98), Jaú (95) and Guiana (89). Napo and Tapajós areas of endemism did not differ in extrapolated numbers of species (Figure 2b). Guiana had fewer species than other areas, except for comparisons with Jaú and Xingu (Figure 2b). At the other extreme, Inambari was

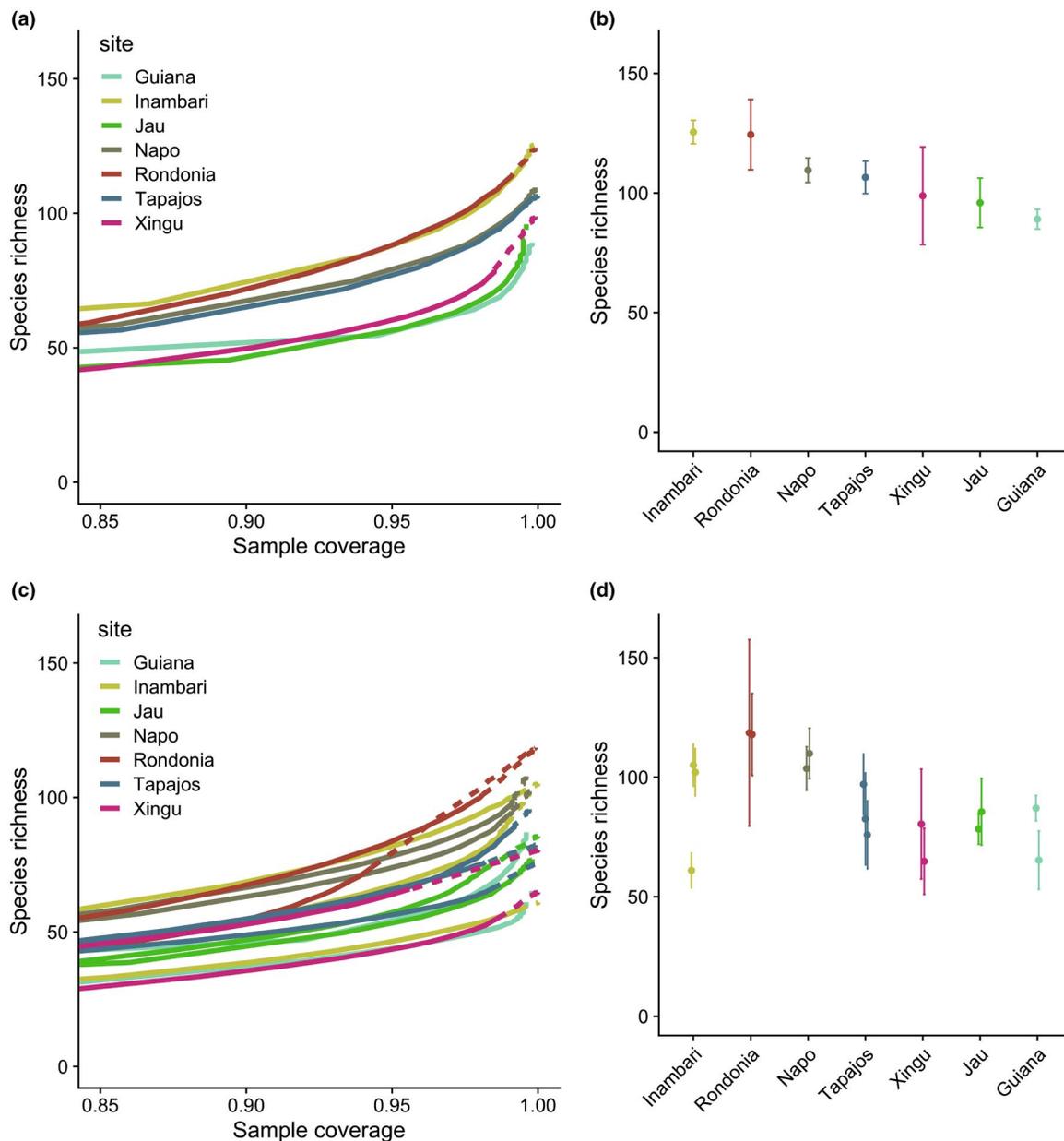


FIGURE 2 (a) Coverage-based rarefaction and extrapolation curves for all areas of endemism. (b) Extrapolation to complete sample coverage. (c) Coverage-based rarefaction and extrapolation curves at the site scale. (d) Extrapolation at the site scale

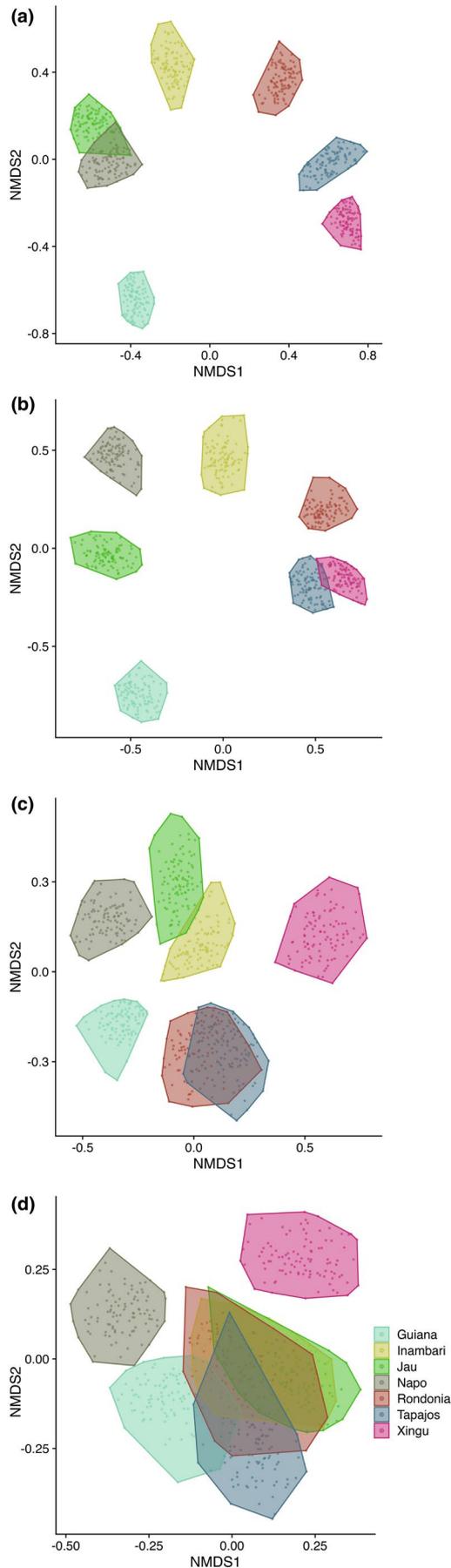


FIGURE 3 Dissimilarity in species composition between areas of endemism. (a) non-metric multidimensional scaling (NMDS) with all species, using capture data. (b) NMDS with all species, using the presence/absence data. (c) NMDS with 51 widely distributed species (i.e. species that occur throughout Amazonia) using capture data. (d) NMDS with 25 widespread species (i.e. only species captured in all areas of endemism) using capture data. Dots represent the sampling units created by the bootstrap of 250 (a, b) and 100 individuals (c, d)

apparently more species-rich than all other areas, except for comparisons with Rondônia. However, this pattern erodes at the site scale (Figure 2c,d). While some sites appear to harbour more species based on a similar number of individuals sampled, there is considerable variation between and within areas (Figure 2c). At the site scale, sample coverage varied from 0.952 (Xingu River - right bank) to 0.997 (Ducke Reserve), and there was no clear pattern between the number of species and individuals captured.

According to the WWF ecoregion map (Olson et al., 2001), each of the seven areas of endemism used here overlap several ecoregions: Guiana (five ecoregions), Inambari (4), Jaú (1), Napo (2), Rondônia (2), Tapajós (2) and Xingu (2). Our sampling points were, therefore, inserted into eight distinct ecoregions. Considering the Inambari area of endemism, our sampling points are located in two distinct ecoregions, which is not the case in any other area (see Figure S3).

Bird species composition based on the number of captures or presence/absence data differed between areas of endemism (Figure 3a,b). The composition based on the number of captures of 51 widely distributed species differed among the Guiana, Inambari, Jaú, Napo and Xingu areas of endemism, while Rondônia and Tapajós were similar (Figure 3c). Likewise, species composition of local assemblages based on the number of captures of 25 widely distributed species (ie, captured in all areas of endemism) differed among Guiana, Napo, Tapajós and Xingu, while Inambari, Jaú and Rondônia were similar (Figure 3d). NMDS results lacking the species complexes maintained the dissimilarity between the areas of endemism, whether those were based on the abundance or presence/absence data (see Figure S1).

The heatmap indicated that Wedge-billed Woodcreeper (*Glyphorynchus spirurus*, 1661 captures) was the most abundant among all widely distributed species recorded across the seven areas of endemism. This species was almost three times more abundant than the second most abundant species (*Dendrocincla merula*, 612 captures). Based on the proportion of captures of each species, Guiana and Napo were clustered together, close to Xingu, which remained isolated, whereas another cluster was formed by Rondônia, Inambari, Jaú and Tapajós areas (Figure 4).

3.2 | Guild proportionality

Most species in our assemblages were insectivores (176; 78.6%), followed by frugivores (17; 7.6%), omnivores (15; 6.7%), nectarivores



FIGURE 4 Dendrogram of widely-distributed species across the seven Amazonian areas of endemism. The dendrogram groups areas of endemism according to species relative abundance. Darker colours indicate higher abundance

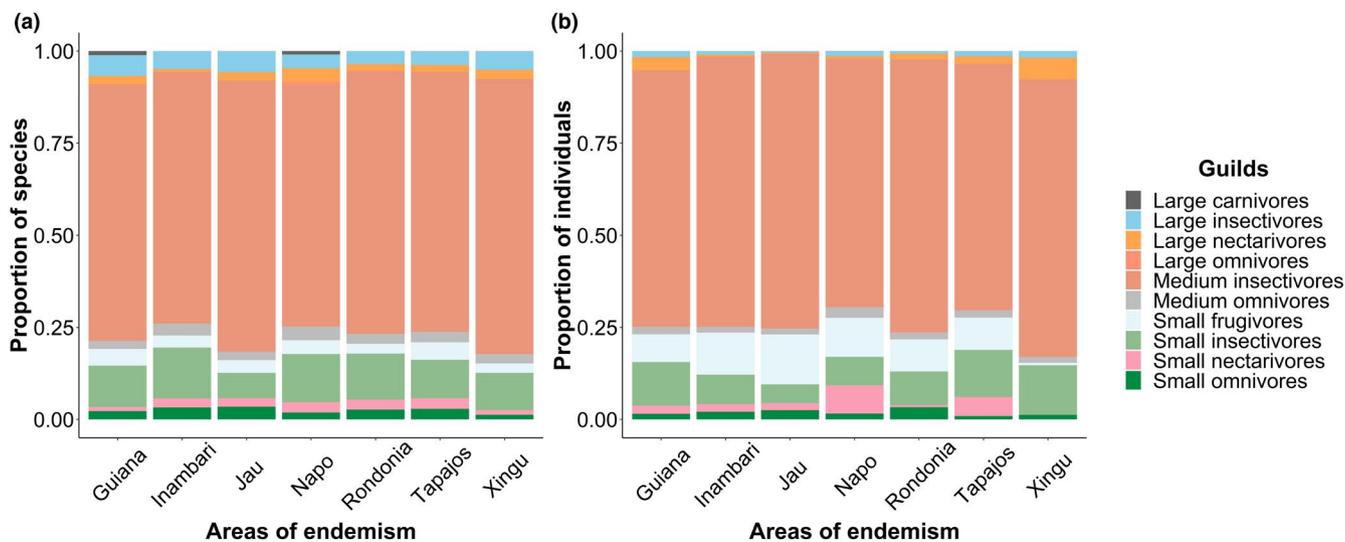
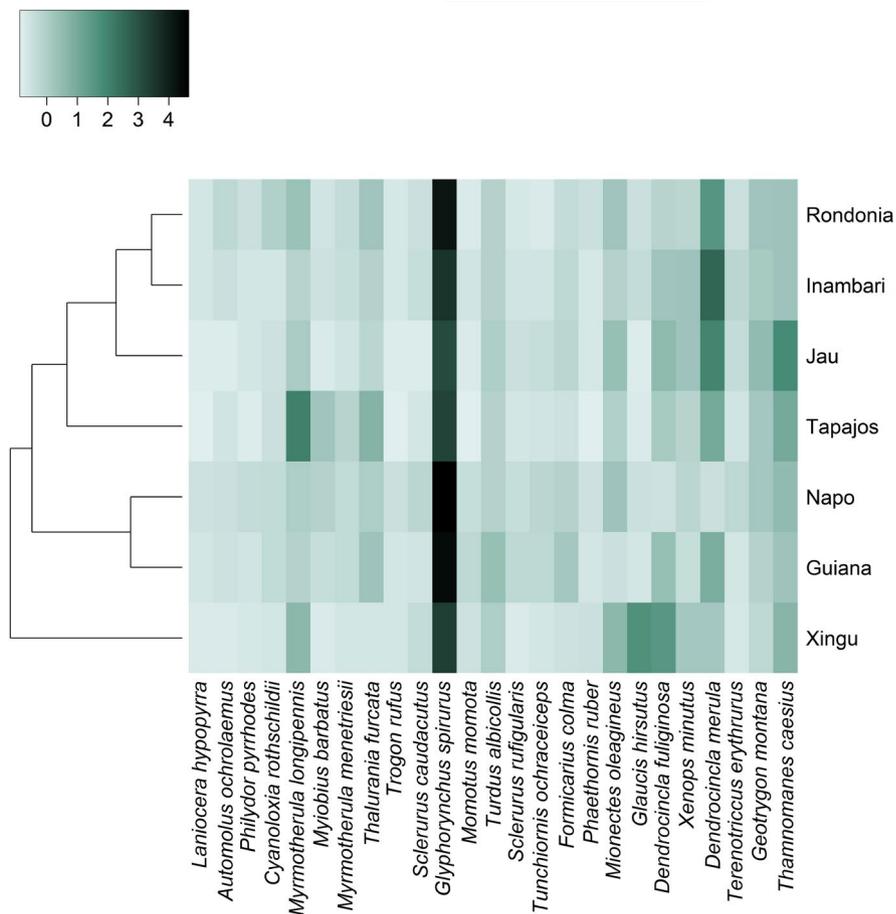


FIGURE 5 Proportion of (a) species and (b) individuals within different guilds created on the basis of dietary mode and body size for the seven Amazonian areas of endemism

(14; 6.2%) and carnivores (2; 0.9%). Despite some variation, the proportion of species (Figure 5a) and individuals (Figure 5b) representing each guild remained similar across all areas of endemism.

We found no differences in the variance of guild proportionality across areas of endemism among the three guild classification schemes (GLM: $p > 0.05$ in all cases). However, there was a general

prevalence of alpha guilds (one proportion z-test, $p < 0.001$), whether we considered (a) only diet and body size (Figure 6a), (b) diet, body size, sociality and foraging substratum (Figure 6b), and (c) only insectivores (Figure 6c). Further, results of the binomial test applied to each area of endemism demonstrated that the significant prevalence of alpha guilds in Guiana and Tapajós remained in all three guild

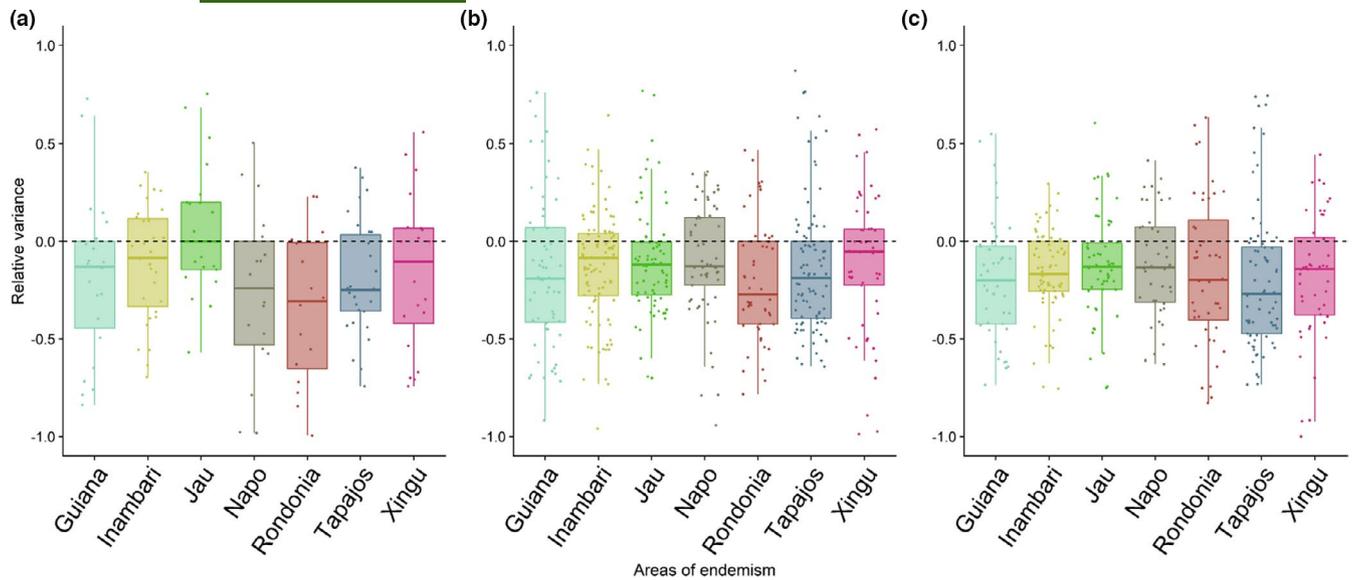


FIGURE 6 Relative variance (RVgp) calculated for seven areas of endemism using (a) diet and body size; (b) diet, body size, sociality and foraging substratum; (c) diet, body size, sociality and foraging substratum, but considering only insectivorous species. Values below and above zero indicate alpha guilds (proportionality) and beta guilds (disproportionality), respectively. Vertical lines represent the minimum and maximum values. Lines inside the boxplot represent the median. The top and bottom of boxplots indicate the 75th and 25th percentiles, respectively. Points are the RVgp values generated for each guild scheme. The end points of the lines (whiskers) is at a distance of 1.5*IQR (inter quartile range, the distance between the 25th and 75th percentiles). Points outside the whiskers are outliers. Dashed horizontal lines indicate the expected value under the null model

TABLE 2 *p*-values of binomial tests for each area of endemism

Guild classification	Guiana	Tapajós	Inambari	Jaú	Rondônia	Napo	Xingu
A	0.016	0.016	0.146	1	0.076	0.096	1
B	<0.001	<0.001	<0.001	<0.001	<0.001	0.430	0.251
C	<0.001	<0.001	<0.001	<0.001	<0.001	0.004	0.026

Note: (A) diet and body size for all species; (B) diet, body size, sociality and foraging substratum for all species; (C) diet, body size, sociality and foraging substratum for only insectivore species.

Bold values are the significant values of binomial tests.

classification schemes. Inambari, Jaú and Rondônia had significant values in cases “b” and “c”, while Napo and Xingu had significant values only in case “c” (Table 2). The general prevalence of alpha guilds was also maintained when we removed the species complexes from the analyses (see Appendix S3).

4 | DISCUSSION

We found distinct patterns of understorey bird species diversity among Amazonian areas of endemism, which was not surprising given the vast distances separating many sampling sites. However, even among different assemblages, the prevalence of alpha guilds within areas of endemism suggests that interspecific competition may be operating in structuring understorey avifaunal assemblages across interfluves. Our data suggest that the structure of local bird assemblages, which possibly resulted from historical processes, may also be maintained by local ecological factors, such as contemporary resource availability.

Exceptional levels of species diversity in southwestern Amazonia that include Inambari and Rondônia was noted for both birds (Stotz et al., 1997) and butterflies (Emmel & Austin, 1990). Historically, the vicariance process of the Amazon, Madeira and Tapajós rivers which delimit the Inambari and Rondônia areas of endemism occurred early on in the formation of the Amazon basin (Campbell Jr. et al., 2006; Latrubesse et al., 2010), unleashing diversification and speciation events over long time periods. According to Stephens and Wiens (2003), richness may be higher in regions occupied earlier by any given clade, with longer timescales to accumulate richness in those regions. Moreover, the time of colonization was found to be a major factor explaining regional richness patterns within clades (Li & Wiens, 2019). Additionally, the high species richness recorded in Inambari may be more related to local environmental conditions. According to the WWF ecoregion map (Olson et al., 2001; Figure S3), our sampling points inserted in the Inambari area of endemism are found in two different ecoregions, which does not occur in other areas even if they are farther apart, like in Xingu and Tapajós. The environmental heterogeneity of the Inambari area may be one of



the factors responsible for the greater expected species richness therein.

Bird species turnover in lowland Amazonia has been addressed in some recent studies, challenging long-held views on the patterns of Amazonian bird distribution. Oliveira et al. (2017) used a database of bird distribution records containing 566 species and, although the authors did not recognize that major rivers delimited areas of endemism, the bird species composition among their main interfluves was also distinct. Fluck et al. (2020) used a database of 1164 passerines and suggested that climate and geographic distance were more important than rivers in determining the composition of Amazonian bird assemblages. However, their results also emphasize the Amazon River as the main driver of beta-diversity across Amazonia, followed by the Negro, Madeira, Xingu, Tapajós and Branco rivers. These studies, however, were based on overlapping hypothetical species geographic range maps or occurrence data and used only presence/absence data. Although our data are limited to understorey birds from *terra firme* forests and restricted to a small region within each area of endemism, our study used a refined taxonomy based on molecular data, as well as field-based real occupancy capture data across a pan-Amazonian scale. Taken as a whole, our results based on capture data support previous studies (Fluck et al., 2020; Oliveira et al., 2017) using presence/absence data, but showing a stronger role of major Amazonian rivers, when compared to smaller tributaries.

The patterns observed among species with wide distributions are associated with differences in the number of captures of these species across areas of endemism, which suggest the influence of environmental filters and/or ecological factors (ter Steege & Zagt, 2002), or the expansion of species' ranges. Since Alfred Russel Wallace's (1854) early observations, several studies have confirmed that large rivers can operate as important natural boundaries for the geographic distributions of birds (Cracraft, 1985; Maximiano et al., 2020) and primates (Boubli et al., 2014; Peres et al., 1996). Given the complexities and the nature of questions addressed, vicariance and evolutionary studies are often focused on small numbers of taxa or clades (Ribas et al., 2012; Silva et al., 2002). Even for understorey birds, which arguably represent the best-studied group of Amazonian vertebrates, the debate as to whether the areas proposed to document patterns of endemism within the Amazon basin can be applied to entire bird assemblages is still open. Our analysis of species composition shows that understorey bird assemblages remain distinct on opposite banks of large rivers, even after excluding infra-generic diversification within species complexes. This indicates that the pattern of species turnover between areas goes well beyond the replacement of species that belong to the same complex and that in addition to vicariance events, dispersal processes have an important role in determining the regional species pool.

The heatmap of widely distributed species highlights the Xingu area of endemism as a separate group, close to the group formed by the Guiana and Napo. These results demonstrated a certain degree of dissimilarity between Guiana, Napo and Xingu, reaffirming divergences in the proportion of captures of these species among areas of endemism. The heatmap also highlighted *G. spirurus* since this

small-bodied woodcreeper was consistently the most abundant species in all areas of endemism. This species is one of the most common understorey birds in Neotropical forests (Blake & Loiselle, 2012). Although it is currently recognized as a single species, Fernandes et al. (2012) pointed to lineages with high genetic differentiation on the opposite banks of major Amazonian rivers, further supporting the importance of major rivers in the diversification process.

Despite high species turnover among the seven areas of endemism, they were all represented by largely invariant proportions of species within guilds, with a higher prevalence of insectivores. The predominance of this guild has also been noted in previous studies conducted using mist-nets in Amazonia (Bierregard, 1990; Robinson & Terborgh, 1990). The similar proportion of guild members across areas of endemism is consistent with results presented by Fluck et al. (2020), who found little variation in the functional diversity of Passerines across Amazonia. This indicates that species turnover occurs between different provinces while maintaining similar ecological functions, suggesting a certain degree of homogeneity in resource-consumer interactions throughout Amazonian *terra firme* forests.

The prevalence of alpha guilds across the seven areas of endemism indicates that the distribution of species among guilds is more similar (guild proportionality) among local assemblages within each area of endemism. Results of guild proportionality considering only diet and body size indicated a significant prevalence of alpha guilds only for Guiana and Tapajós. However, with the refinement of guild categorization, a prevalence of alpha guilds was also observed in Inambari, Jaú and Rondônia. This refinement in guild designation ensured the grouping of species that presumably compete more directly for resources, joining species with similar body size and social behaviour that consume the same food type in a similar substrate. Among insectivores, there was a significant prevalence of alpha guilds in all areas of endemism. Insectivores are the most abundant and species-rich group of understorey birds, and interspecific competition can be stronger within this guild. This proportionality suggests that interspecific competition and resource availability are more important than environmental heterogeneity in structuring these assemblages (Fox & Brown, 1993; Wilson, 1989, 1999; Wilson & Whittaker, 1995).

If interspecific competition is important in structuring local assemblages, the proportion of species within guilds remains constant because species already present preclude or inhibit similar species (ie, from the same guild) from subsequently entering the assemblage (Wilson, 1989). Thus, species complexes, which in this study are mainly taxonomic substitutes between the interfluves, often have the same ecological functions and could influence the overall guild proportionality. However, the general prevalence of alpha guilds remains similar even after species complexes were removed, suggesting that interspecific competition and resource availability may be operating in structuring local assemblages, illuminating the mechanisms of coexistence and maintenance of understorey bird diversity in Amazonia. In fact, congeneric birds that co-occur in Amazonian *terra firme* forests diverge in several morphological measures, which

are possibly related to differences in resource use within the same general habitat (Bierregard, 1988). Cases of interspecific territoriality and habitat occupation models between congeneric bird species, in which the largest species occupy the most productive end of habitat gradients and the smallest species occupy less productive habitats (Robinson & Terborgh, 1995), also suggest the role of competition in structuring understory bird assemblages.

The prevalence of alpha guilds among areas of endemism does not mean that other processes, such as habitat heterogeneity (Tews et al., 2004) and environmental conditions (Veech & Crist, 2007) are not operating. Our results focused on a broader scale and on locations with little or no detectable anthropogenic disturbance to create a baseline of species assembly for *terra firme* forests, which is the most abundant and probably most heterogeneous forest type in Amazonia (Tuomisto et al., 2019). However, it is well documented that bird assemblages change with environmental characteristics (Menger et al., 2017), forest fragmentation (Cintra et al., 2013), ecological succession (Borges et al., 2021) and wildfires (Barlow & Peres, 2004), showing that environmental heterogeneity contributes to maintaining the diversity of understory bird species.

Areas of endemism are proposed units of the evolutionary history of the Amazonian biota, being delimited as a function of a set of endemic species. Here we show that, although historical events defined the regional pool of species in each area, ecological processes are also at play, selecting those species that coexist in local assemblages. The numbers of species per guild were in general more proportional than expected by chance within each area of endemism, suggesting that competitive exclusion may be involved in structuring local assemblages. However, environmental filtering related to resources availability and vegetation structure within *terra firme* forests could not be discarded as important in selecting bird species in local assemblages. Our study highlights the importance of integrating the concepts of historical biogeography with ecological processes to improve our understanding of the factors that generate and maintain the diversity of the world's richest avifauna.

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CONFLICT OF INTEREST

The authors declare that they do not have any conflict of interest.

DATA AVAILABILITY STATEMENT

Most of the data are already published in other studies, as cited in the text. Another part of the data is not published. However, these were provided to us only for this study, and publication in any repository is not authorized. <https://doi.org/10.5061/dryad.p8cz8w9rv>

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BIOSKETCH

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SUPPORTING INFORMATION

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