

Bird assemblages on Amazonian river islands: Patterns of species diversity and composition

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Abstract

The principles of island biogeography are rarely applied to the animal assemblages of Amazonian river islands. Here, we compare bird assemblages of Amazonian river islands with a variety of mainland habitats. We also examine how bird species diversity and composition are related to island physical attributes. Birds were sampled with mist nets and qualitative censuses on 11 river islands and 24 mainland sites on the lower reaches of the Rio Negro in the Brazilian Amazon. Island bird assemblages were characterized by lower species richness and a higher abundance of a few dominant species. Additionally, the species composition of the islands was distinct from that of the mainland, including the nearby floodplain habitats. The number of bird species increased with island size and habitat diversity, and decreased with degree of isolation. In addition, small islands tended to harbor an impoverished subset of the species present on larger ones. Bird species diversity and composition on Amazonian river islands are likely influenced by the ecological succession and historical events affecting island formation. Considering their small total area across the Amazon basin, these insular fluvial communities could be disproportionately threatened by river channel disturbances related to climate change or hydroelectric dam development.

Abstract in Portuguese is available with online material.

KEYWORDS

Amazon floodplains, climate change, habitat specialization, hydroelectric dams, Rio Negro

1 | INTRODUCTION

Niche-based hypotheses for the concentration of biological diversity in the tropics generally assume that niche width of tropical species is narrow compared with that of temperate species, allowing for the coexistence of a high number of species (Barlow et al., 2018; Turner & Hawkins, 2004). Historically, ornithological studies provide some support for niche-based explanations for high tropical species diversity (Orians, 1969; Terborgh, 1980). Indeed, empirical comparisons of bird assemblages in tropical and temperate regions generally confirm that the niches of tropical birds are narrow and tropical birds have specialized resource requirements that

are absent from temperate ecosystems (Marra & Remsen, 1997; Terborgh, 1980).

Habitat specialization is also related to tropical bird niche diversification (Klopfer & MacArthur, 1960; Marra & Remsen, 1997; Pigot, Trisos & Tobias, 2016), and regions with high species diversity such as the Amazon are ideal for examining the influence of habitat specialization on patterns of species diversity. Indeed, a remarkable feature of the rich Amazonian avifauna is the high degree of specialization among habitats such as continuous upland forests (Blake, 2007; Cohn-Haft, Whittaker & Stouffer, 1997) and patchily distributed habitats such as white-sand *campinas* (Borges et al., 2016; Oren, 1981), savanna enclaves (Sanaiotti & Cintra, 2001; Santos & Silva,

2007), and bamboo forests (Cockle & Areta, 2013; Kratter, 1997). Habitat specialization influences the distribution of Amazonian birds (Stotz, Fitzpatrick, Parker & Moskovits, 1996), and habitat heterogeneity predicts variation in bird species richness and composition in different parts of the Amazon basin (Rahbek & Graves, 2001).

Floodplain vegetation covers 14% of the Amazon basin (Hess et al., 2015) and contributes substantially to regional biodiversity. For example, at least 15% of the non-aquatic bird species are flooded-habitat specialists across the Amazon (Remsen & Parker, 1983). The Amazonian floodplains show high heterogeneity in plant physiognomy (e.g., herbaceous open areas and forests with variable canopy heights), and these habitats are used by distinct groups of birds, increasing species turnover within floodplains (Petermann, 1997; Robinson & Terborgh, 1997).

River islands are conspicuous components of Amazonian floodplains and may occupy extensive areas of some tributaries. The islands of the Rio Negro, for example, form the two largest fluvial archipelagos in the world, each containing hundreds of islands (Latrubesse & Franzinelli, 2005).

Rosenberg (1990) was a pioneer in calling attention to the avifauna of fluvial islands, identifying 18 bird species whose distributions are apparently restricted to islands in the Peruvian Amazon. Further observations confirm that these and other species have

their natural histories intimately linked with riverine islands (Cintra, Sanaiotti & Cohn-Haft, 2007; Petermann, 1997; Zimmer & Isler, 2003). In addition, birds specialized on river islands show distinct patterns of genetic diversity among Amazon tributaries (Choueri et al., 2017). Preferential use of fluvial islands, therefore, represents an example of niche specialization by tropical birds with implications for the understanding of the ecological and evolutionary diversification of birds within the Amazon basin.

Recently, the biodiversity of Amazonian river islands has received increasing attention (Choueri et al., 2017; Cintra et al., 2007; Nunes, de Carvalho, Vaz-de-Mello, Dáttilo & Izzo, 2014; Rabelo, Aragón, Bicca-Marques & Nelson, 2019; Rabelo, Bicca-Marques, Aragón & Nelson, 2017; Rocha et al., 2014). This is a welcome development, since biodiversity studies of fluvial islands have important conservation implications. Due to their intrinsically fragmented nature, fluvial islands are likely more sensitive to river channel disturbances (e.g., hydroelectric dam building) than continuous floodplains or other mainland habitats. Therefore, to define effective conservation strategies for this habitat type, it is important to investigate the extent and nature by which river island biodiversity differs from other major regional environments.

Here, we present an analysis of bird assemblages on fluvial islands in the Rio Negro, Central Amazon. We applied principles of

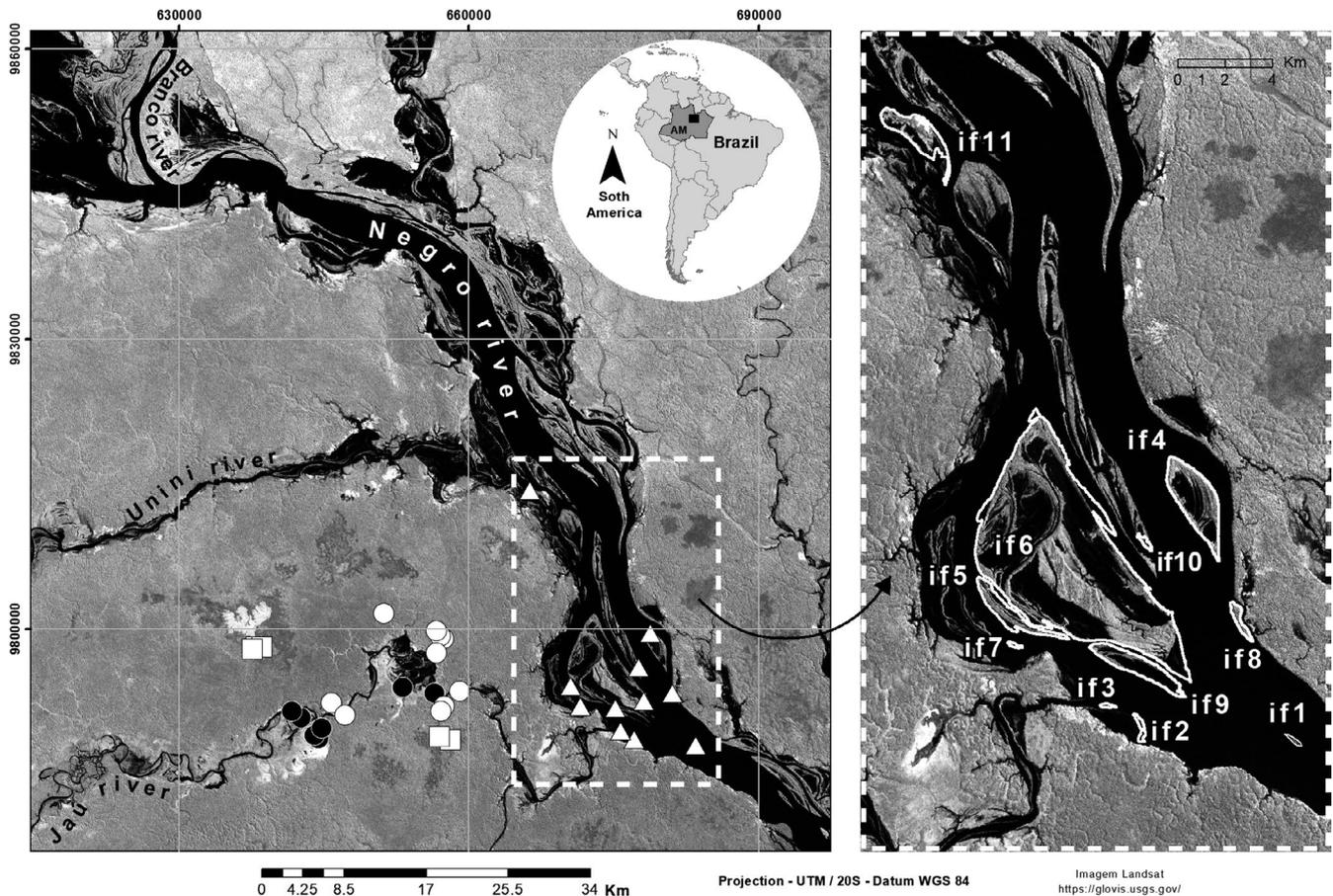


FIGURE 1 Distribution of study sites in the major habitats of the eastern part of Jaú National Park. Habitats types are *terra firme* forest (white circles), blackwater flooded forests (black circles), white-sand soil forests (white squares), and fluvial islands (white triangles)

TABLE 1 Descriptive data on the studied fluvial islands in the Rio Negro, Brazilian Amazon

Island names/codes	Area (ha)	Isolation (% water) ^a	No of captures	Number of species (total)
Camutirana (if1)	5.57	100	No capture	14
Dalva (if3)	8.15	97	No capture	25
Ponta do Coandu (if10)	9.00	83	No capture	25
Do Dino (if7)	10.58	100	No capture	21
Cauixi (if2)	17.35	80	No capture	48
Jussara (if8)	47.35	73	310	125
Panema (if9)	150.00	86	36	72
Do Boi (if5)	165.00	83	26	61
Prosperança (if11)	219.00	93	30	55
Das Onças (if4)	471.00	100	247	85
Caroçal/Tucubá (if6)	13,214.00	90	74	64

^aCalculated as percentage of water inside a 500-m buffer zone around each island.

island biogeography (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007) to investigate whether bird species richness, abundance, and composition on fluvial islands were distinct from those on mainland habitats and how bird assemblage metrics are related to island physical attributes. To achieve this, we compared bird survey data collected on fluvial islands and several mainland habitats on the lower reaches of the Rio Negro. The questions guiding the study were as follows: (a) Are bird species richness and abundance distinct between island and mainland systems?; (b) do island avifaunas have a distinct species composition or are only a subset of those from regional mainland habitats?; (c) what is the contribution of different mainland habitats as sources of individuals and species to colonize islands?; and (d) how are bird species richness and composition related to physical attributes of the islands such as size and degree of isolation?

2 | METHODS

2.1 | Study region

Birds were sampled on the island and mainland habitats within Jaú National Park, a protected area on the lower Rio Negro, Brazil (Figure 1). Water in this reach of the Rio Negro is acidic and sediment-poor. Islands originated either as sandbars stabilized by vegetation or as incised alluvial terraces (Cunha, 2017; Latrubesse & Franzinelli, 2005). Most of the islands studied were developed via sedimentation, except Ilha Jussara (no. 8 in Figure 1), which was likely an old terrace detached from the mainland. Islands experience seasonal inundation by the Rio Negro and remain totally or partially submerged between March and June. The islands achieve maximum exposure between August and February.

Soils of the selected islands are composed of alternating layers of sand and clay. Smaller islands support shrubs and low-canopy trees, while larger islands support high-canopy forests. Both vegetation structure and floristic composition are affected by the

annual flooding duration which, in turn, depends on local topography (Piedade, Junk, Adis & Parolin, 2005).

Birds were sampled on 11 islands which varied in size (Table 1, Figure 1) and 24 mainland sites. Mainland habitats consisted of forests seasonally inundated by blackwater rivers (BWF), *terra firme* forests (TFF), and white-sand soils forests (WSF). Descriptions of the structure and floristic composition of these habitats are given in Borges (2013) and references therein.

2.2 | Bird sampling

We surveyed birds in island interiors on foot and used motorboats to survey island margins. We documented species presence on the islands with photographs, sound recordings, and voucher specimens deposited in the bird collection of the National Institute of Amazonian Research (INPA). Photographs and tape recordings of representative samples of species are available in WikiAves website (www.wikiaves.com.br). We visited each site at least three occasions from 2000 to 2014. In addition to these presence-absence surveys, we established capture stations on six larger islands consisting of two continuous net lines with eight mist nets each. Birds were sampled opportunistically, always in the dry months (August to December) when the islands were above water. Sampling efforts for each site are presented in Table 2. Details of the methods used for sampling birds in mainland habitats are available in Borges (2013). Subsequent analyses follow the bird taxonomy of Piacentini et al. (2015).

2.3 | Data analysis

We analyzed data only from islands and mainland sites that were simultaneously sampled with mist nets and qualitative censuses, with the exception of five small islands where mist nets were not effective due to low bird abundance. Only presence-absence data from these small islands were analyzed. Species lists obtained for each site contained both mist net records and qualitative census data. We

Habitat	No of sites	Sampling effort (days)	No of captures	No of species	
				Total	Mean (range)
Fluvial islands (FI)	11	58	723	193	54 (14–125)
Blackwater flooded forests (BWF)	7	24	307	153	70 (48–81)
Terra firme forests (TFF)	10	30	1,144	168	87 (79–94)
White-sand soil forests (WSF)	7	26	329	159	79 (56–94)
Mainland habitat totals	24	80	1,780	253	–
Totals	35	138	2,503	319	–

TABLE 2 Bird sampling effort and general data on bird assemblages in fluvial islands and mainland sites

analyzed presence–absence (captures plus qualitative census) and abundance data (only captures) separately.

We included the following physical characteristics of each island in analysis, following Si, Baselga and Ding (2015): area in hectares, percentage of water in a 500-m buffer zone around each island (a measure of isolation), and number of habitat types present. Area and isolation were measured in ArcView software using a Landsat satellite images from July 2001. We categorized island habitats as follows: (a) sandbanks, (b) muddy banks, (c) sparse vegetation growing over sand or muddy banks, (d) internal lakes with shrub vegetation around the margins, (e) aggregations of jauari palms (*Astrocaryum jauari*), (f) clumps of *Heliconia* spp. in the understory, (g) presence of cecropia trees (*Cecropia* spp), (h) anthropogenic secondary vegetation, (i) large treefall gaps, and (j) stands of understory vines.

We estimated species richness in different habitats with sampling curves and their respective confidence intervals. We generated sampling curves using EstimateS (Colwell, 2013), applying the Mao Tau function with the number of field days as the unit of sampling effort. Non-overlapping confidence intervals among habitats imply statistically significant differences in species richness (Colwell, 2013).

We analyzed dominance patterns by examining abundance curves with each species ranked in decreasing order of relative abundance (Clarke, 1990). We built relative abundance curves using capture data for each study site. We computed dissimilarity distances for each pair of curves using a modified Manhattan distance (Clarke, 1990). We then examined the resulting dissimilarity matrix with an analysis of similarity (ANOSIM) to test for differences between four groups of sites corresponding to different habitat types. ANOSIM computes an R statistic that ranges from 0 to 1, with large values indicating increasing dissimilarity between compared samples (Clarke & Warwick, 2006). We assessed statistical differences in abundance distributions between groups of samples through a permutation procedure detailed in Clarke and Warwick (2006).

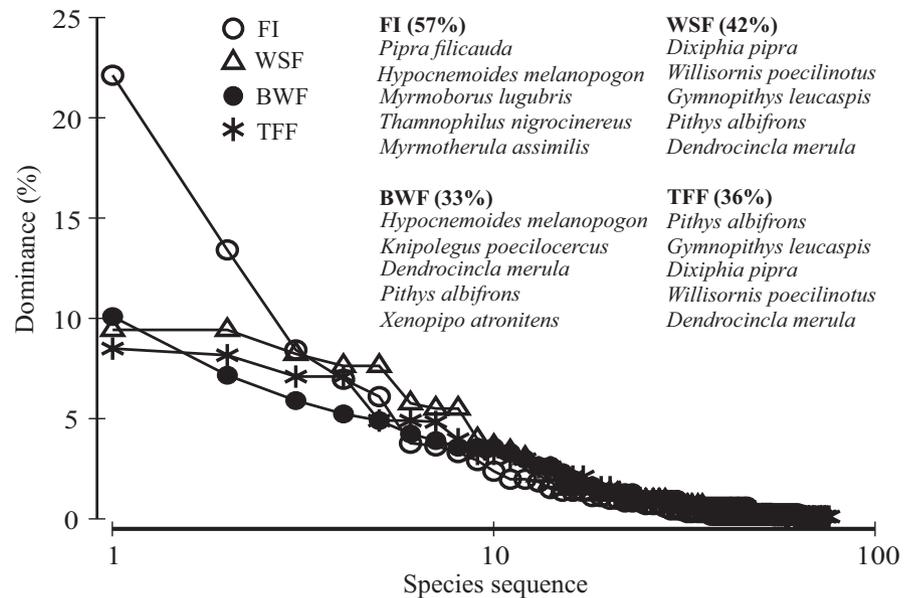
We examined variation in species composition between sites with NMDS (non-metric multidimensional scaling) ordinations and ANOSIM tests using distinct dissimilarity metrics and datasets. Only species found in at least four sites, or with a minimum of

four captured individuals, were used in ordinations. For mist net samples, we standardized captures by total captures at each site. We square-root-transformed the data to equalize the contribution of abundant and rare species, and used the Bray–Curtis index as a measure of dissimilarity. For presence–absence data, we used two dissimilarity metrics: the Jaccard index and the BjtU index. This latter metric is not affected by differences in number of species among sites (Baselga, 2012), a desirable property due to the high variability in species richness among our sites. We used ANOSIM analysis (see above) with these dissimilarity matrices to test for differences in species composition between islands and mainland habitats.

We assessed potential colonization patterns in islands by characterizing assemblages according to bird habitat preference categories given in Borges and Almeida (2011), simplified as follows: (a) birds likely to have colonized the islands from blackwater flooded forests; (b) species likely to have dispersed from the *terra firme* forests; (c) habitat generalists, a category including species associated with more than one habitat type; and (d) birds likely dispersed from other islands, comprised of species recorded exclusively on islands.

We examined the relationships between bird assemblage metrics and island attributes using complementary approaches. First, we tested the relationship between species richness and island attributes using linear regressions. In addition, we tested whether islands bird assemblages showed significant nested distributions that occur when the species composition at species-poor sites represents a subset of those in richer ones (Ulrich, Almeida-Neto & Gotelli, 2009). To examine the effects of island attributes on the relative nesting of species compositions, we ordered presence–absence matrices by species richness, island area, and degree of isolation. We used these matrices to calculate nestedness metric based on overlap and decreasing fill (NODF) metrics whose values vary from 0 to 100, with larger values indicating an increasing tendency toward nestedness (Almeida-Neto, Guimarães, Guimarães, Loyola & Ulrich, 2008). We assessed statistical significance of NODF indices with a shuffled column (SC) null model that tested whether a particular site ordering leads to a higher degree of nestedness than expected by chance (Strona, Galli, Seveso, Montano & Fattorini, 2014).

FIGURE 2 Dominance curves of river islands and the mainland habitats. The species listed are the five most abundant with percentage of total captures of each habitat. Abbreviations: FI (fluvial islands), BWF (blackwater flooded forests), TFF (terra firme forest), WSF (white-sand soil forests)



3 | RESULTS

3.1 | Island bird assemblages

We recorded 319 bird species of which 193 were in fluvial islands and 253 in mainland habitats (Borges et al., 2019). Similar species richness values were recorded from islands and mainland habitats sampled with similar effort (Figure S1). When all mainland habitats were pooled into a single category (i. e. general mainland), the species richness in the fluvial islands was significantly lower than that of the mainland (Figure S1).

Relative species abundance distributions differed between habitats (Global $R = 0.44$, $p < .01$: See dominance curves, Figure 2). Paired comparisons indicated significantly higher dominance on islands compared with *terra firme* forests ($R = 0.77$, $p < .01$) and white-sand soil forest ($R = 0.54$, $p < .01$). However, no difference was found in the abundance distributions between islands and blackwater flooded forest ($R = 0.09$, $p = .17$). The five most commonly captured birds on the islands comprised more than half of all individuals, a higher proportion than in other habitats (Figure 2).

Bird species compositions on islands were distinct from those of mainland habitats (Table S1), a pattern observed across dissimilarity metrics (Figure 3). The distribution of sites in the ordination space was not greatly changed when the analysis was controlled for differences in number of species between sites (Figure 3b,d). The species composition of larger islands (>50 ha) was apparently distinct from that of smaller islands (Figure 3c). However, this distinction disappeared after controlling for species richness differences (Figure 3d).

Blackwater flooded forest is the main habitat source for most bird species that colonize islands, especially the smaller than 50 hectares (Figure S2). Habitat preferences among species on larger islands tended to be more diversified (Figure S2). An exception to this trend was the small Ilha Jussara (if8, 47.35 ha) which houses a rich

avifauna assembled from diverse source habitats, includes a large proportion of *terra firme* forest species (Figure S2)

3.2 | Bird assemblages and island attributes

Species richness increased with island area and habitat diversity (Figure 4). Habitat diversity is partially explained by island area since these two attributes are inter-correlated (R^2 adjusted = 0.35, $p = .03$). Species richness had a marginally negative association with island isolation (Figure 4). One island (Ilha das Onças, if4) strongly influenced the correlation, and excluding it from the analysis made the influence of island isolation on species richness more evident (R^2 adjusted = 0.52, $p = .01$).

Bird assemblages in islands and mainland sites with low numbers of species were often a subset of those species present at the species-rich sites (NODF observed = 51.81 vs. NODF randomized = 25.86 for mainland sites and 64.78 vs. 32.68 for islands, $p < .001$ in both comparisons). This nested pattern was significantly associated with island size, since most species present on small islands were also found on larger ones (NODF observed = 49.44 vs. NODF randomized = 32.30, $p < .05$). Nested arrangement, however, was not related to island isolation (NODF observed = 45.50 vs. NODF randomized = 33.21, $p > .05$).

4 | DISCUSSION

4.1 | Bird assemblages on Amazonian river islands

Island bird assemblages were characterized by lower species richness compared with mainland. Also, a greater number of bird species colonized larger islands that had greater habitat diversity compared with smaller ones.

Bird assemblages on islands were distinct from mainland habitats, even when compared with adjacent blackwater flooded forest habitats (Figure 3). This distinct species composition results from

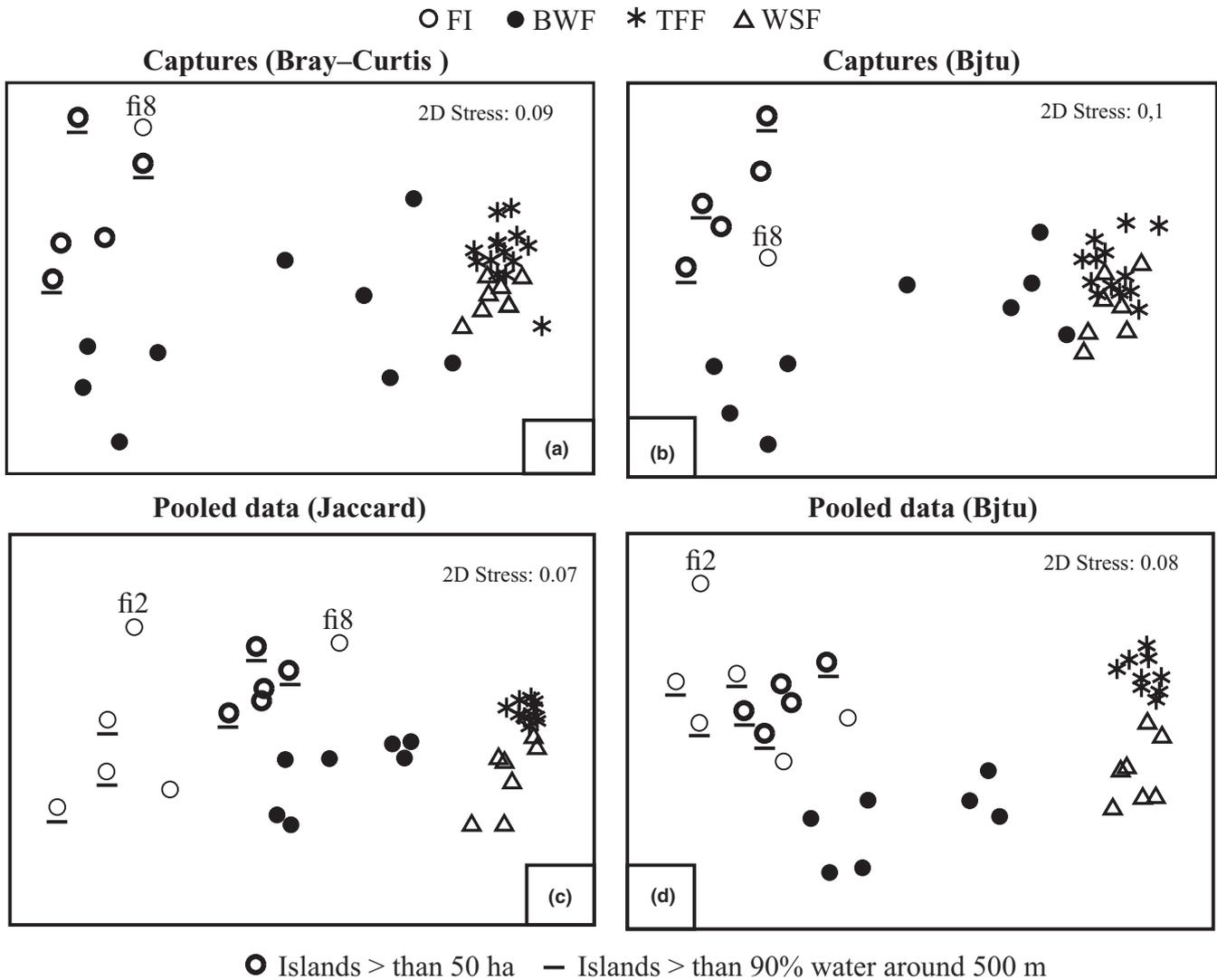


FIGURE 3 Non-metric multidimensional scale (NMDS) plots of bird assemblages in islands and mainland habitats. Analysis based on (a) capture data using Bray–Curtis similarity, (b) capture data using Bjtu index, (c) presence–absence data using Jaccard similarity, and (d) presence–absence data using Bjtu index. Abbreviations are the same as in Figure 2

differential occupancy of islands by some bird species. We suspect that some species are more abundant on the islands compared with the mainland. Indeed, some species recorded exclusively on islands during the sampling period (e.g., *Pipra filicauda* and *Schiffornis major*) were rare at mainland sites in Jaú National Park (Borges & Almeida, 2011).

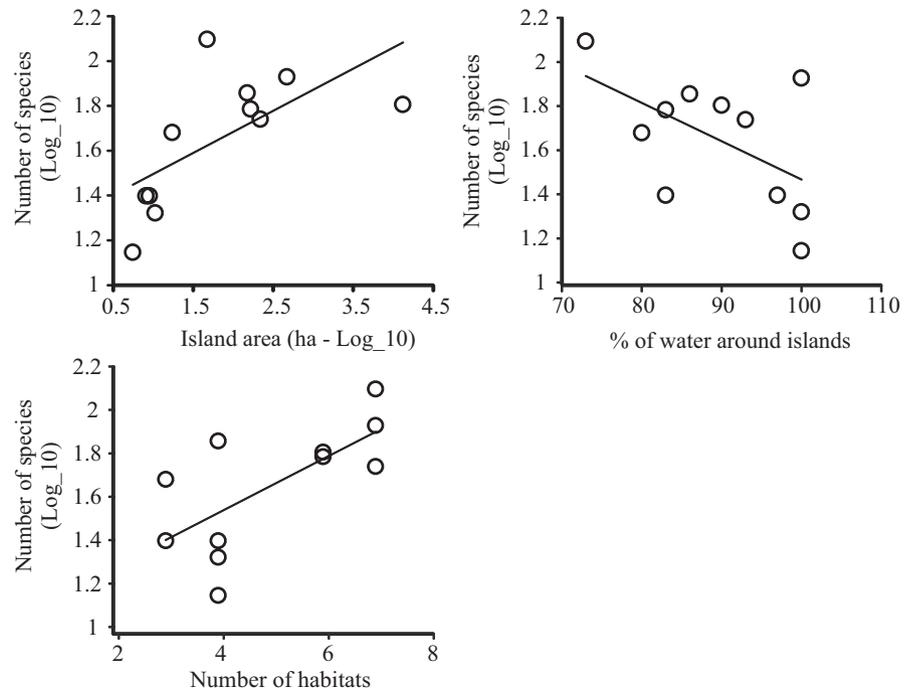
Habitat specialization may help explain the distinctiveness of the island bird assemblage. The distributions of five species recorded in this study (*Myrmotherula klagesi*, *Myrmotherula assimilis*, *Thamnophilus nigrocinereus*, *Myrmoborus lugubris*, and *Stigmatura napensis*) appear to be strongly associated with fluvial islands (Rosenberg, 1990; Zimmer & Isler, 2003). Also, three of the five most captured species on islands were exclusively recorded on islands and are considered obligate island species across the Amazon (Rosenberg, 1990; Zimmer & Isler, 2003). Another three species are potentially good candidates for consideration as regional island specialists: a hummingbird (*Phaethornis rufurumi*), a

flycatcher (*Tolmomyias sulphurescens*), and a curassow (*Pauxi tomentosa*). Although these species are found in mainland habitats and are habitat generalists in other parts of their ranges (Borges & Almeida, 2011; Laranjeiras et al., 2014), they are especially common and widespread on islands of the lower Rio Negro (Cintra et al., 2007).

Nested pattern between species-rich and species-poor sites was linked to island area, but not to the degree of isolation, suggesting that this system is extinction-driven rather than colonization-driven (Bruun & Moen, 2003). Indeed, differential extinctions explained vertebrate distributions on artificial islands created by fragmentation of continuous forests by hydroelectric dams (Aurélio-Silva, Anciães, Henriques, Benchimol & Peres, 2016; Bueno, Dantas, Henriques & Peres, 2018; Lima et al., 2015; Palmeirim, Vieira & Peres, 2017; Si et al., 2015).

However, extinction-related processes are less-than-satisfactory explanations for the community composition of Rio Negro islands

FIGURE 4 Relationships between bird species richness and island size (r^2 adjusted = 0.36, $p = .03$), island degree of isolation (r^2 adjusted = 0.22, $p = .08$), and habitat diversity (r^2 adjusted = 0.41, $p = .02$)



because the islands likely developed slowly from sandbars (Cunha, 2017). Since habitat diversity increased with island area in this dataset, it is possible that the observed nested pattern results from island ecological succession. Specific habitats necessary for successful colonization of some bird species could be absent on smaller islands. Larger islands, on the other hand, are potentially older and in more advanced phases of succession, and so could contain a more complete sample of regional habitats available for colonization by a greater number of bird species.

The passive sampling effect, in which the probability that a species will colonize an island is proportional to its regional abundance, provides another possible explanation for the nested patterns (Ulrich et al., 2009). Indeed, occupancy of Amazonian fluvial islands by mammal species is predicted by regional abundance (Rabelo et al., 2019). The relative abundance of captured birds on studied islands and in the nearby blackwater flooded forest was positively correlated (Spearman rank correlation $R_s = 0.51$, $p < .001$) which also suggests that passive sampling could affect the observed nested composition patterns.

We hypothesize, therefore, that the association between the nested species distribution of birds and island area could be explained by increasing habitat diversity related to ecological succession. Furthermore, we expect island colonization events by birds are, at least partially, mediated by the passive sampling effect. Quantitative data on bird abundance and habitat diversity collected from a greater number of islands are necessary for an adequate test of this hypothesis.

4.2 | River island biogeography

Animal and plant assemblages and individual species that colonize islands all have certain characteristics that distinguish them from

their mainland counterparts, including (a) lower species diversity, (b) species with disproportionately high population density, (c) elevated endemism rates, and (d) greater incidence of flightlessness, gigantism, dwarfism, and low aggressiveness (Whittaker & Fernández-Palacios, 2007). How these general characteristics are manifest in the bird assemblages of the Amazonian river islands? Detailed answers to this question are not possible given our incomplete knowledge of such island bird assemblages. However, provisional responses useful for spurring further investigations are offered here. Since the area of effective sampling on island and mainland sites was not standardized, it is not possible to disentangle the contribution of area and habitat coverage *per se* to species diversity patterns (Fahrig, 2013; Rabelo et al., 2017). However, islands had lower bird species diversity compared to mainland sites sampled with similar effort. It is important to emphasize that area is not a fixed attribute of river islands, since the seasonal fluctuation in the water level altered the area available to terrestrial organisms. In this sense, birds on Amazonian river islands must deal with an additional environmental filter rarely encountered on other types of islands. How birds cope with such seasonal fluctuations in area/habitat availability on riverine islands is still not well understood.

Islands generally house species with higher population densities compared with the mainland (Adler & Levins, 1994). Elevated densities of birds specialized in fluvial islands have been recorded in the western Amazon (Armacost & Capparella, 2012; Rosenberg, 1990). Capture analysis for the current study indicates that bird assemblages on the islands show higher dominance compared with the mainland habitats. Some of the most commonly captured bird species in this study were island specialists across the Amazon (Rosenberg, 1990), suggesting higher densities of species better adapted to exploit island resources compared with non-specialists.

Endemism is difficult to evaluate in the avifauna of Amazonian river islands. The Amazonian floodplains, including its islands, are subject to intense dynamism linked to fluctuation in river levels and sediment discharges (Junk et al., 2011). Birds evolved extensive dispersal abilities to cope with such dynamism, which enhances gene flow between bird populations (Aleixo, 2006; Cadena, Gutiérrez-Pinto, Dávila & Chesser, 2011). In this sense, is not likely that riverine islands provide the sufficient isolation to restrict gene flow between populations and promote differentiation.

However, a recent study has shown that birds specialized in the use of river islands evolved in distinct lineages among different Amazon tributaries (Choueri et al., 2017). This population structure among island specialists suggests that historical events, such as fluctuations in sea level, climate change, and tectonic activity (Bertani, Rossetti, Hayakawa & Cohen, 2015; Nogueira, Silveira & Guimarães, 2013), are relevant to the interpretation of current distribution of these species (Choueri et al., 2017). Endemism at the intraspecific lineage level, therefore, could be an important characteristic of birds specialized in river islands as indicated by preliminary studies (Choueri et al., 2017; Thom et al., 2018).

5 | CONCLUSION

Amazonian river islands house a distinct assemblage of bird species even compared with nearby continuous floodplain habitats. Bird species richness and composition are well predicted by island size and habitat diversity. Patterns of bird species diversity and composition on Amazonian river islands are likely associated with ecological succession and historical events related to island formation. Considering their small area across the Amazon basin, the fluvial island environment is disproportionately threatened by river channel disturbances such as climate change events (Flores et al., 2017), and hydroelectric dam construction (Macedo & Castello, 2015). We do not yet understand how such events affect river island biodiversity. Furthermore, it remains to be determined whether the patterns observed in bird assemblages could be applied to other animal or plant assemblages of river islands.

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Nogueira Neto (1923–2019), a leading Brazilian environmentalist responsible for the creation of several protected areas in Brazil, including Anavilhanas National Park that protected one of the largest river island systems in the world.

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j14g206> (Borges, Baccaro, Moreira & Lacerda Choueri, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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