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Effects of a major Amazonian river confluence on the distribution of floodplain forest avifauna

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Abstract

Aim: Although 'river color' or water type is an important determinant of Amazonian floodplain biodiversity, the relevance of mixing distinct water types at river confluences to the distribution of terrestrial floodplain fauna has been largely overlooked. We investigated how the influx of a sediment-rich whitewater tributary affects the floodplain forest avifauna along the world's largest blackwater river.

Location: Northwestern Brazilian Amazon.

Taxon: Birds.

Methods: We sampled floodplain avifauna and retrieved estimates of sediment concentration in the water (the main parameter in river-water classification) at 52 sites, along the Negro (blackwater) and Branco (whitewater) rivers, above and below their confluence. We compared species richness and composition using analyses of variance, ordinations, generalized linear models and indicator species analyses.

Results: Bird species composition on the lower Rio Negro (below the confluence) was distinct from both the upper Negro (above the confluence) and the Branco, and species richness on the Negro increased below the confluence. Typical whitewater bird species occurring on the Branco were found exclusively or predominantly along the left side of the lower Rio Negro, where the Branco's muddy waters seem to be channelled. Overall avian compositional variation among sites was correlated with sediment concentration in the water, a determinant of floodplain forest structure.

Main conclusions: The influx of the muddy waters of the Rio Branco into the Rio Negro promotes the co-occurrence of bird species that are segregated by river type upstream, increasing species richness at the landscape scale. Rather than just representing a potential blackwater barrier between whitewater systems, the lower Rio Negro comprises a unique biogeographical transition zone, with a mixed avifauna occurring in a mosaic of varied floodplain forest types. Our results suggest that confluences of large rivers of distinct water types represent a significant factor determining species distributional boundaries and geographic patterns of Amazonian floodplain biodiversity.

KEYWORDS

birds, Brazilian Amazon, fluvial islands, indicator species, Rio Branco, Rio Negro, river color, sediment load

1 | INTRODUCTION

Identifying key geographical features that shape biodiversity is a major challenge in Amazonia (Tuomisto & Ruokolainen, 1997), the world's largest and most diverse tropical forest and hydrographic basin (Antonelli et al., 2018; Goulding et al., 2003) . For the floodplain systems, which cover around 15% of the biome (Hess et al., 2015), river 'color' or water type has offered a simple but fundamental starting point. Draining different geological formations and containing water with distinct attributes, Amazonian 'white-', 'black-', and 'clearwater' rivers create varied floodplain landscapes. Floodplains along whitewater rivers with heavy sediment loads, such as the Rio Madeira, are highly productive and contain a diversity of vegetation types, including tall dense forests, with rich and abundant fauna; conversely, floodplains along sediment-depleted rivers, such as the Rio Negro (blackwater) or the Rio Tapajós (clearwater), are less productive, with fewer vegetation types, lower forests, and a relatively scarce fauna (Goulding et al., 2003; Haugaasen & Peres, 2005; Junk et al., 2011; Prance, 1979; Sioli, 1968).

Rivers of distinct water types, however, meet one another (see Venticinque et al., 2016), and such river confluences could have important implications for floodplain systems. By affecting hydrogeological dynamics, including sediment distribution, confluences are expected to promote habitat heterogeneity, enhancing species richness (Benda et al., 2004; Gascon & Smith, 2004; Rice et al., 2008). This is the case for electric fishes, with higher diversity at tributary mouths along the main channel of the Amazon river (Fernandes et al., 2004). Nevertheless, no other study has evaluated confluence effects in the basin, and the relevance of mixing distinct water types for distributions of floodplain terrestrial fauna has been largely overlooked.

Birds represent a conspicuous and relatively well-known component of Amazonian floodplains' biodiversity. More than 400 species have been reported to occur in river-created habitats, including more than 100 specialized and many range-restricted species (Cohn-Haft et al., 2007; Remsen & Parker, 1983; Stattersfield et al., 2005; Stotz et al., 1996). Although river type is a strong predictor of avian species composition, with numerous species indicating distinct types (Laranjeiras et al., 2019), the effects of river confluences on avian communities remain undescribed. This is particularly surprising considering that most major Amazonian rivers are, in fact, formed by tributaries of distinct water types (see Ventincique et al., 2016).

The Rio Negro, the world's largest nutrient-poor blackwater river, in the northwestern Brazilian Amazon, offers an iconic opportunity to study the effect of river confluences on the floodplain avifauna. The Negro's largest tributary is the muddy nutrient-rich whitewater Rio Branco (Goulding et al., 2003; Venticinque et al., 2016). The avifauna of the lower section of the Rio Negro, below the mouth of the Rio Branco, has been presented as if typical of blackwater floodplain forests (Borges et al., 2019; Cintra et al., 2007), contrasting strongly with that of whitewater rivers, such as the upper Amazon River (see Cohn-Haft et al., 2007; Petermann, 1997). Our own observations, on the other hand, suggest that the lower Negro avifauna is somewhat similar to that of the Rio Branco, being similar to the Amazon, and distinct from that found along upstream portions of the Negro (Laranjeiras et al., 2014; Naka et al., 2007, 2020). This could reflect the influence of the Branco's sediment-rich muddy-waters, which are visible for dozens or even hundreds of kilometres along the lower Rio Negro's left (eastern) margin (Latrubesse & Franzinelli, 2005; Latrubesse & Stevaux, 2015). However, few ornithological data are available from the Rio Negro floodplains above the mouth of the Rio Branco (Laranjeiras et al., 2017), and any possible differences between upper and lower stretches have never been tested.

Here we investigated if and how the entrance of the Rio Branco affects species richness and composition of the floodplain forest avifauna along the Rio Negro. Specifically, we ask the following questions: (1) Are there changes in avifauna along the Rio Negro, downstream from the mouth of the Rio Branco? (2) Are potential changes more evident along the lower Negro's left margin, where the muddy waters from the Rio Branco appear to be channelled? (3) Are potential changes related to the sediment load in the water (the main parameter in river-water classification)? (4) Do any changes represent an admixture of black- and whitewater avifaunas? To address these questions, we conducted standardized avian sampling of floodplains of both riverbanks and on nearby islands, above and below the confluence of the two rivers, and estimated sediment concentration in the water using satellite imagery from throughout the sampling area. Exploring variation in all detected resident bird species and, specifically, in floodplain specialists and in species that were previously identified as indicators of white- or blackwater tributaries, we expected that: (1) the avifauna of the lower Rio Negro would be distinct from that found on the upper section (above the mouth of the Rio Branco); (2) avian communities on opposite sides of the lower Rio Negro would differ from one another; (3) sediment concentration would correlate with species composition and richness of white- or blackwater indicator species, and predict them better than does a simple classification of water type; and (4) the lower Negro would share species with both the upper Negro and the Branco, including both black- and whitewater indicator species. Finally, considering the distribution of distinct rivers and their confluences throughout Amazonia, we discuss implications of this for the distribution and conservation of floodplain birds and overall biodiversity.

2 | MATERIALS AND METHODS

2.1 | Study region

This study was conducted in the north western Brazilian Amazon (Figure 1), where we focused on the floodplains of the Rio Negro, above and below the mouth of the Rio Branco. With most tributaries draining sandy soil lowlands, the Rio Negro is a typical blackwater (nutrient-poor) river (Goulding et al., 2003; Junk et al., 2015). In contrast to most of the basin, the headwaters of the Rio Branco and several of its tributaries are located in the Guianan Shield mountains, draining areas of presumably more clayey soil (Ferreira et al., 2007; Oliveira et al., 2001; Venticinque et al., 2016). Based on geomorphology, the Rio Negro can be divided in lower, middle and upper sections, with the mouth of the Branco marking the boundary between the middle and the lower sections (Franzinelli & Igreja, 2002). Here, however, we refer to the section above the confluence (including the middle section) as 'upper Rio Negro'. These river stretches flow through sedimentary deposits and are characterized by the presence of the world's two largest fluvial archipelagos: Mariuá, above the mouth of Rio Branco, and Anavilhanas below (Latrubesse & Stevaux, 2015).

Human population densities are very low around the confluence of the Negro and Branco rivers and anthropogenic impacts on river floodplains are restricted to small areas (Junk et al., 2015). Selective logging occurs along the Negro (Goulding et al., 2003), mostly near Manaus, which is about 320 km downstream from the mouth of the Rio Branco (Scabin et al., 2012), whereas fires are becoming more prevalent throughout (Flores et al., 2012, 2016). Nevertheless, our sampling was restricted to sites without obvious anthropogenic impacts (see below).

Climate throughout the study area is warm and wet, with a mean annual temperature of 27°C and mean annual precipitation ranging from 2,350 mm, in the lower Rio Negro around Novo Airão, to 2,550 mm above the confluence with the Rio Branco, near Barcelos (INMET, 2019). Rainfall concentrates from January to May and river water level begins to fall in August or September, with the low-water period extending from October to February; waters start to rise in March, staying high until July (Goulding et al., 2003; Junk et al., 2011).

2.2 | Avifauna sampling design

We sampled the avifauna at 40 sites along the Rio Negro (17 on the upper and 23 on the lower section) and 12 sites on the Rio Branco (Table S1, Figure 1). Sites were distributed both on riverbanks and on nearby islands, from 5 to 200 km from the confluence. As many as four sites were grouped at a given distance from the confluence: on the left (northern or eastern) and right (southern or western) banks,

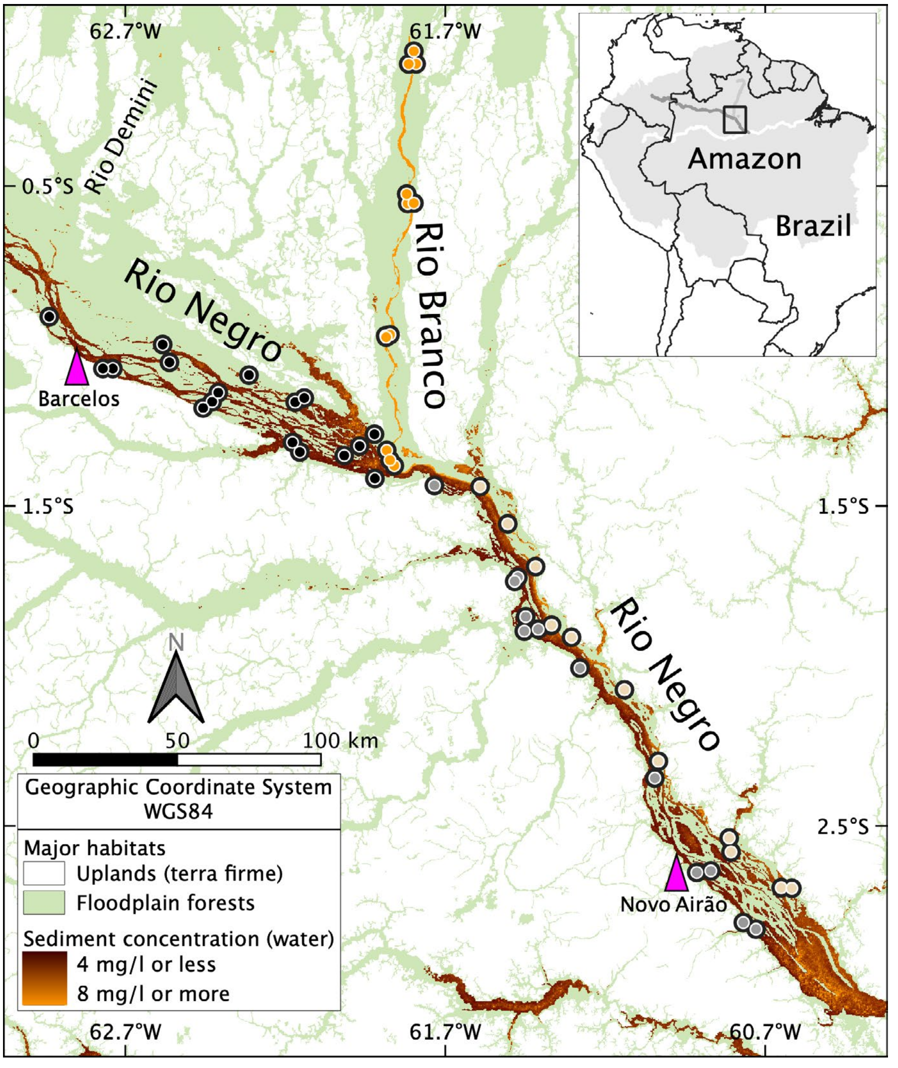

FIGURE 1 Study region (black square in inset) at the confluence of the Negro and Branco rivers (dark and medium grey lines in inset, respectively), in the context of the main channel of the Amazon river (white line in inset) and Amazon biome (pale grey in inset). We sampled the avifauna at 40 sites along the Rio Negro, at distinct distances from the mouth of the Rio Branco, above (17 sites, black dots) and below (12 sites on the right bank, grey dots; 11 sites on the left, beige dots). Twelve sites (orange dots) in the Rio Branco were also sampled. Pink triangles indicate the location of two cities along the Rio Negro. Major habitats are based on Hess et al. (2015) and sediment concentrations in the water (trimmed to highlight variation within Rio Negro) are based on an empirical correlation available in Fassoni-Andrade and Paiva (2019)

and up to two islands (Figure 1). All sites within the same section were at least 1 km apart.

Sampling was undertaken during six expeditions, between 2012 and 2017 (see Table S1). All expeditions were conducted between May and October, during the dry season, in the high- or falling-water periods (Goulding et al., 2003), optimizing access to sampling sites and partially controlling for seasonal variation. Although we did not evaluate potential variation in bird detection related to water level, we sampled both rivers over similar hydrological periods (Table S1) and so expect no biases in our results. We also expect no biases regarding potential inter-annual variation in bird detection, because some sites on both sections of the Rio Negro were sampled during the same expeditions, mostly in 2016 and 2017.

At each of the 52 sampling sites, we conducted ten 15-min point-counts (see archived data for exact coordinates), with an unlimited radius of detection. Point-counts were distributed every 500–1000 m along the riverbanks or islands (see details of point-count protocols in Laranjeiras et al., 2019). Within most sites, we surveyed all 10 points on the same day, during a single non-rainy morning, beginning before sunrise at first light (5:30) and ending mid-morning (roughly 9:30), noting all bird species seen or heard (presence–absence in each point; see archived data). For logistical reasons, we surveyed six Rio Negro sites (two on the lower and four on the upper section) in the late afternoon (16:00–18:30) of two not necessarily consecutive days. For all analyses, we combined data from all ten point-counts at a given site, providing a single list of birds for each site (see below). All surveys were led by TOL (48 out of 52) or LNN (with other participants; see Table S1), both of whom have more than 10 years of experience in conducting Amazonian avian inventories.

2.3 | Estimates of sediment concentration

We retrieved estimates of surface suspended sediment concentration in river water (hereafter, sediment concentration) from satellite imagery for each site. Estimates were based on an empirical correlation between the red-light reflectance of rasterized satellite imagery (at a 250-m spatial resolution) and sediment concentration in the water in gauge stations, provided by Fassoni-Andrade and Paiva (2019). In each pixel, images provide the mean value for a 15-year time series, covering the high-water period (from May to August). For each of our sampling sites, we calculated the mean value for all pixels within a 1.8-km radius buffer around the central coordinate of the site. Because estimates are valid only for pixels in open water, we found this buffer zone to be the minimum necessary to cover a representative group of pixels (minimum of four, average of 38; see Table S1) around the floodplain forests, avoiding overlap with the buffer of other sites or waters on the opposite side of the river. We only considered pixels that were identified as open water in more than 30% of the time series images. We used mean values to reduce the noise resultant from the correlation's low adjustment at low sediment concentration levels (see Fassoni-Andrade & Paiva, 2019). The retrieved estimates (see Table S1) were congruent with recent field measures on the lower Rio Negro (see Marinho et al., 2020) and the standard deviation of the estimates for each site (Table S1) was not dependent on the number of valid pixels within the buffer ($p > 0.05$).

2.4 | Data analyses

We analysed the variation in species richness and composition of the avifauna considering all detected resident species (excluding known migrants) and a subset of floodplain avian specialists (see Table S2). Floodplain specialists are species that occur exclusively or predominantly in this habitat, according to Remsen and Parker (1983), Parker et al. (1996) and our own field experience in the region (see Laranjeiras et al., 2014, 2017; Naka et al., 2020). By analysing floodplain specialists alone, we avoided the known role of the Negro and Branco rivers as physical barriers for *terra-firme* forest birds (Haffer, 1974; Naka, 2011; Naka et al., 2012; Naka & Brumfield, 2018).

We also analysed the richness of species that are typical of black- or whitewater floodplains (hereafter, black- or whitewater species, respectively; see Table S2). These included previously identified indicator species (which are significantly more frequent or exclusively found in one of the two river types; see Laranjeiras et al., 2019) and other floodplain specialists that were known, above the confluence, only from the Rio Branco (see Naka et al., 2007, 2020).

We assessed sampling efficacy using randomized sample-based rarefaction curves (Kindt & Coe, 2005). To compare species richness between sections of the Rio Negro (lower vs. upper) and the Rio Branco, and between opposite sides of the lower Rio Negro, we applied a nonparametric Wilcoxon–Mann–Whitney test, followed by a pairwise test.

We visualized variation in species composition among sites by reducing data dimensionality through non-metric multi-dimensional scaling (two-axis NMDS ordination), using the Jaccard dissimilarity index (for presence–absence data) and the Bray–Curtis index (for abundance data). Abundance data for each species was represented by the number of point-counts in a single site in which that species was detected (0–10), and not the total number of individuals detected. Total number of points per site with detections is a proxy for actual abundance, offering advantages over using raw numbers of individuals under this sampling design. First, because most detections were auditory and point surveys lasted 15 min, it was difficult to avoid double counting individuals. Also, our sample unit was the site and not the points; this assumes that 10 consecutive points capture the normal variation within a site, and counting points with presence instead of total individuals deemphasizes very local phenomena, such as microhabitat differences among points, presence of single fruiting trees filled with birds or a large flock at a particular point. Overall, our impression is that large concentrations of individuals of any species at any given site were rare and that most species were represented by a single individual or a pair at any given point.

To assess the statistical significance of observed differences in avian species composition in the comparisons, we ran a Permutational

Analysis of Variance (Anderson, 2001; McArdle & Anderson, 2001), followed by a pairwise test using a derived function (Arbizu, 2019). This analysis uses pseudo-*F* values to compare within and among-group similarity, assessing significance by permutation.

We used a model ranking approach (generalized linear models) to verify if the sediment concentration in the water explains the variation in avian species composition around the confluence. We considered six response variables: four were the first axis scores of each of two ordinations (Jaccard or Bray–Curtis index Gaussian distribution), for all species and for only floodplain specialists; the other two variables were species richness of whitewater and blackwater indicator species (Poisson distribution). For each of the six response variables, we contrasted alternative simple models, including as predictor variable either: (1) sediment concentration; (2) water type; (3) geographic distance of sampled sites from the confluence; or (4) a constant (null model). In addition, we included an interaction model, to verify if the effects of sediment concentration depend on the water type (Table 2). Models for each dependent variable were ranked using the Akaike information criterion, with adjustment for small sample size (AICc; Burnham & Anderson, 2002). Most plausible models were identified considering dAICc $\leqslant 2$ (Burnham & Anderson, 2002).

To identify which species characterized avian dissimilarities between river sections, we performed an indicator species analysis. This analysis generates a value between 0 and 1 for each species, where 0 indicates no association with either group of sites, and 1 indicates both complete fidelity to one of the groups and representation at every site in that group (Dufrêne & Legendre, 1997). Statistical significance of the indicator value was assessed through 10,000 permutations, and the analysis was performed allowing site group combinations.

We carried out all data analyses using the R language platform version 3.5 (R Core Team, 2016). We used the *kruskall.test* function from the *stats* package (version 3.3.2) to run the Kruskal–Wallis test. We used the package *vegan* (Oksanen et al., 2015) to construct rarefaction curves (*specaccum* function), to build distance matrices based on Bray–Curtis and Jaccard indexes (*vegdist* function), and to run the NMDS (*metaMDS* function) and the *permanova* (*adonis* function). We ran the pairwise tests using the *pairwise.adonis* function (Arbizu, 2019). We performed generalized linear models, using the *glm* function (*stats* package) and model ranking using the *AICctab* function of *bbmle* package (Bolker, 2020). We ran Indicator Species Analysis using the *multipatt* (IndVal.g) function of the *indicspecies* package (De Cáceres et al., 2015).

3 | RESULTS

During our surveys, we recorded 9,235 detections of 303 bird species, including 94 floodplain forest specialists (Table S2, archived data). Although we found no significant differences in species richness per site between river sections (Figure 2a), total avian species richness was higher along both the Rio Branco and lower Rio Negro than on the upper Negro, independent of survey effort (Figure 3a). Moreover, the species richness of both floodplain specialists and of whitewater species was significantly higher on the Rio Branco and on the left side of the lower Rio Negro than on the right side or on the upper Negro (Figure 2b and c). The total species richness of blackwater bird species was similar between sections of the Rio Negro (Figure 3b), but blackwater species richness per site was higher on the upper Rio Negro than in any other section (Figure 2d).

Avian species composition differed between sections of the Rio Negro (Table 1), despite a wide overlap in the ordinations (Figure 4). Some sites on the eastern side below the confluence, particularly those on the islands, were the closest, in terms of avian species composition, to sites on the Rio Branco (Figure 4). Differences between opposite sides of the lower Rio Negro were significant when considering the entire community (Table 1), but not for the subset of floodplain specialists (Table 1). Similar results (significant for the entire community; non-significant for floodplain specialists) were found for the differences between the right side of the lower Rio Negro and the section above the confluence (Table 1).

Sediment concentration, better than water type or geographic distance of sampled sites from the confluence, explained the variation in avian species composition (for both dissimilarity indexes and species subsets) and in the species richness of white- and blackwater bird species, given simple models (Table 2). The models with interaction of sediment concentration and water type were top-ranked overall (Table 2, Figure 5), indicating the effects of sediment concentration differed between rivers.

The indicator species analysis identified 23 species as indicators of the left side of the lower Rio Negro, with 11 being shared with the Rio Branco, including six whitewater species (Figure 6, Table S3). In contrast, 16 species were identified as indicators of the upper Rio Negro, with eight being shared with the right side of the lower section, including six blackwater species (Figure 6, Table S3).

4 | DISCUSSION

Confluences of large rivers are striking hydrogeological phenomena, with potential impacts on the ecology and biogeography of aquatic and floodplain habitats (Benda et al., 2004; Park & Latrubesse, 2015; Rice et al., 2008). Here our results demonstrate the implications of such phenomena for the distribution of the floodplain forest avifauna in the northwestern Brazilian Amazon. The input of the whitewater sediment-rich Rio Branco into the Rio Negro (the world's largest blackwater river) promotes species diversity and a distinct mixed avifauna. Regardless of the well-known role of the Negro and Branco rivers as barriers for *terra-firme* bird species distributions (Haffer, 1974; Naka, 2011; Naka et al., 2012; Naka & Brumfield, 2018), bird species that are typical of whitewater floodplains occurred predominantly, or exclusively, on the left riverbank or nearby islands of the lower Rio Negro, on the same side into which the Rio Branco flows and where its muddy waters seem to be

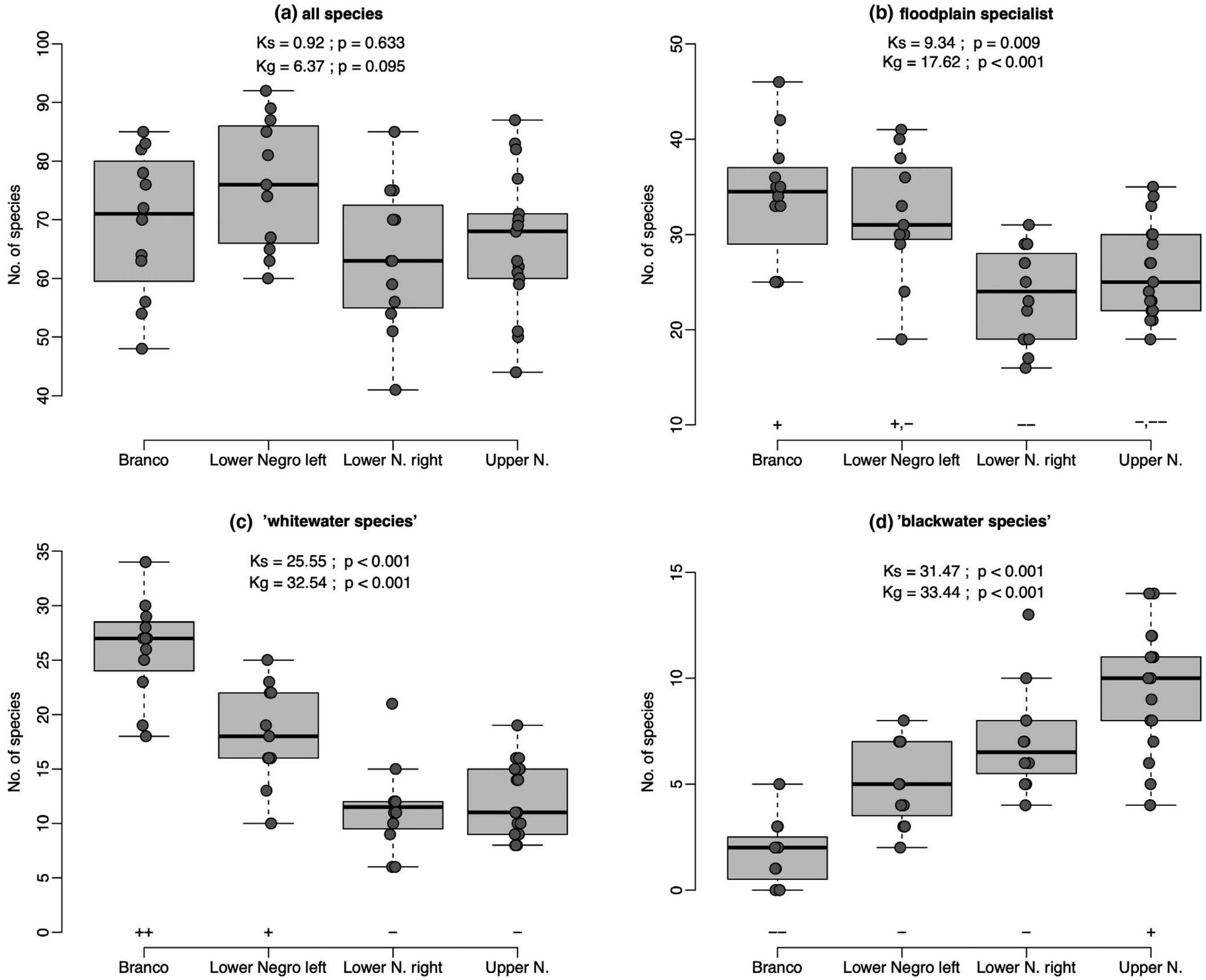

FIGURE 2 Boxplots showing the variation in total numbers of (a) all resident bird species, (b) floodplain specialists, (c) whitewater indicator species and (d) blackwater indicator species, along distinct sections of the Rio Negro and the Rio Branco (Brazilian Amazon). Results of Kruskal–Wallis tests with level of significance are shown: 'Ks' for comparison between sections (lower vs. upper Rio Negro vs. Rio Branco) and 'Kg' for comparisons given separately opposite sides of the lower Rio Negro. Non-significant differences among sections in post hoc pairwise comparison are indicated by use of the same symbol ("++", "+", "-", "--")

channelled. These results are similar to those found for Amazonian fishes (Fernandes et al., 2004), indicating that confluences of larges rivers not only affect aquatic species, but also the distribution of floodplain terrestrial biodiversity.

A mixed avifauna in the lower Rio Negro and the tight correlation between sediment concentration and species composition indicate the importance of the dynamics and distribution of nutrient-rich sediments. It has been suggested that the influx of sediments from the Rio Branco contributed to the formation, and contributes to the maintenance, of river islands in the lower Rio Negro (Leenheer & Santos, 1980; Cunha & Sawakuchi, 2017; Latrubesse & Franzinelli, 2005; Marinho, 2019). Likewise, it also seems to have influenced fertility, floristic composition and physiognomy of the landscape (Junk et al., 2011; Montero & Latrubesse, 2013; Oliveira et al., 2001). This influence likely created similar conditions (micro-habitats) to those found along the Rio Branco itself, allowing a blackwater floodplain to be colonized and occupied by species often associated with sediment-rich rivers. Our findings for birds are consistent with the distinct floristic compositions found between the lower and upper Negro (Montero & Latrubesse, 2013; Montero et al., 2014; Scudeller & Vegas-Vilarrúbia, 2018).

The importance of absolute values of sediment concentration in the water, on the other hand, should be interpreted with caution. Current sediment load in the Negro and Branco rivers seems to be much lower than it was in the mid-Holocene (~7,000 years ago; Cunha & Sawakuchi, 2017; Latrubesse & Franzinelli, 2005; Marinho, 2019). It is not clear if the current productivity, floodplain forest structure and associated avifauna result from current water sediment loads or reflect past increased rates of sediment deposition. Here we used spatial variation in this parameter to predict differences in the

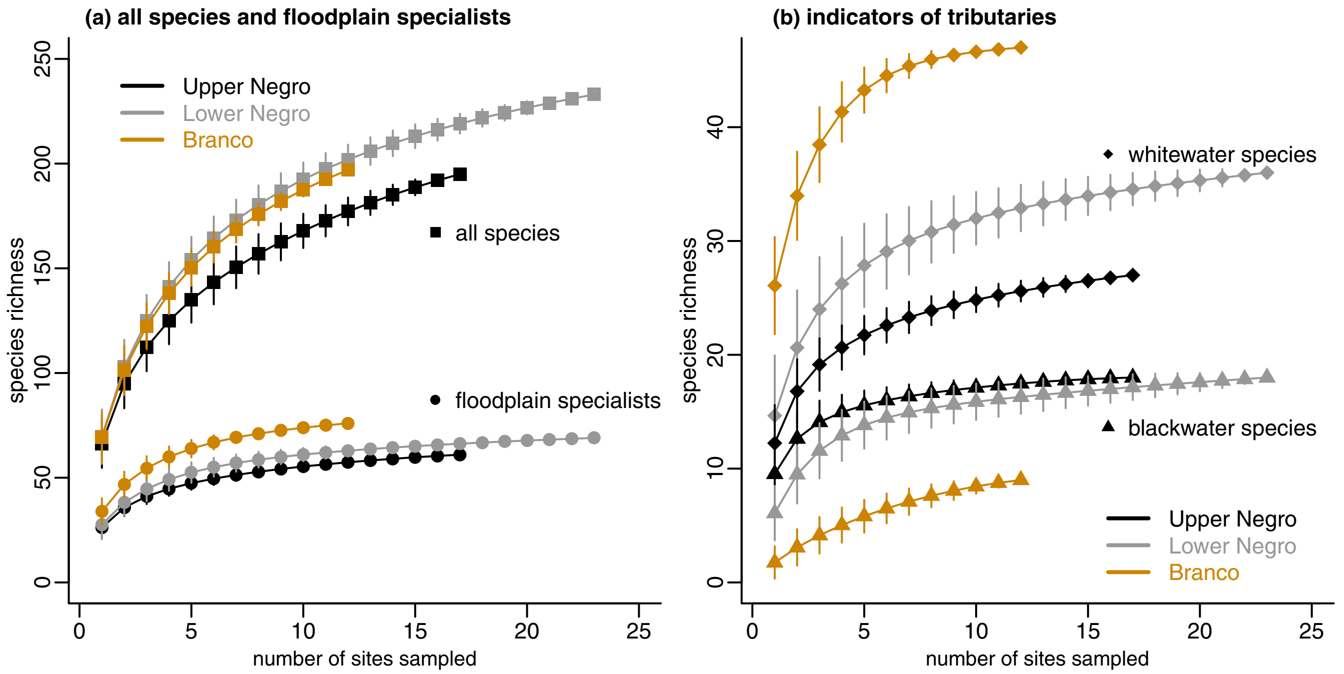

FIGURE 3 Species accumulation curves with increased sampling for (a) all resident bird species and floodplain specialists and for (b) whitewater and blackwater indicator species, along the Negro and Branco rivers (Brazilian Amazon)

TABLE 1 Statistics of permutational analyses of variance in multiple pairwise comparisons of bird species composition among distinct sections of the Rio Negro and Rio Branco (Brazilian Amazon), considering abundance (bc; Bray–Curtis index) and presence–absence (jac; Jaccard index) data for all detected species and for floodplain specialists, including the pseudo-F measure of differentiation level, adjustment (r^2) and significance level (p adjusted). Comparisons are ordered according to their pseudo-*F* values for all species (Jaccard index)

Pairwise comparison	All species				Floodpain specialists			
	Pseudo-F		r^2		Pseudo-F		r^2	
	jac	bc	jac	bc	jac	bc	jac	bc
Lower Negro vs. Branco	5.76	8.91	0.15[a]	0.21[a]	9.45	12.17	0.22[a]	0.27[a]
Upper Negro vs. Branco	5.73	8.93	0.18[a]	0.25[a]	10.24	10.79	0.27[a]	0.29[a]
Lower Negro (right) vs. Branco	5.51	8.78	0.20[a]	0.29[a]	7.31	11.50	0.25[a]	0.34[a]
Lower Negro (left) vs.Branco	4.52	6.80	0.18[a]	0.24[a]	6.03	8.79	0.22[a]	0.30[a]
Lower Negro (left) vs. Upper *N.*	3.45	4.70	0.12[a]	0.15[a]	4.04	5.31	0.13[a]	0.17[a]
Lower Negro vs. Upper *N.*	2.85	3.62	0.07[a]	0.09[a]	3.53	4.27	0.09[a]	0.10[a]
Lower Negro (left) vs. L. *N.* (right)	2.14	2.78	0.09[c]	0.12[a]	1.96	2.39	0.09[d]	0.10[d]
Lower Negro (right) vs. Upper *N.*	1.97	2.33	0.07[b]	0.08[b]	2.03	2.38	0.07[c]	0.08[c]

[a]p adjusted: ⩽0.01. [b]p adjusted: ⩽0.05. [c]p adjusted ⩽0.1. [d]p adjusted: >0.1.

avifauna between sites. Impacts of historical variation of sediment load on the floodplain forest structure and productivity and on the avifauna in a given site remain to be evaluated. Nevertheless, despite potential historical changes in those values, current spatial distribution of sediment concentrations remains a powerful predictor of species diversity.

4.1 | Biogeographical implications

The input of sediment-rich waters from the Rio Branco into the Rio Negro affects the overall distribution of floodplain birds. Two floodplain specialists, Ash-breasted Antbird (*Myrmoborus lugubris*) and Klages's Antwren (*Myrmotherula klagesi*), are distributed throughout the lower Negro and lower Branco, but are absent from upstream of their confluence or from elsewhere in the Rio Negro basin (see BirdLife-HBW, 2016). Other species, such as the Plain-crowned Spinetail (*Synallaxis gujanensis*) and the Gray-headed Tanager (*Eucometis penicillata*), appeared more locally below the mouth of the Rio Branco, but were recently discovered from other whitewater tributaries of the Negro, such as the Rio Demeni (Laranjeiras et al., 2019). These distribution patterns suggest that the floodplain forest in the Anavilhanas archipelago, located on the lower Rio Negro, may represent a dispersal corridor or stepping-stone, allowing expanded ranges or connecting populations of birds that are more prevalent in whitewater floodplains.

Such a dispersal corridor, however, may have been more important in the past than today, because several whitewater species appear to be isolated on the Rio Branco (Naka et al., 2007, 2020; this study). These include four bird species that are specialized on early-successional stages of the floodplain forest: White-bellied Spinetail (*Mazaria propinqua*), Lesser Wagtail Tyrant (*Stigmatura napensis*), River Tyrannulet (*Serpophaga hypoleuca*), and Bicolored Conebill (*Conirostrum bicolor*). These ephemeral habitats depend on the deposition dynamics of sediments (Rosenberg, 1990), and are currently scarce or completely absent along the Rio Negro (pers. obs.). The formation of Anavilhanas islands in a geologically recent

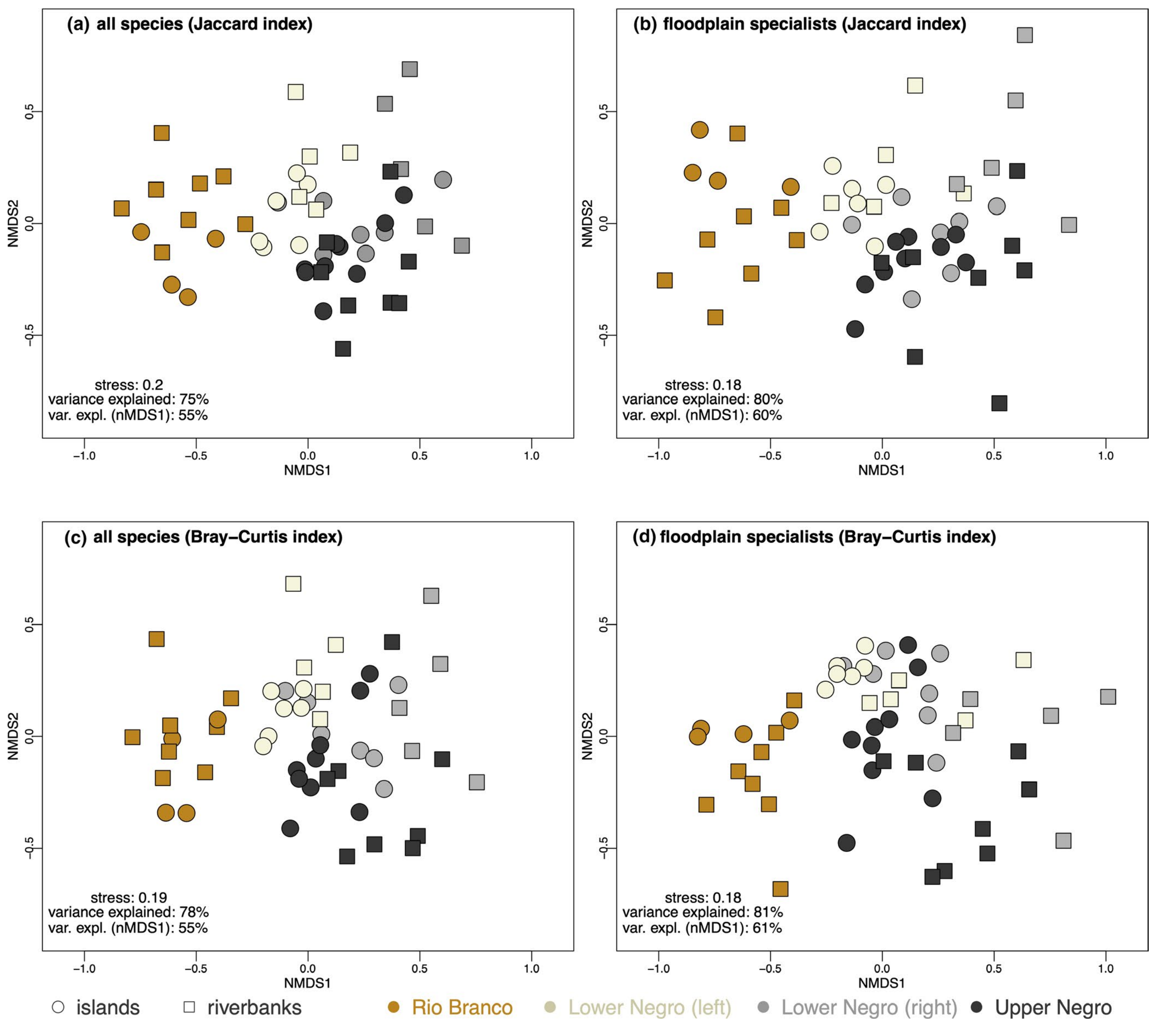

FIGURE 4 Ordinations (NMDS) of 52 sites, on islands and on riverbanks, along the Negro and Branco rivers (Brazilian Amazon), based on presence–absence (a and b) and on abundance data (c and d) for all resident bird species (a and c) and for floodplain specialists (b and d)

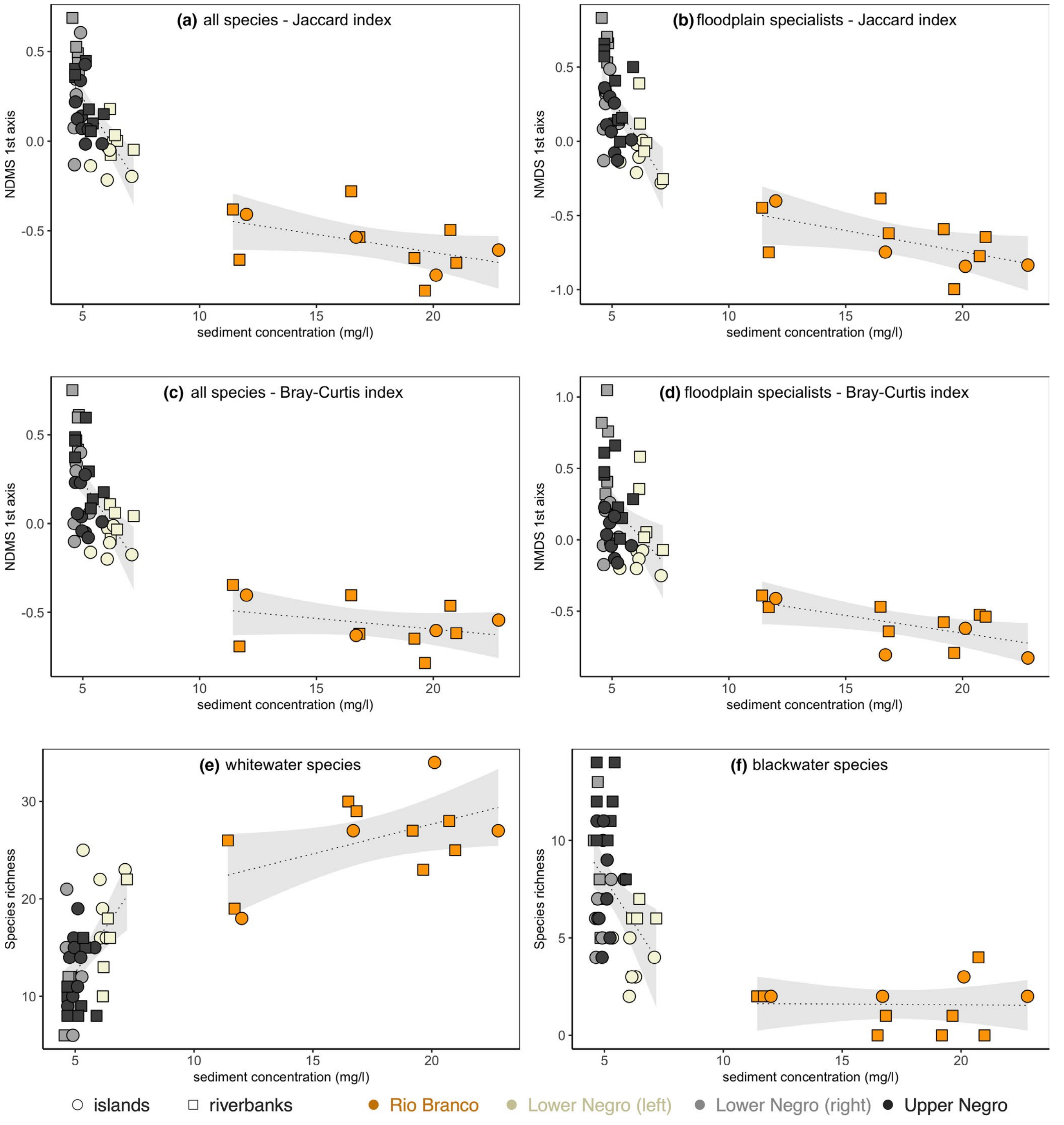

FIGURE 5 Relationships between floodplain avifauna and sediment concentration in the water that floods the forests along Negro and Branco rivers (Brazilian Amazon), considering as response variables: (a) the ordination first-axis scores for all species (Jaccard index); (b) the ordination first-axis scores for floodplain specialists (Jaccard index); (c) the ordination first-axis scores for all species (Bray–Curtis index); (d) the ordination first-axis scores for floodplain specialists (Bray–Curtis index); (e) species richness of whitewater indicator species and (f) species richness of blackwater indicator species. Predictor lines are shown for the top-ranked models (which included interaction with water type; see Table 2)

past, when the sediment load was likely much higher (Cunha & Sawakuchi, 2017; Latrubesse & Franzinelli, 2005; Marinho, 2019), may have offered these habitats temporarily and contributed to the establishment of these populations, from the main Amazon river system. Ongoing population genetic analyses should shed light into the probable origin of these populations (Leilton Luna and collaborators, pers. comm.).

Overall, the avifauna of the lower Rio Negro seems to represent a unique biogeographical transition zone. This avifauna is not more similar to that of the Rio Branco than to that of the upper Negro,

TABLE 2 Alternative models (generalized linear models) that were contrasted to explain variation in avian species composition along the Negro and Branco rivers (Brazilian Amazon). Response variables were: the first-axis scores of each of two ordinations, using Jaccard (jac) and Bray–Curtis (bc) indexes, for all species (NMDS1 all species) and only for floodplain specialists (NMDS1 flood. esp.), and the species richness of whitewater and blackwater indicator species. Alternative predictor variables were the sediment concentration in river water, water type (black vs. white), the distance of the sampled sites from the confluence, or a constant (null model). Models are ranked according the Akaike Information Criteria (dAICc) for the NMDS first axis for all species (Jaccard index). Statistics include: degrees of freedom (*df*)

Response variable	NMDS1 all species				NMDS1 flood. esp.				Species richness			
	Jac		bc		jac		bc		whitewater		blackwater	
Model (predictors)	dAICc	*df*	dAICc	*df*	dAICc	*df*	dAICc	*df*	dAICc	*df*	dAICc	*df*
Water type*sediments	0	5	0	5	0	5	0	5	0	4	0	4
Sediments	15.78	3	13.92	3	12.6	3	2.75	3	10.08	2	2.74	2
Water type	21.02	3	15.14	3	19.2	3	6	3	16.17	2	5.65	2
Null	79.09	2	68.37	2	72.19	2	47.95	2	91.99	1	71.39	1
Distance	81.33	3	70.62	3	74.37	3	49.55	3	93.95	2	67.38	2

contradicting our previous expectations (Laranjeiras et al., 2014; Naka et al., 2007; Naka et al., 2016). Despite significant differences between sections, many more floodplain specialists are shared between the two sections of the Rio Negro than either section shares with the Branco, and several species occurred exclusively on the Rio Branco (see Table S3). Nevertheless, the avifauna of the Rio Negro as a whole should not be interpreted as typical of blackwater floodplains. More than 20 species that are indicators of whitewater tributaries occurred widely along the river, including above the mouth of the Rio Branco (see Table S2). Surprisingly, satellite imagery also indicates differences in sediment concentrations on opposite sides of the upper Rio Negro (see Figure 1, Table S1). This likely represents the contribution of other whitewater tributaries upstream, such as the Rio Demeni, reinforcing the importance of sediment distribution (see above). Thus, rather than just representing a potential blackwater barrier between whitewater systems, the Rio Negro comprises a mosaic of varied floodplain forests, connecting and holding important populations of both black- and whitewater bird species.

4.2 | Implications for conservation

Given the importance of sediments to define patterns of bird diversity, the Rio Negro floodplains are extremely vulnerable. Although most of the lower Rio Negro is already within protected areas (Goulding et al., 2003), government plans to dam the Rio Branco and some of its tributaries may have devastating impacts on the floodplains downstream. Dams alter flooding regimes and retain sediments, thus drastically altering floodplain ecosystems (Assahira et al., 2017; Forsberg et al., 2017; Latrubesse et al., 2017; Lobo et al., 2019; Marinho, 2019; Resende et al., 2019). As we have shown, bird species composition above and below the confluence of the Negro and Branco rivers are broadly correlated with sediment loads. Bird species associated with higher sediment levels will likely suffer considerable population impacts, including species with highly restricted ranges, such as Klages's Antwren, an already threatened Brazilian endemic species (BirdLife International, 2018; Laranjeiras & Naka, 2018) . If the dam on the Rio Branco is built, in addition to the impacts on populations of several whitewater birds within the Rio Branco itself (Naka et al., 2020), no protected area on the lower Rio Negro will likely sustain the micro-habitats used by these species with subsequently reduced sediment loads. The connectivity between whitewater systems, apparently fostered by current sediment inputs, will be drastically reduced and the islands themselves could gradually erode away.

4.3 | Are major river confluences biogeographical phenomena in Amazonia?

Our results suggest that other major confluences are likely to affect the distribution of the floodplain avifauna throughout the Amazon basin. The Rio Negro itself meets the Amazon river, creating not only the much more famous and contrasting 'meeting of the waters' of two of the world's largest rivers (Goulding et al., 2003), but also effectively forming a different, enormous river with distinctive floodplain forests (Albernaz & Costa, 2007; Albernaz et al., 2012; Dunne et al., 1998), inhabited by a unique avifauna (Cohn-Haft et al., 2007). Numerous bird species occurring on the upper or lower Amazon River, such as the Scarlet-crowned Barbet (*Capito aurovirens*) and Varzea Piculet (*Picumnus varzeae*), respectively, also meet their known range limits near the Negro-Amazon confluence (BirdLife-HBW, 2016; Cohn-Haft et al., 2007). These mixing waters coexist for hundreds of kilometres (Park & Latrubesse, 2015), and seem to express past habitat discontinuities that were sufficient to isolate populations and promote diversification in floodplain specialized birds (Thom et al., 2020). Although the Rio Negro is the only major Amazonian blackwater river with whitewater tributaries, several other confluences of contrasting large rivers occur throughout the Amazon, such as that of the Mamoré and Guaporé rivers and of the Tapajós with the Amazon river (see Venticinque et al., 2016). Most such sites have not been studied carefully, and

FIGURE 6 Bird indicator species of specific sections of the Rio Negro or the Rio Branco (Brazilian Amazon), ordered according to their indicator value (from highest to lowest), including only those previously identified as indicators of white- (in orange) or blackwater (in black) tributaries or other floodplain specialists (in green). Detailed data are presented in the Table S3

these phenomena emerge as a key factor to explain boundaries of species' distributions and geographic patterns of Amazonian floodplain biodiversity.

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DATA AVAILABILITY STATEMENT

We certify that we have provided an accurate representation of our methods and raw data are available at ebird.org and Dryad Digital Repository: https://doi.org/10.5061/dryad.bk3j9kd9d (Laranjeiras, Naka, Leite, & Cohn-Haft, 2021).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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