



## RESEARCH PAPER

Journal of  
Biogeography

WILEY

# Climate as a major driver of avian diversity in riparian Amazonian habitats along an environmental gradient

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## Funding information

Fundação Estadual de Meio Ambiente e dos Recursos Hídricos (FEMARH); Fundação Boticário de Proteção à Natureza, Grant/Award Number: 934-2012.1; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Chico Mendes Institute of Biodiversity Conservation (ICMBio), Grant/Award Number: MPC-014.007; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 480496/2012-9 and 484219/2011-1; Rufford Foundation, Grant/Award Number: 19908-1

Handling Editor: Camila Ribas

## Abstract

**Aim:** To investigate the influence of bioclimatic, productivity and topographic variables on avian diversity patterns in riparian habitats along a savanna/humid forest environmental gradient. We investigate how this gradient affects patterns of taxonomic and phylogenetic alpha and beta diversities, and whether the changes observed along the river are the result of taxonomic (and phylogenetic) replacement or nestedness-resultant dissimilarities. We also explore a potential ecological mechanism to account for differences in species richness along the gradient.

**Location:** Basin of the Rio Branco, northern Amazonia, Brazil.

**Taxa:** An avian community of 325 bird species.

**Methods:** We sampled avian communities using standardized avian point counts at 16 localities, systematically distributed along the Rio Branco and two of its major tributaries. We compared patterns of species richness using rarefied numbers of species detected, and patterns of phylogenetic diversity with a community-wide consensus tree. In addition, we partitioned beta diversity in species replacement and nestedness-resultant dissimilarities. We reduced predictor variables using a principal components analysis, correlating locality scores with changes in diversity. We tested the effect of climatic variables on beta diversity with a distance-based redundancy analysis (dbRDA).

**Results:** Patterns of avian composition and species richness were highly correlated with climatic and productivity variables. We found more bird species in less arid localities with higher annual precipitation, and in areas with lower annual temperatures, lower evapotranspiration and less temperature variation throughout the year. Despite differences in species richness, the number of individuals remained relatively similar along the gradient. However, species-rich localities presented lower average species frequency and median avian biomass. Patterns of taxonomic and phylogenetic beta diversity were correlated with the climatic gradient and were due to species replacements.

**Main conclusions:** Climate represents a major player in structuring avian communities along the Rio Branco, affecting distinct levels of avian diversity organization. We found evidence of species packing, a mechanism to fit more species in the communities. Patterns of species replacement highlight the importance of transitional zones

along the gradient and stress their importance as future buffer zones, vital for the survival of bird species under future human-induced climatic conditions.

#### KEYWORDS

alpha diversity, Amazonia, beta diversity, birds, Rio Branco, Roraima, species packing, species turnover

## 1 | INTRODUCTION

Spatial changes in patterns of species richness represent a universal feature of biodiversity. At continental scales, environmental variables associated with altitudinal and latitudinal gradients usually determine diversity patterns, which follow the general observation that warmer regions support more species than temperate ones (Wallace, 1876). Habitat heterogeneity, productivity and climate are often considered primary drivers of current diversity patterns (Hawkins, Porter, & Diniz-Filho, 2003; Körner, 2007). Classic studies have already shown the strong relationship between habitat heterogeneity (e.g. number of habitats or micro-habitats) and species diversity (Pianka, 1966; Simpson, 1964). More recently, climate and associated energy supplies and productivity have been considered important drivers of ecological gradients worldwide, influencing biome and habitat boundaries and therefore constraining patterns of species distribution over broad geographic scales (Rahbek & Graves, 2001). However, data collected at continental scales are often too coarse to fully unveil the potential effect of climate on biome boundaries and on species diversity patterns.

Under the climate-based energy hypothesis, rainfall appears as one of the main drivers of species richness (Hawkins et al., 2003). Even subtle changes in rainfall patterns or other climatic variables can affect forest structure and plant species composition (ter Steege et al., 2003). Therefore, understanding how climatic variables correlate with patterns of biological diversity at fine scales may be particularly useful in a world affected by global warming and climate change (De Frenne et al., 2013). Temperature and rainfall are already changing worldwide (Weltzin et al., 2003) and reports forecast dramatic climatic alterations in the Amazon basin due to agricultural expansion and the accumulation of carbon in the atmosphere (Duffy, Brando, Asner, & Field., 2015; Salati & Vose, 1984). There is ample evidence that those changes in rainfall patterns will double or triple drought events in the Amazon in the next decades (Correa, de Paiva, Espinoza, & Collischonn, 2017; Duffy et al., 2015; Easterling et al., 2000). Therefore, it is crucial to understand the natural (non-human induced) variation in species richness and composition along environmental gradients (De Frenne et al., 2013), before human-made climate changes influence the boundaries of natural biomes. Furthermore, because climatic variables are easy to measure and have reliable historical data, it is possible to model and predict future changes in species distributions due to changes in critical climatic variables (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Parmesan, 2006; Thomas, 2010).

The Amazon basin is one of the world's most humid places, with high levels of rainfall and water vapour, contributing ~15% of the global freshwater reaching the oceans (Molinier, Guyot, Oliveira, & Guimarães, 1996). The mean annual rainfall for the whole basin is around 2,200 ( $\pm$  138) mm/year (Espinoza Villar et al., 2009). While some areas in north-eastern and western Amazonia receive higher levels of rainfall (3,000 mm/year and more), other areas receive considerably less. For instance, the plains along the border between Peru and Bolivia and the Brazilian state of Roraima and the adjacent region in Guyana represent some of the driest regions in the Amazon, receiving less than 1,500 mm of rainfall every year (Espinoza Villar et al., 2009). The relatively dry region located along the Brazil/Guyana border hosts the Roraima-Rupununi savannas, which are drained by the Essequibo River in Guyana, and the Rio Branco in Brazil. Despite being relatively short by Amazonian standards, the Rio Branco (~550 km) crosses three distinct geomorphological regions and one of the largest climatic gradients in the entire Amazon. Rainfall, for example, increases from 1,400 to 2,600 mm/year from the upper to the lower sections of the Rio Branco. The combination of geomorphology and climate has a dramatic effect on the vegetation: drier areas on top of the Boa Vista Formation are dominated by savannas and gallery forests and the more humid areas on the sedimentary basin are covered by tall humid forest and seasonally floodplain forest along the river.

Possibly the most interesting feature of the riparian avifauna along the Rio Branco is the differentiation between the avifauna on the upper and lower sections of the river (Naka et al., 2020). Several bird species associated with gallery forests are common along the river margins on the upper Rio Branco but absent on the lower sections of the river. Similarly, many bird species are widespread on the lower Rio Branco's floodplain forests but do not occur further north. This phenomenon creates two rather distinct avifaunas along the river, overlain by a steep climatic gradient. The species and climatic transitions along the Rio Branco offer a unique opportunity to understand, in considerable detail, how rainfall and other environmental variables affect patterns of species replacements and diversity.

Patterns of beta diversity, which relate to the change in species identity and relative abundance among sites (Whittaker, 1960), may reflect two different phenomena, including species replacement (turnover) and species loss (nestedness; Baselga, 2010; Baselga, Jiménez-Valverde, & Niccolini, 2007; Harrison, Ross, & Lawton, 1992). Nestedness occurs when the biota of one region (or set of sites) represents a subset of the species present at the other region (Wright & Reeves, 1992), which implies that there

is a loss of species across the gradient (see Legendre, 2014, for a historical review of nestedness). Spatial turnover, on the other hand, occurs when there are species replacements across the gradient (Baselga, 2010). More recently, species replacement patterns have included phylogenetic information to understand the contribution of species' evolutionary history to present-day patterns, allowing the evaluation of both ecological and evolutionary questions (Cavender-Bares, Ackerly, & Kozak, 2012; Chiu, Jost, & Chao, 2014).

Changes in patterns of species diversity, however, raise a fundamental question, which is how biotic assemblages manage to pack more species in the same geographic space (MacArthur & Levins, 1967). Productivity has been pointed out as a potential driver of species richness (Connell & Orias, 1964), but the causal mechanisms behind such relationship remain controversial (Grace et al., 2016). Another quite different phenomenon, however, are the mechanisms that may allow a system to sustain more species, without a significant raise in species abundance. One such phenomenon is known as species packing, where more productive environments allow the coexistence of more species, without supporting more individuals. Potential mechanisms include establishing an upper limit in the abundance of each species, allowing more species in the system (Paine, 1966; Schoener, 1965) or allowing a higher degree of niche specialization, resulting in tighter niches (MacArthur & Levins, 1967).

In this study, we used standardized avian surveys (point counts) to evaluate patterns of riparian bird diversity along a broad environmental gradient. We systematically distributed these surveys throughout the entire length of the Rio Branco and its two main tributaries, the Uraricoera and Tacutu rivers. In a previous study (Naka et al., 2020), we have shown that geomorphology can explain differences in species composition between the upper and lower sections of the Rio Branco. Here, we ask how the environmental gradient present on top of these geomorphologic units affects taxonomic and phylogenetic alpha and beta avian diversities along the river. We also investigate whether the changes observed in avian species assemblages along the river are the result of taxonomic (and phylogenetic) replacement or nestedness-resultant dissimilarities. Finally, we evaluate an ecological mechanism that may allow differences in avian diversity along the gradient. We interpret these results considering future climatic changes expected to occur in the next decades in addition to planned infrastructure projects for the Rio Branco basin, including a major hydroelectric dam and an associated hydroway that will likely affect the distribution of species in dramatic ways.

## 2 | MATERIALS AND METHODS

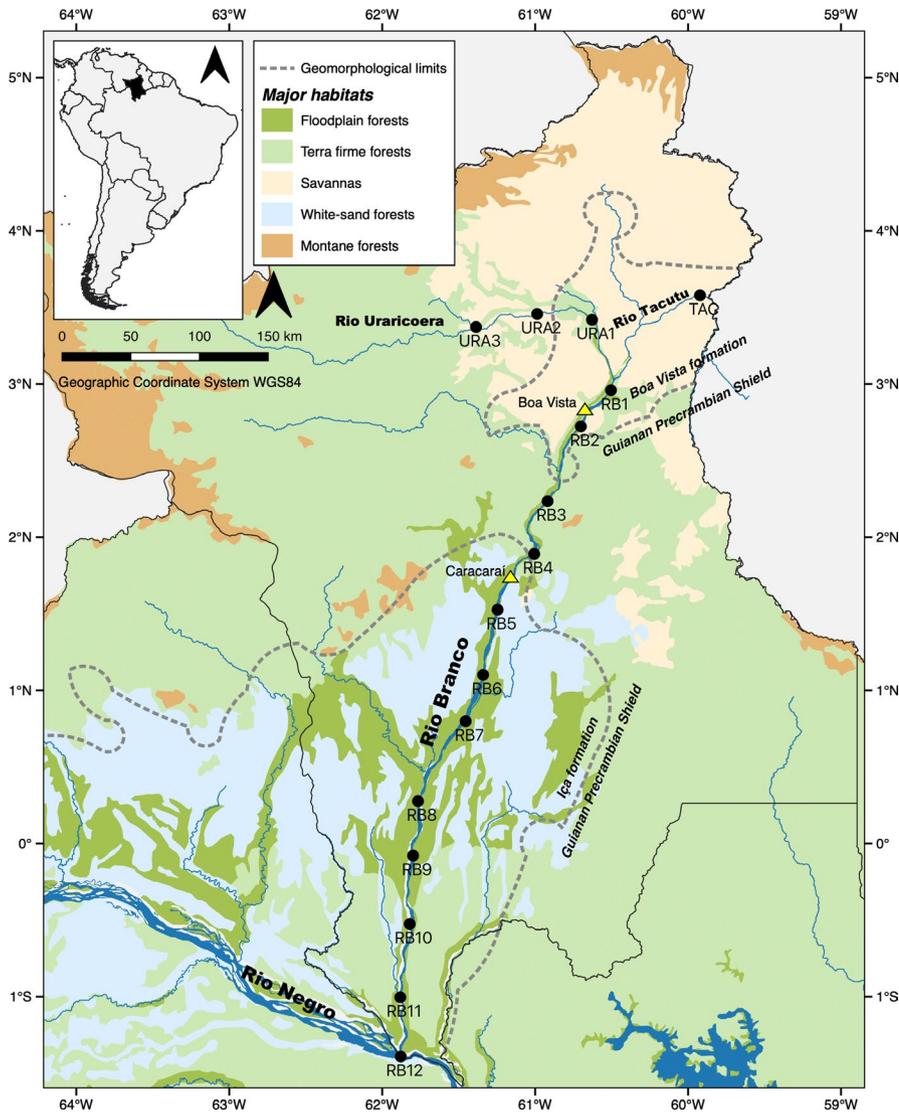
### 2.1 | Study area

The Rio Branco is a relatively minor river by Amazonian standards, ranking 18th among the 20 longest rivers in the Amazon basin (Goulding, Barthem, & Ferreira, 2003). As its Portuguese name

suggests, it is generally considered a whitewater river due to its muddy appearance, but due to seasonal changes in its chemical characteristics, it is also considered a clearwater river during the dry season (Ríos-Villamizar, Piedade, Da Costa, Adeney, & Junk, 2013). The Rio Branco originates in the Roraima-Rupununi savannas from the convergence of its two upper tributaries, the Uraricoera and Tacutu Rivers (Figure 1). The Rio Branco runs in a north-south direction for its entire course until reaching the Rio Negro. While the Tacutu drains the savannas, the Uraricoera drains the savannas and the Sierra de Parima in the Guayan Highlands. According to its geomorphological features, the Rio Branco can be divided into upper, middle, and lower sections (Cremon, de Fátima Rossetti, de Oliveira Sawakuchi, & Cohen, 2016). The upper Rio Branco runs for ~100 km, from the confluence of its two upper tributaries to the Rio Mucajá. This section runs on top of the Boa Vista geological formation (Melo, Schaeffer, Vale, & Uchoa, 2010), located in an area of low rainfall (less than 1,400 mm/year). The riverine vegetation along this section is made of narrow stretches of gallery forests, which are structurally similar to the vegetation present along the lower sections of the Uraricoera and Tacutu rivers. The middle Rio Branco runs for ~150 km, cutting through Precambrian rocks of the Guiana Shield and forming several rapids before reaching the city of Caracará. This section can be considered somewhat intermediate with taller forests intermingled with semi-deciduous forests. The lower section of the river flows for ~300 km on top of sedimentary rocks of the Solimões Formation, extending all the way to the Rio Negro (Figure 1). Here, the river floodplains are covered with tall seasonally flooded forests (Cremon et al., 2016). South of Caracará, rainfall increases considerably, reaching up to 2,600 mm/year (Table 1). Like other Amazonian rivers, seasonal fluctuations in the level of the river can oscillate from 8 to 10 m between the low-water and high-water seasons (Junk, Bayley, & Sparks, 1989). The general flatness of the basin results in extensive areas influenced by seasonal flooding. Depending on the topography, the Rio Branco floodplains may remain underwater from a few days to several months every year, creating a complex mosaic of habitats that include barren beaches and sand-bar scrubs to flooded and transitional forests (Junk et al., 2011). A more detailed description of the study region and the several habitats found along the river's margins (including images) are available in our recent study (Naka et al., 2020).

### 2.2 | The avifauna of the Rio Branco

The avifauna of the Rio Branco is well known, with a fairly complete list of bird species (Naka et al., 2006; Laranjeiras et al., 2014). To date, a total of 439 bird species have been recorded in riverine habitats along this river and its main tributaries (Naka et al., 2020). Although the Rio Branco represents a well-known biogeographical barrier for terra-firme forest avian taxa (Naka, 2011; Naka, Bechtoldt, Henriques, & Brumfield, 2012; Naka & Brumfield, 2018), the river does not seem to present a biogeographical boundary for riparian and riverine bird species.



**FIGURE 1** Map of the Rio Branco basin in northern Amazonia, including 16 sampling localities where avian surveys were conducted (black dots). Light brown background represents the Roraima/Rupununi savannas, located within the Boa Vista geological formation. Light green background represents Amazonian lowlands dominated by terra-firme forests and light blue represent white-sand forests (*Campinas*). Dark green along rivers depicts riverine forests, which are formed by gallery forest on the upper Rio Branco (RB 1-2) and its two tributaries, the Uraricoera (Ura 1-3) and Tacutu (TAC) rivers, and by floodplain forest along the lower Rio Branco (RB 5-12). The two localities between Mucajai and Caracará (RB 3-4) represent the ecotone. Yellow triangles represent major cities along the river

### 2.3 | Avian surveys

We conducted standardized avian censuses (point counts) along 16 localities systematically distributed every 50 km along the entire length of the Rio Branco and the lower sections of the Uraricoera and Tacutu rivers (Table 1, Figure 1). We established 12 sampling localities along the 550 km of the Rio Branco, three sampling localities along the lower 150 km of the Rio Uraricoera and a single locality along the Rio Tacutu, 100 km from its mouth (Figure 1). Each locality along the Branco and Uraricoera rivers was sampled by approximately 30 point counts, including 10 on each bank of the river and 10 located on river islands (Table 1). At each locality, point counts were systematically established every 500 m, covering ~5 km of river. Given the lack of islands on the Rio Tacutu, we only sampled this river with 20 point counts (10 on each side of the river). The sampling of the Rio Branco was completed in 2013, whereas the sampling on the Uraricoera and Tacutu rivers occurred in 2014 and 2015. All samples were conducted during the dry seasons. However, given that most species are year-long residents in the area (Naka et al., 2020), we expect no seasonal effects on our sampling. During point counts, which lasted 15 min, we recorded all species

seen or heard in an unlimited radius. Censuses were conducted from the shore, usually penetrating a few metres into the forest, to minimize the effect of forest structure on species detectability. Although not all species connected to flooded environments favour the river margins, by doing acoustic surveys, we were able to detect most species regardless of their specific microhabitat preference. Point counts started at dawn (between 5:30–5:45 a.m.), and mostly finished before 10 a.m. All surveys were conducted by at least one experienced observer (LNN or TOL).

### 2.4 | Environmental data

We obtained climate data from WorldClim 2.0 (Fick & Hijmans, 2017) using a 1-km spatial resolution. Initially, we obtained all 19 bioclimatic variables derived from monthly temperature and precipitation average for the years 1970–2000 (see Table S1), representing annual trends, seasonality and extreme values (Fick & Hijmans, 2017). In addition, we obtained five variables from the ENVIREM database (Title & Bemmels, 2018), including annual potential evapotranspiration (PET), aridity (degree of water deficit) and terrain roughness index

**TABLE 1** Average and total number of bird species and individuals detected per survey and locality, based on 467 surveys conducted in 16 localities along the Rio Branco (RB1 to RB12) and its two major tributaries, the Uraricoera (URA1 to URA3) and Tacutú (TAC) rivers

Locality	No. surveys	Mean no. spp (total spp. obs.)	Mean no. ind (total ind. obs.)	Rarefied phylogenetic diversity (PD)	Median biomass (g)	Ave. spp frequency
TAC	20	14.7 ± 2.1 (73)	14.95 ± 2.14 (299)	735.953	204.7	0.201
URA3	30	16.37 ± 1.76 (116)	16.47 ± 1.81 (494)	941.570	137.8	0.080
URA2	30	17.17 ± 2.31 (113)	17.57 ± 2.46 (527)	860.665	186.1	0.152
URA1	30	15 ± 1.95 (91)	15.1 ± 1.98 (453)	761.174	148.1	0.165
RB1	30	17.8 ± 2.47 (117)	18.07 ± 2.56 (542)	746.792	179.35	0.152
RB2	30	15.93 ± 3.44 (116)	16.27 ± 3.74 (488)	777.192	121.2	0.115
RB3	30	13.13 ± 2.65 (119)	13.17 ± 2.67 (395)	781.453	99.3	0.131
RB4	30	11.6 ± 2.51 (109)	11.87 ± 2.8 (256)	788.264	133.4	0.124
RB5	30	12.83 ± 2.09 (100)	13.07 ± 2.15 (392)	762.301	77.3	0.137
RB6	30	14.5 ± 1.33 (130)	14.57 ± 1.37 (437)	901.174	141.4	0.110
RB7	30	11.77 ± 2 (122)	11.87 ± 2.02 (356)	900.697	145.4	0.106
RB8	29	12.76 ± 2.64 (113)	12.76 ± 2.64 (370)	850.642	124.2	0.128
RB9	30	15.93 ± 2.5 (136)	15.97 ± 2.5 (479)	812.886	99.9	0.112
RB10	29	15.21 ± 2.37 (132)	15.38 ± 2.41 (446)	766.163	112.8	0.096
RB11	30	15.43 ± 1.57 (118)	15.47 ± 1.57 (464)	828.202	153.5	0.113
RB12	29	13.66 ± 2.73 (116)	13.9 ± 2.88 (403)	696.013	89.2	0.117

(a measure of topographic variation; Title & Bemmels, 2018). Prior to the analyses described below, we removed climatic/topographic variables with correlation higher than 0.9, resulting in 12 non-correlated variables (Table S1, Figure S1).

## 2.5 | Bird phylogeny

We built a phylogenetic tree with the 325 species detected on our point counts (Appendix S1), using the 'Phylogeny Subset' tool available at [www.birdtree.org](http://www.birdtree.org) from a world bird phylogeny of 9,993 species (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). This tool generates 10,000 trees combining a backbone phylogeny with 158 clades (Hackett et al., 2008) and calibrated molecular trees from sequence data with 15 genes (Jetz et al., 2012). Species without genetic data were included in the tree using their taxonomic information to generate a consensus tree. Although this approach is not devoted of criticisms (Davies, Kraft, Salamin, & Wolkovich, 2012), it remains a useful tool to investigate phylogenetic community structure. Earlier critical problems with node calibration have been corrected in the Phylogeny Subset program. We generated 1,000 trees from 325 sampled species to build a consensus tree with branch lengths using the Maximum Clade Credibility Tree with the software Mesquite 3.04 (Maddison & Maddison, 2016).

## 2.6 | Data analysis

Prior to analyses, we used a principal components analysis (PCA) using 11 bioclimatic/energetic and one topographic variable, to

reduce the number of predictor variables in the model and avoid the inflation of model fit due to the large number of correlated variables (Quinn & Keough, 2002). We retained the first three PCA axes, which accounted for >90% of the total inertia. Then, we used the PCA scores of each site as predictor (climatic or topographic) variables to explain the observed changes in taxonomic and phylogenetic diversities (See Table S2 and Figure S2).

We used Hill numbers (the so-called effective number of species) integrated with rarefaction (both interpolation and extrapolation) to test whether climatic variables represented by the three first axes of the PCA affect avian taxonomic and phylogenetic alpha and beta diversities. We used an individual-based method with Shannon index (order  $q = 1$ ) to avoid the effect of the number of individuals detected (Chao et al., 2014), which varied from 256 to 542 individuals among sites (Table 1). By rarefying and extrapolating with Hill numbers from both taxonomic and phylogenetic diversities, we obtained a standardized measure of alpha diversity to be used as the dependent variable in generalized least squares (GLS) models. We constructed two models, one including spatially correlated residuals [`mod.Ratio <- nlme:glms(interpolated_richness ~ PC1 + PC2 + PC3, correlation = corRatio(form = ~Longitude + Latitude, nugget = TRUE), data = dat)`], and another without using spatial autocorrelation [`mod.simple <- nlme:glms(interpolated_richness ~ PC1 + PC2 + PC3, data = dat)`]. We compared models with other correlation classes, such as spherical, linear, exponential and Gaussian spatial correlation (Pinheiro & Bates, 2000). Then, we compared the six models (five with correlation structure and one without any correlation structure) with model selection (AIC) to retain the best model to investigate the effect of climatic variables (PCs) on the rarefied (both

interpolated and extrapolated) taxonomic and phylogenetic diversities. By allowing correlated residuals with GLS, we improved model adequacy and avoided spurious interpretations caused by the spatial structure in the response variable. Both for rarefied species richness and rarefied phylogenetic diversity, simple linear models (without spatial autocorrelation) performed better than more complex ones and were therefore used in the analyses (Table S3).

To test the effect of climatic variables on taxonomic and phylogenetic beta diversity, we used distance-based redundancy analysis (dbRDA). We first partitioned beta diversity into replacement (originally called turnover) and nestedness-resultant (originally called nestedness) components (Baselga, 2010), using the Jaccard dissimilarity index. It is important to emphasize that the decomposition of beta diversity into these two components has been hotly debated in the literature. One of the limitations of this method is that it overestimates species turnover compared with another method proposed by Podani and Schmera (2011) which, in turn, underestimates turnover. Importantly, both indices increase monotonically to changes in community composition, as it is desirable for beta diversity calculation (Legendre & De Cáceres, 2013). We calculated turnover components using Podani and Schmera's index and found high similarity with Baselga's values ( $r = 0.86$ ). Thus, we decided to use the decomposition proposed by Baselga, as they have also included phylogenetic decomposition using the same mathematical procedure. Leprieur et al. (2012) generalized this method and included a quantification of true lineage turnover (similar to species replacement component of the taxonomic beta diversity) and phylogenetic diversity gradients (similar to the nestedness-resultant component of the taxonomic beta diversity).

To compare taxonomic and phylogenetic replacement and nestedness-resultant dissimilarity among sites along the Rio Branco and its tributaries, we used the four beta diversity matrices (i.e. distance matrices of taxonomic and phylogenetic diversities for both replacement and nestedness-resultant dissimilarities) as dependent variables in the dbRDA. However, because spatial autocorrelation can explain both changes in species composition and climatic gradients, we obtained spatial vectors by implementing Moran's eigenvector maps (MEM) that used conditional variables in dbRDA (Bauman, Drouet, Dray, & Vleminckx, 2018). Variables were obtained in the MEM approach by diagonalizing a double-centred spatial weighting matrix (Dray et al., 2012). We used an optimized method proposed by Bauman et al. (2018) that compares the accuracy of different weighting matrices to identify a higher *r-square* estimation. In addition, we used a *p*-value correction method for multiple tests to account for type I error rates (Bauman et al., 2018).

To represent changes in species along the environmental gradient, we used a non-metric multidimensional scaling (NMDS) applied to a Sorensen dissimilarity index that was computed based on a species by site presence/absence matrix. We selected two dimensions ( $k = 2$ ) for scaling and used site scores as a response

variable to represent species composition. Then, we regressed the scores of the first NMDS axis against the climatic gradient (PC1 axis).

To evaluate whether species rarity changed along the climatic gradient, we calculated the frequency of occurrence of all species by adding the number of times a given species was detected at each locality divided by the number of points surveyed at each locality, resulting in a value ranging from, for example, 0.033 (found at one point out of 30 surveyed in a locality) to 1 (found in every survey). Finally, we calculated the mean of frequencies at each locality, excluding species not found at a given locality. Avian average biomass (available in the Appendix S1) was obtained from specimen data from the Rio Branco, retrieved from three Brazilian ornithological collections, complemented by data from other localities, when specimens were not available (see Naka et al., 2020, for a complete list of modern specimens available from the Rio Branco).

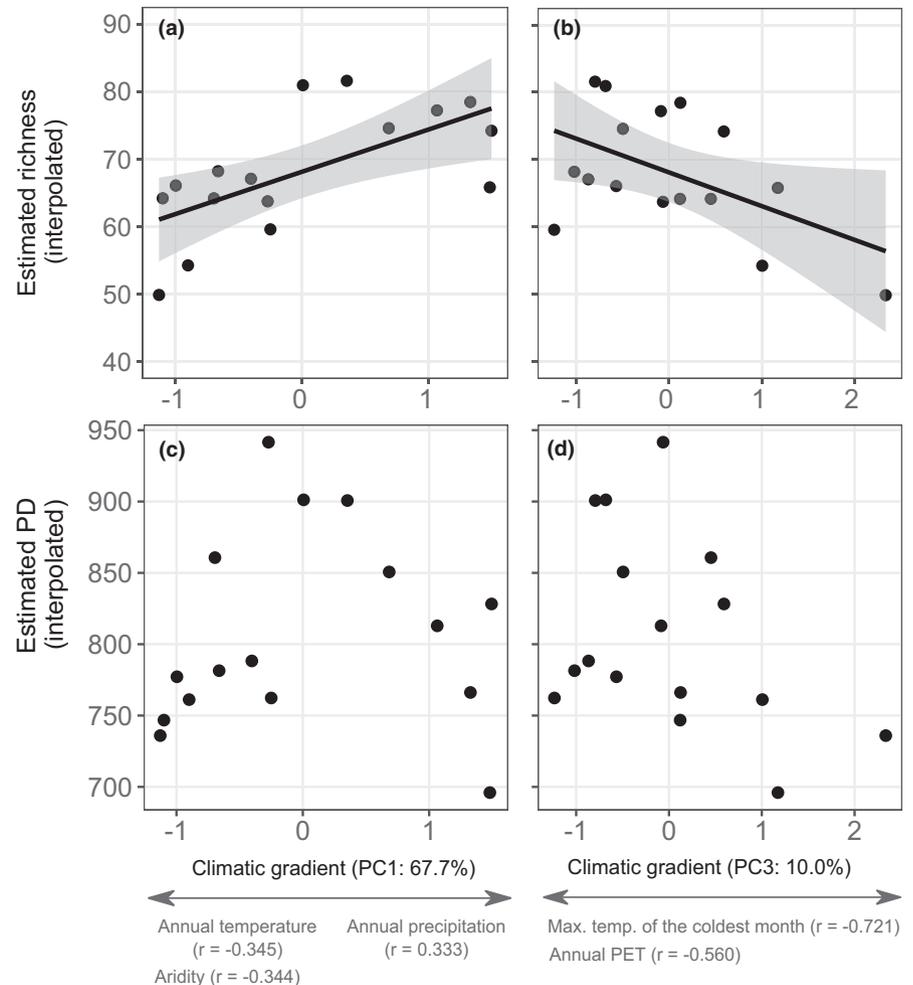
All statistical analyses were conducted in R, using several packages, including *vegan* (Oksanen et al., 2019), *adespatial* (Dray et al., 2019), *iNEXT* (Hsieh, Ma, & Chao, 2019) and *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2019).

### 3 | RESULTS

#### 3.1 | Patterns of species richness and phylogenetic diversity

We conducted a total of 467 avian surveys (point counts) throughout the Rio Branco and its two northern tributaries, where we detected 325 bird species (Appendix S1). On average, we detected  $14.61 \pm 1.84$  species and  $14.77 \pm 1.88$  individuals per 15-min survey (Table 1, Figure S3). We found no significant difference in the number of species or individuals recorded per survey along the climatic gradient (Figure S3), but we observed a large variation in the number of species and individuals detected per locality even for equal number of surveys, ranging from 91 to 136 species (data not corrected by number of individuals) and 256 to 542 individuals detected in 30 independent surveys. When corrected by sample size (individual-based interpolated data), we found a correlation between the estimated number of species per locality and the climatic gradient (represented by the first ( $F_{1,9} = 15.04$ ,  $p = 0.004$ ) and third ( $F_{1,9} = 10.05$ ,  $p = 0.0081$ ) PCA axes), which encompass variables such as Aridity, Annual Temperature, Isothermality, annual PET and Annual Precipitation (Figure 2a,b, Table S2). However, there was no correlation between the rarefied phylogenetic diversity and the first ( $F_{1,12} = 0.006$ ,  $p = 0.801$ ) and third ( $F_{1,12} = 2.72$ ,  $p = 0.126$ ) PC axes (Figure 2c,d). Briefly, we found more bird species in less arid localities with higher annual precipitation, and in areas with lower annual temperatures, lower evapotranspiration and less temperature variation throughout the year (Table 1, Table S2).

**FIGURE 2** Estimated species richness and phylogenetic diversity (interpolated data) in relation to axes 1 and 3 of the PCA, which represent a climatic gradient (a and c) and a productivity and temperature gradient (b and d) respectively. Points represent our surveyed localities ( $n = 16$ ); grey areas refer to confidence intervals, and black lines denote significant relationships



### 3.2 | Species packing

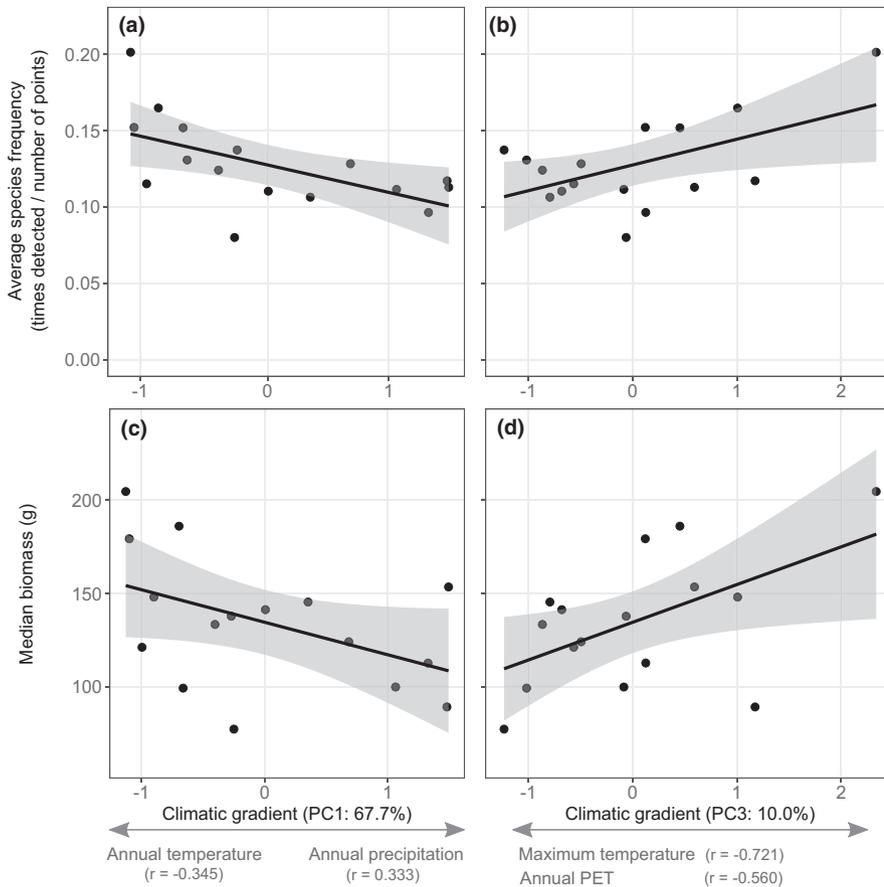
The observed increase in the number of species along the climatic gradient occurred without a significant increase in the numbers of individuals (Table 1). At the same time, we detected a reduction in the average species frequency along the gradient, which responded to all climatic axes (PC1:  $F_{1,9} = 22.139$ ,  $p = 0.001$ , PC2:  $F_{1,9} = 5.634$ ,  $p = 0.042$  and PC3:  $F_{1,9} = 22.139$ ,  $p = 0.001$ ). The average species frequency per locality dropped from 0.20 at one end of the gradient (drier, hotter areas) to around 0.10 at the other end (more humid, cooler areas; Table 1, Figure 3a,b). We also found a reduction in the median avian biomass per locality along the third axis of the PCA (PC3:  $F_{1,9} = 11.358$ ,  $p = 0.008$ ) and a marginally significant relationship with the first axis (PC1:  $F_{1,9} = 8.436$ ,  $p = 0.075$ ). Median avian biomass ranged from over 200 g on the upper Rio Branco to nearly 90 g on the lower section of the river (Table 1, Figure 3c,d).

### 3.3 | Taxonomic and phylogenetic beta diversities

The environmental gradient also represents a major player in structuring avian communities (Figure 4). The first axis of the NMDS is highly correlated with the first and third axes of the PCA and

the environmental variables they represent (PC1:  $F_{1,12} = 92.41$ ,  $p < 0.001$ , PC3:  $F_{1,12} = 33.712$ ,  $p < 0.001$ , Global Adj.  $R^2 = 0.89$ ; see Table S2).

Partitioning of beta diversity shows that most of the variation in the avifauna observed along the environmental gradient is the result of species replacement ( $\beta$ -sim), which accounts for 93% of the variation, whereas nestedness-resultant ( $\beta$ -nes) accounts for only 7%. Patterns of both taxonomic and phylogenetic cross-site variations are positively correlated with climatic variables, such as rainfall and temperature. Species replacement was correlated with PC1 and PC3 axes (Adj.  $R^2 = 0.283$ ; PC1:  $F_{1,12} = 3.804$ ,  $p = 0.01$ ; PC3:  $F_{1,12} = 2.624$ ,  $p = 0.041$ ), whereas PC3 determined the variation in the phylogenetic gradient (a nestedness-component of phylogenetic diversity; Adj.  $R^2 = 0.238$ ; PC3:  $F_{1,12} = 3.431$ ,  $p = 0.05$ ). The main climatic variables correlated with PC1 and PC3 were rainfall and minimum temperature of the warmest month respectively (Figure 5a). This means that the higher the difference in rainfall and temperature between sites, the more different their avifaunas will be in terms of species composition. All three PCA axes were significantly correlated with phylogenetic replacement (Adj.  $R^2 = 0.225$ ; PC1:  $F_{1,12} = 2.427$ ,  $p = 0.03$ ; PC2:  $F_{1,12} = 1.888$ ,  $p = 0.057$ ; PC3:  $F_{1,12} = 2.033$ ,  $p = 0.033$ ; Figure 5b). This gradient, however, generally did not affect the nestedness-resultant



**FIGURE 3** Relationship between average species frequency and median biomass at each locality and the climatic gradient (PC1 and PC3 axes). Average species frequency (a and b) and median biomass (c and d) decrease along the Rio Branco and its major tributaries, with mean annual precipitation, lower average annual temperatures and with lower evapotranspiration. Points represent our surveyed localities ( $n = 16$ ); grey areas refer to confidence intervals, and black lines denote significant relationships

phylogenetic dissimilarity, except marginally for PC3 (PC1:  $F_{1,12} = 1.147$ ,  $p = 0.317$ ; PC2:  $F_{1,12} = 1.079$ ,  $p = 0.338$ ; PC3:  $F_{1,12} = 3.489$ ,  $p = 0.061$ ).

## 4 | DISCUSSION

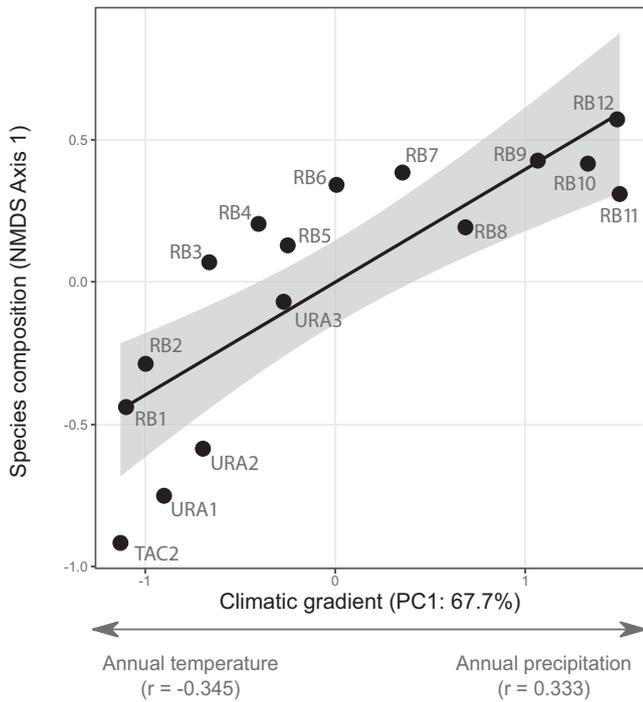
There is ample evidence that current environmental conditions account for a significant proportion of the variation in the distribution of species at both local (alpha diversity) and regional (gamma and beta diversity) scales (Hawkins et al., 2003; Rahbek & Graves, 2001). Here, we investigated the patterns of avian variation along an environmental gradient that coincides with the course of a major Amazonian river, the Rio Branco. The study site's situation provided a unique opportunity to investigate changes in the patterns of alpha and beta diversity using a single species pool in a single geographic unit, obtained at the same time frame. Four key findings of our study are worth highlighting. First, despite the presence of two distinct environmental units (gallery forests on the Boa Vista geological formation and floodplain forest on the sedimentary basin), climate represents a major player in structuring avian communities along the river. Second, we found that changes in species numbers occurred without significant increases in the number of individuals. Third, we found that diversity patterns along the environmental gradient are mainly the result of species replacements, rather than loss of species. And finally, the environmental transition between the lower and

upper sections of the Rio Branco highlights the importance of transitional zones as buffers for future changes in climatic conditions.

### 4.1 | Climatic drivers of avian diversity

In a previous study, we showed that geomorphology was a powerful predictor of species composition along the Rio Branco (Naka et al., 2020). Here, we show that on top of the different geomorphological units present along the river, there is a climatic gradient, and that a substantial amount of the variation observed in avian alpha and beta diversity along the Rio Branco can be explained by aridity, temperature, isothermality, precipitation and evapotranspiration. Importantly, these variables likely affect biological communities in different ways and have a key function determining vegetation structure (ter Steege et al., 2003), which provides specific habitats for the biota, including birds (Hořák et al., 2019).

Accordingly, the structure of the vegetation also changes along the environmental gradient studied, from narrow gallery forests on the drier and warmer upper stretches of the Rio Branco to wide floodplain forests on the more humid and more productive lower portions of the river. Ongoing botanical studies point out that variables, such as above-ground biomass, average tree height, number of trees per area unit and tree species composition, also vary along this gradient (Farias, 2014; Pereira, 2016), and these variables are likely to directly affect the structure of avian communities as



**FIGURE 4** Relationship between avian species composition at the localities studied (axis 1 of the NMDS) and the climatic gradient (PC1 axis), represented by annual temperature and precipitation, along the Rio Branco and its major tributaries. Points represent our surveyed localities ( $n = 16$ ); grey areas refer to confidence intervals, and black lines denote significant relationships

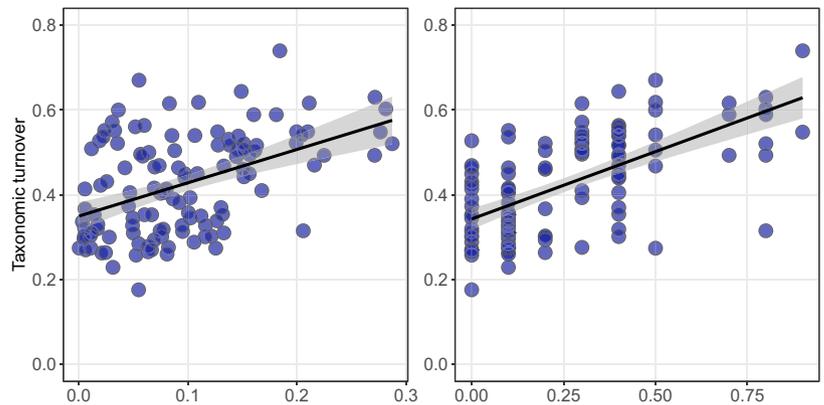
has been shown in other tropical forests (Hořák et al., 2019). Also, among the most important factors defining structural complexity and productivity of alluvial vegetation, are the physicochemical parameters of river water (e.g. suspended sediments and nutrients concentration), which also define local avian diversity and species composition (Laranjeiras, Naka, & Cohn-Haft, 2019). Two additional variables that are worth exploring are (a) the flooding regimes along the river, which are known to vary along the Rio Branco, and (b) the presence of river islands dominated by *Cecropia* spp. along the lower Rio Branco, which provide specific habitats for river-island specialists (Robinson & Terborgh, 1997; Rosenberg, 1990).

Although several confounding factors may be in play along the environmental gradient studied, climatic variables seem to be a fundamental factor defining species distributions and community assemblages. Given that climatic changes are already happening, and are expected to accelerate in the next decades, understanding the role of climatic variables on ecotone delimitation and the boundaries of adjacent biomes may allow us to understand and model future changes in the distribution of biodiversity due to global climate change.

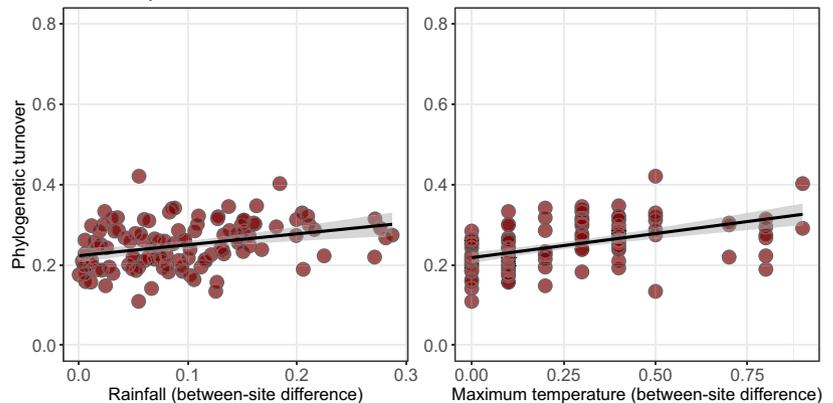
### 4.2 | Species packing

A number of studies have shown geographical patterns of increasing species richness with increasing energy availability or habitat productivity (Lawton, 1990). The higher species richness found along

#### (a) Taxonomic ( $R^2_{adj} = 0.254$ )



#### (b) Phylogenetic ( $R^2_{adj} = 0.225$ )



**FIGURE 5** Relationship between taxonomic (a) and phylogenetic (b) replacement and two climatic variables (annual rainfall and maximum temperature) obtained from the climatic gradient. The use of specific variables allows us to better understand how changes in specific variables can affect species turnover. Each point on the graph represents a cross-site comparison (beta diversity) among our 16 surveyed localities; grey areas refer to confidence intervals, and black lines denote significant relationships



the lower Rio Branco coincides with the areas with higher productivity, and are therefore consistent with such observations. Two variables, however, are key in determining how energy and other limiting resources are allocated: body size and population density (Brown & Maurer, 1986). Although we observed more species in more productive areas, this increase did not occur as a result of detecting more individuals. Interestingly, this increase was correlated with significant reductions in (a) average species frequency and (b) median biomass. These results are consistent with well-accepted generalized relationships between population density, body size and species richness (Lawton, 1989). On the other hand, smaller body size distributions have also been interpreted in light of habitat specialization and tighter niches (Aarssen & Schamp, 2002; Brown, 1995).

### 4.3 | Species turnover across the transition zone

Our results on taxonomic and phylogenetic beta diversity provide strong evidence that changes in species composition along the environmental gradient are the result of species and lineage replacements, rather than the result of species loss. This finding is particularly important because (a) it reflects the importance of all habitats (despite their species richness) for the overall conservation of biodiversity, and (b) it highlights the important role of transition zones and ecotones. Despite our previous observations that two distinct avifaunas are supported by riverine habitats along the Rio Branco (Naka, Cohn-Haft, Whittaker, Barnett, & Torres, 2007; Naka et al., 2020), it seems that the avifaunal change observed along the river is a response to a set of continuous variables acting upon a soft boundary. In that sense, our results suggest that avian communities along the Rio Branco act as idiosyncratic assemblages, as envisioned by Gleason (1939) where each taxon presents species-specific ranges, rather than a shared hard-bounded unit, as suggested by Clements (1916).

Transitional regions, such as those found between the gallery and the floodplain forests along the Rio Branco, can potentially act as important buffer zones for biodiversity (Kark, Allnut, Levin, Manne, & Williams, 2007). This is particularly relevant in the face of global warming and the dramatic climatic changes that are already taking place worldwide. Available models from the Central American highlands suggest that many species may become extinct because they will lack buffer zones to move to, following projected range shifts (Colwell et al., 2008). In such a scenario, transition zones and ecotones will represent vital buffer zones for the biota, and as such, these areas will need to be protected. Both, the upper and lower Rio Branco are home to several habitat specialist birds, including at least 22 bird species of conservation concern (Naka et al., 2020), and two critically endangered species (BirdLife International, 2018). How all these species will respond to future climatic changes will depend on their capacity to conduct range shifts, if necessary.

Worryingly, the transitional zone between the upper and lower Rio Branco is under immediate threat, due to the plans of the Brazilian Government to build a hydroelectric dam on the Rio Branco. The

proposed location of the dam is on top of the Bem Querer rapids, a geological feature that defines the boundary between the Guiana Shield and the sedimentary basin of the Rio Branco (Cremon et al., 2016). If built, this dam will permanently flood most of the upper Rio Branco, disrupt the natural flood pulse of the river, reduce suspended sediments/nutrients transport downstream and wholly eliminate the transitional ecological zones of this ecological and evolutionary hotspot.

## 5 | CONCLUSIONS

Our results provide evidence that climatic variables represent a powerful predictor of avian species composition and are key to shape current patterns of alpha and beta avian diversities on a major Amazonian river. Specifically, we found that along the steep climatic gradient on the Rio Branco, more humid and less hot localities host more bird species. The increase in the number of species, however, cannot be explained by higher number of individuals. Our data are consistent with an ecological mechanism known as species packing, which allows for an increase in species, at the expense of increased rarity and lower median biomass in the communities. Also, species turnover along the gradient indicates that all portions of the river contribute to the overall species diversity. The strong relationship between climate and avian diversity suggests that the expected future changes in rainfall regimes due to human-induced climate change will likely demand shifts in species distributions along the Rio Branco and its tributaries. Under such a scenario, we highlight the importance of transition zones as potential buffers accommodating these shifts, particularly for species adapted to specific climatic conditions along the gradient. Worryingly, the potential construction of a hydroelectric dam right within the transitional region will strongly reduce this buffer zone, preventing species to adapt to new climatic conditions.

## ACKNOWLEDGEMENTS

We thank several people involved in our field expeditions, including field assistants, cooks, boatmen and other fellow researchers. Among these, we acknowledge the joined efforts of Carolina V. de Castilho, Sofia de Castilho Naka, Mario Cohn-Haft, Marcela F. Torres, Priscila Azarak, Hugo Frias and Lilian Cruz, who participated in some of the expeditions. We are particularly indebted to Agnaldo de Souza, Maxwell Santos, Hamilton de Melo and the late Sebastián Salvino for their assistance in the field. Several people from the Chico Mendes Institute of Biodiversity Conservation (ICMbio) were key to the success of our trips, including Beatriz Ribeiro Lisboa, Antonio Lisboa, Erica Tiekko Fijisaki, Inara Santos, Romerio Briglia, Antônio Galdino and Renata Bocorny. We are also grateful to Lisa Davenport, for her editorial and grammatical corrections on an earlier version of this manuscript. This work was supported by funding granted to L.N.N, including the Fundação Boticário de Proteção à Natureza (934-2012.1), the Brazilian Research Council, CNPq (484219/2011-1 and 480496/2012-9), the Fundação Estadual de

Meio Ambiente e dos Recursos Hídricos, FEMARH and to T.O.L., including funding from the Chico Mendes Institute of Biodiversity Conservation (ICMBio), through the Diretoria de Pesquisa, Avaliação e Monitoramento da Biodiversidade (MPC-014.007), and the Rufford Foundation (19908-1). G.R.L. and L.N.N. are particular grateful to Maria Gracimar Pacheco, Coordinator of the Graduate Program on Biological Diversity at the Universidade Federal do Amazonas. As graduate students, A.C.P. and T.O.L. received MSc and PhD fellowships granted by the Coordination for the Improvement of Higher Education Personnel (CAPES) respectively, whereas G.R.L. received a MSc fellowship from Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM).

#### DATA AVAILABILITY STATEMENT

We certify that we have provided an accurate representation of our methods and that we provide our raw data (presence/absence matrix and frequency values per locality) in the Appendix S1.

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## BIOSKETCH

We are interested in the fields of ecology, biogeography and evolutionary biology. Our main goal is to integrate these fields by (a) recognizing and synthesizing avian distribution patterns, paying particular attention to contact zones and phylogeographic breaks; (b) understanding how environmental gradients along ecotones define avian species distributions, affecting patterns of taxonomic, phylogenetic and functional diversity; and (c) unveiling the evolutionary mechanisms and processes that shaped the distribution of current biotas, both at the species and community levels. Please visit our website at <https://www.ornitlab.org/research>. Author contributions: LNN, TOL and FP contributed to the study design; LNN, TOL, AP and GRL collected the data; LNN, TOL and TGS decided on statistical analyses, which were run and coded by TLS. LNN drafted the manuscript, with help from TOL and TGS. All authors reviewed and approved the manuscript.

## SUPPORTING INFORMATION

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

**How to cite this article:** Naka LN, Laranjeiras TO, Rodrigues Lima G, Plaskievicz A, Pinto F, Gonçalves-Souza T. Climate as a major driver of avian diversity in riparian Amazonian habitats along an environmental gradient. *J Biogeogr.* 2020;00:1–13. <https://doi.org/10.1111/jbi.13957>