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# Effect of Two Geologically Distinct Amazonian Rivers in Shaping Forest Understorey Bird Assemblages

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## ABSTRACT

**Aim:** The effects of rivers as barriers for species dispersal can be expected to vary according to both species traits and the characteristics of rivers themselves. In this context, our aim was to investigate dissimilarities in species composition across opposite banks of two major Amazonian rivers, the Juruá and the Tapajós, and relate them to each river's characteristics and history.

**Location:** The study was conducted in upland forests on opposite banks of two contrasting Amazonian rivers: the Juruá and the Tapajós. The Juruá River, a highly meandering and sediment-rich river, drains the Solimões sedimentary basin. In contrast, the Tapajós River is an entrenched, low-sediment river flowing through the cratonic region of the ancient Brazilian shield. These rivers represent distinct geomorphological and geological settings, allowing us to assess their differential effects on bird species compositions.

**Time Period:** Data were collected over multiple time periods, spanning several decades. The earliest surveys were conducted in the 1990s. Additional data were collected in 2012 and 2013, followed by a more recent sampling effort in 2022.

**Major Taxa Studied:** Upland forest bird assemblages, including species with different ecological traits, such as varying body sizes, diets and dispersal abilities, ensure an evaluation of how species characteristics interact with riverine features in shaping bird community structure.

**Methods:** We used standardised bird surveys to assess taxon (genus, species and subspecies) composition of upland bird assemblages on both sides of each river. Occupancy and abundance data were obtained using mist-net lines. Differences in composition were analysed using statistical methods to assess community dissimilarity and test for significant differences between opposite margins. We assessed the relative contributions of river basins, geographical distances and environmental variables in explaining dissimilarities in bird taxon composition across the Juruá and Tapajós rivers.

**Results:** We found significant differences in bird assemblages between the opposite margins of the stable Tapajós, but not between the margins of the more dynamic Juruá. These findings suggest that the Tapajós, with its entrenched channel and long-term geological stability, acts as a stronger biogeographic barrier than the Juruá, which has a broader floodplain but a more dynamic and meandering course. The less pronounced barrier effect of the Juruá is likely due to its dynamic current and historical geomorphological processes, which facilitate species dispersal across the river and its floodplain.

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**Main Conclusions:** Our findings are consistent with the notion that geomorphological history and fluvimorphic stability can influence the strength of Amazonian rivers as biogeographic barriers, but broader replication is needed to generalise this pattern across the Amazon basin. Rivers with a more dynamic and shifting course, like the Juruá, appear to exert weaker dispersal limitations, whereas stable rivers, like the Tapajós, create more pronounced differences in species composition. This supports the notion that rivers experiencing a more dynamic history exert a weaker geographic barrier effect, and that geomorphological setting and landscape history are important determinants of the effect of Amazonian rivers on the dispersal and diversification of Amazonian vertebrate taxa.

## 1 | Introduction

Rivers are quintessential elements of Amazonian landscapes. The Amazon River has over 1100 tributaries, 17 of which are over 1500 km long, forming the world's largest river basin, which covers more than 6,000,000 km<sup>2</sup> (Fassoni-Andrade et al. 2021). Amazonian rivers directly control ecosystem processes in their floodplains through their often-prolonged annual flood pulses and play a significant role in the regional and global climatic systems (Malhi et al. 2021). Amazonian rivers are also crucial drivers of evolutionary processes that have led to the exceptional biodiversity found throughout the region Capparella (1988). Large rivers in Amazonia function as natural barriers that reduce or prevent the dispersal of many forest species, constraining their geographic ranges (Wallace 1852; Cracraft 1985; Avila-Pires 1995; Haffer 1997; Godinho and da Silva 2018; Nazareno et al. 2019; Moncrieff et al. 2024; Helenbrook and Valdez 2025). Based on such congruent patterns of distribution, the riverine barrier hypothesis proposes that large rivers act as physical barriers, severely limiting gene flow between populations on opposite sides of the river, thereby leading to classic allopatric speciation over time (Sick 1967; Ayres and Clutton-Brock 1992; Weir et al. 2024). However, comparative studies have found different diversification ages for different species groups across the same river, suggesting that congruent distributional patterns may result from a variety of processes. These could, for example, result from secondary contact between populations whose diversification was not directly linked to the presence of rivers, or from habitat heterogeneity on opposite margins (Tuomisto and Ruokolainen 1997; Smith et al. 2014; Naka and Brumfield 2018).

Beyond their role in speciation and diversification, large rivers are responsible for generating high levels of environmental heterogeneity within Amazonia, further contributing to species-rich local assemblages and the high levels of landscape-scale beta-diversity observed across the region (Salo et al. 1986; Kalliola et al. 1992; Tuomisto et al. 1995; Wittmann et al. 2010; Ribas et al. 2025). This diversity is particularly evident when comparing the two main environments of Amazonia: floodplain (*várzea* and *igapó*) forests, which experience seasonal flooding, and upland (*terra firme*) forests, which are beyond the reach of even the highest floods (Junk et al. 2011). These habitats differ significantly in habitat structure, primary and secondary productivity, and resource availability (Haugaasen and Peres 2005). This difference is most notable in the forest vertebrate communities they support. Compared to floodplain forests, *terra firme* forests typically host higher vertebrate species diversity but often lower overall animal biomass density (Peres 2000). Ground-dwelling, understory mixed-species flocks and ant-following birds are often lacking in floodplain forests, as the undergrowth is often entirely submerged by a 10–15 m flood pulse and therefore unavailable to terrestrial vertebrates for up

to half of the year (Borges and Carvalhaes 2000). Although less species-rich, floodplain forests host bird species that are uniquely adapted to the seasonally flooded environment (Remsen and Parker 1983; Beja et al. 2009).

The extent to which rivers act as effective barriers to dispersal for upland forest birds is likely influenced by several factors. These include characteristics of the river itself, such as its channel width (Weir et al. 2015) and flow rate (Mourthé et al. 2022), as well as the dispersal ability of the species on either side (Burney and Brumfield 2009). The geological history of the river and its surrounding landscape is also relevant, especially how long ago the river was formed and how its floodplain changed through time (Ruokolainen et al. 2019; Ribas et al. 2022, 2025; Musher 2025). These factors can vary greatly across species and river systems. Taxonomic resolution also influences the interpretation of rivers as barriers: finer taxonomic resolutions can potentially reveal more subtle patterns than coarser taxonomic levels, as the effects of the dispersal barrier accumulate or diminish over evolutionary time (Rull 2011; Ribas et al. 2025).

Recent advances in the availability of species distribution data, molecular techniques and remote sensing have revealed new patterns that challenge the traditional understanding of river barriers. Some distribution patterns are not aligned with the current locations of large river channels but are instead associated with their ancient courses, reflecting underlying geological formations that influence soil characteristics, vegetation and biota, creating cascading effects (Kopuchian et al. 2020). Furthermore, the type of terrain drained by a river can be a key factor in understanding the processes structuring the surrounding biota. Rivers draining dynamic sedimentary basins meander through more changeable courses and exhibit rapid deposition that results in lateral meandering channel migration across the floodplain over time, which facilitates cross-bank gene flow, thereby reducing their effectiveness as a barrier, especially for species that occur along the floodplains (Peres et al. 1996; Gascon et al. 2000; Ribas et al. 2025). Conversely, entrenched river channels draining older, more stable terrains are less likely to undergo such changes and may present stronger barriers to dispersal (Ruokolainen et al. 2019; Ribas et al. 2025).

The avifauna that occurs in upland *terra firme* Amazonian forests has been central to the discussion about the role of riverine barriers in driving current distributions and/or inducing diversification (Ribas et al. 2025). Patterns of endemism for upland forest birds were recognised decades ago and continue to be refined and characterised through recent studies (Haffer 1969, 1974; da Silva et al. 2005; Borges and Da Silva 2012; Rego et al. 2024). Several of the recognised bird areas of endemism have their limits coinciding with large

Amazonian rivers such as the Amazonas, Negro, Madeira and Tapajós (Ribas et al. 2025), and studies on bird communities have suggested that the presence of a riverine barrier is the main factor influencing variation in upland forest bird community composition (Dambros et al. 2021; Maximiano et al. 2020; Almeida et al. 2024). However, environmental heterogeneity is also known to play a key role in shaping bird community structure in the Amazon, often interacting with dispersal-limiting factors to influence patterns of species composition (Pomara et al. 2014). Nonetheless, a controlled comparison of bird communities on opposite margins along rivers with distinct histories and geomorphology has not been done yet.

Here, we compare upland forest bird assemblages across two Amazonian rivers with markedly divergent evolutionary histories, focusing on how their contrasting geological dynamics influence patterns of species composition, rather than attempting a basin-wide assessment of fluvial geomorphological effects. The Juruá River runs over dynamic sedimentary terrains in central Amazonia and is characterised by high sediment loads and a recent history of river avulsions (Ruokolainen et al. 2019; Rossetti et al. 2021; Ribas et al. 2025). In contrast, the Tapajós River runs over stable terrains in the Brazilian shield of eastern Amazonia and carries low sediment loads along a relatively constrained floodplain (Ribas et al. 2025). Both rivers have similar discharges and are flanked by closed canopy Amazonian forests. We hypothesised that bird communities separated by the Juruá River would be more similar than those separated by the Tapajós, due to their distinct geological contexts. We assessed the relative contributions of river basins, geographical distances and environmental variables (e.g., soil nutrient concentration, Landsat bands) in explaining dissimilarities in bird species composition across the Juruá and Tapajós rivers. To control for ecological traits, such as dispersal capacity, we analysed both the entire bird assemblage and key functional groups separately. We also tested the effect of taxonomic resolution in the interpretation of results.

Our primary research questions were: (i) How does bird composition vary between and within basins? (ii) What factors are associated with variation in bird composition across basins? (iii) Are there compositional differences between bird functional groups? (iv) To what extent do riverine barriers and environmental factors explain the observed variation in community composition? and (v) To what extent does taxonomic resolution influence the interpretations of differences in community composition?

## 2 | Methods

### 2.1 | Study Areas

Sampling design included sites on both margins of the Juruá and the Tapajós, two major first-order southern tributaries of the Amazon River with geologically distinct drainage sub-basins (Figure 1).

The Juruá is a whitewater river with a high sediment load (189.2 tons/km<sup>2</sup>/year). The forests seasonally flooded by whitewater

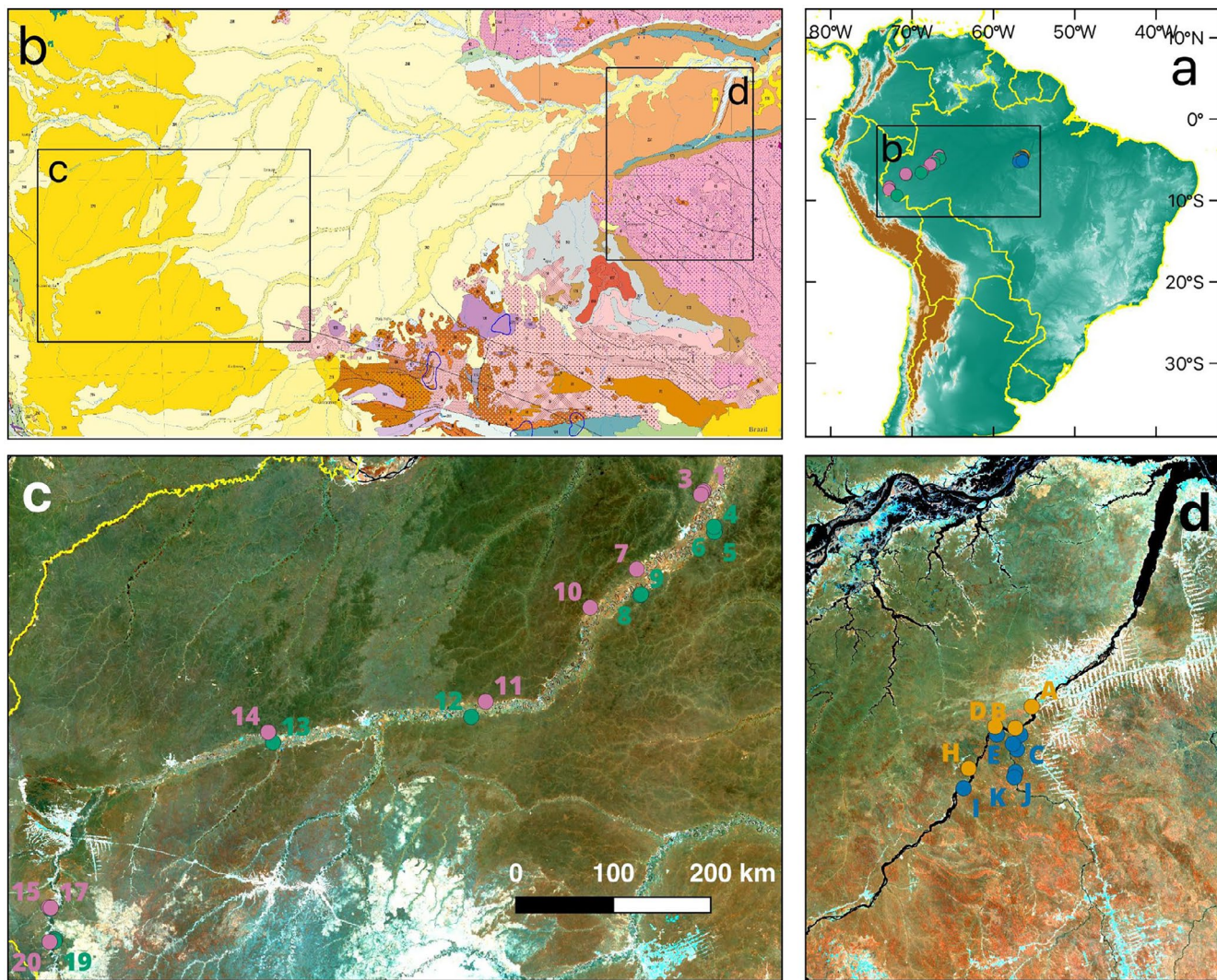
rivers are highly productive and referred to as *várzeas*. The Juruá runs through the Solimões sedimentary basin, a relatively young and erodible plain, and is characterised by endless meanders and frequent formation of oxbow lakes. The Juruá River is 3283 km long, carries a mean discharge of 8440 m<sup>3</sup>/s, and its basin drains about 185,000 km<sup>2</sup> (Latrubesse and Franzinelli 2005). Although channel width at the site localities surveyed here was on average 357 m ( $\pm 56$  m), the width of the floodplain and the river channel together, which constitute an effective barrier for upland forest taxa, on average add up to 21 km. The channel width can vary greatly along the river due to the sinuosity in its entire course, and at its mouth can reach 620 m.

As a clearwater river, the Tapajós discharges transparent to greenish waters carrying low amounts of suspended sediments and dissolved solids (12.2 tons/km<sup>2</sup>/year). Seasonally flooded forests along clearwater rivers are referred to as *igapós*, which are sustained by intermediate fertility soils (Junk et al. 2011). A large portion of the Tapajós, including the study region, flows within the deeply weathered Brazilian Shield, which was formed some ~1 billion years ago. The Tapajós is 1784 km in length, and it drains a basin area of ~490,000 km<sup>2</sup>, accounting for 7% of all Amazonian freshwater and transporting a mean discharge of 13,500 m<sup>3</sup>/s (Latrubesse and Franzinelli 2005) through a stable and relatively linear channel (sinuosity index  $\approx 1.3$  vs. 3 along the Juruá). At its mouth, the Tapajós River is characterised by a 21-km wide ria lake, narrowing down to a ~2 km width upstream of this lake. The channel width at the localities surveyed here was on average 2409 ( $\pm 269$ ) m, and the width of the floodplain and river channel together around 8 km.

### 2.2 | Bird Sampling

Bird occupancy and abundance data were obtained using mist-net lines (12 m long; 36 mm mesh size) that were placed in the understorey (up to 2.5 m in height above the ground). Mist-nets provide a more effective and less biased method than personal observations, but successful captures are primarily limited to understorey and mid-strata birds, with rare incidences of sub-canopy to canopy birds (Bibby et al. 2000). Along the Juruá River, data were collected during two field seasons (throughout 1991–1992 and July 2022), both of which included sites on both sides of the river. In the first field season, each site was sampled using a net-line of 16 mist nets set up end-to-end and operated from dawn to dusk (~06:00 to 18:00 h) for three consecutive days. In the second field season, data were obtained using three net-lines of 20 mist-nets each, which were also operated for 3 days from dawn to dusk (~06:00 to 17:00 h), except on the third day, when they were closed at 12:00 h. Along the Tapajós River, each site was sampled more than once (throughout 2012 and 2013), with five net-lines of 10 mist-nets each operated from 06:00 to 12:00 h for three consecutive days (see Maximiano et al. 2020 for details). All mist-net lines examined here were operated on *terra firme* forest environments, thereby excluding bird species specialised to floodplain (*várzea* and *igapó*) forests.

We identified all birds to the species level, harmonising overall species-level taxonomy updated by the Brazilian Ornithological Records Committee (CBRO) (Pacheco et al. 2021). The subspecies classification followed Rego et al. (2024). Vouchers of



**FIGURE 1** | (a) Map of South America with elevation above sea-level as the background (source: <https://www.earthdata.nasa.gov/data/instruments/srtm>); the region shown in panel (b) is limited by the rectangle. (b) Geological map of the study region (Source: <https://ccgm.org/en/2023/02/26/mapping-the-geology-of-south-america/>); rectangles show the extents of panels (c, d) the most relevant geological units are siliciclastic sedimentary rocks and unconsolidated deposits (mid yellow: Quaternary; pale yellow: Neogene to Quaternary; dark yellow: Neogene) in the Juruá area; and rhyolitic and granitic rocks of Orosirian age (pink) in the Tapajós area, where Paleogene siliciclastic sedimentary rocks and unconsolidated deposits of Paleogene age (orange) dominate north of the sampled area. (c) Sampling localities along the Juruá River (pink: Northern bank, green: Southern bank). (d) Sampling localities along the Tapajós River (orange: Northern bank, blue: Southern bank). Panels (c, d) are on the same scale, and their background is a Landsat TM/ETM+ composite (Van Doninck and Tuomisto 2018). Coordinates of the sampling localities are listed in Table S1.

each recorded species were collected for all sampling plots in the Tapajós River and during the second field season in the Juruá River. Specimens were collected under the appropriate licences #66/2012 and #73696, issued by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) and the Chico Mendes Institute for Biodiversity Conservation (ICMbio), respectively, and were all deposited at the Bird Collection of the National Institute for Amazonian Research (INPA).

### 2.3 | Species Subsets

We classified all species in terms of both their (i) trophic modes: frugivores, granivores, insectivores, omnivores, nectarivores and predators/vertivores (birds that feed on vertebrates: lizards,

amphibians, fish and other birds) and (ii) body size based on their adult body mass: small (1–29g), medium (30–100g) and large (> 100g; Wilman et al. 2014). These traits were selected because they directly or indirectly influence species dispersal capacity (Terborgh et al. 1990).

### 2.4 | Environmental Variables

To assess the influence of environmental variables on the species composition of bird assemblages across riverbanks, we used remote sensing products and models of plant species composition for each bird sampling point. This allowed us to explore the degree to which environmental heterogeneity contributes to patterns of dissimilarity across riverbanks in comparison to the river barrier effect.

Surface reflectance as measured with Landsat satellites has been found to correlate with edaphic properties, vegetation structure and plant species composition in Amazonia, and can therefore be used as a proxy of habitat variation (Higgins et al. 2011; Tuomisto, Poulsen, Ruokolainen, et al. 2003; Tuomisto, Ruokolainen, Aguilar, et al. 2003; Tuomisto et al. 2019). We used data from a Landsat composite (Figure 1c,d) that covers the entire Amazon at 30-m resolution (Van Doninck and Tuomisto 2018). We also used data derived from the Shuttle Radar Topography Mission (SRTM), which provides elevation information with a spatial resolution of approximately 30 m.

Soil nutrient concentration influences the productivity of the forest, vegetation structure and other characteristics as well as the availability of food resources for birds (Pomara et al. 2012) and arboreal mammals (Peres 2008). We extracted the sum of bases (Ca + Mg + K) from two different maps developed by Zuquim et al. (2019, 2023). Both maps are based on the interpolation of field-measured and plant-derived soil values for the entire Amazon basin. The older map (Zuquim et al. 2019; hereafter 'soil 2019') modelled gradual spatial variation between data points using kriging, which is a simple interpolation method that works well in densely sampled areas but is prone to miss abrupt changes in data-poor areas. The newer map (Zuquim et al. 2023; hereafter 'soil 2023') used a more sophisticated interpolation method based on machine learning that took advantage of covariates, such as topography and remote sensing, which made it possible to detect abrupt changes even in areas with large sampling gaps.

Finally, since vegetation heterogeneity can be perceived differently by different organismal groups, we used as predictors the main compositional gradients of palms, ferns (including 'fern allies', i.e., lycophytes) and melastomes (plants of the Melastomataceae family). Palms are a major source of nutrient intake for many frugivorous birds and are also used as nesting, roosting and perching sites (Snow 1981; Brightsmith and Cáceres 2017; van der Hoek et al. 2019; Glória and Tozetti 2021). Furthermore, some abundant palm species can be used as effective biodiversity surrogates for bird communities, as their distributions are strongly correlated with bird assemblages (Menger et al. 2024). Ferns and melastomes, in turn, are general indicators of habitat characteristics (Tuomisto, Poulsen, Ruokolainen, et al. 2003; Tuomisto, Ruokolainen, Aguilar, et al. 2003; Tuomisto, Ruokolainen, and Yli-Halla 2003; Pomara et al. 2012; Zuquim et al. 2014). Compositional gradients were available for the Juruá region from an earlier study that modelled them using machine learning to spatialise locally observed community composition with environmental and remotely sensed predictors (Zuquim et al. 2021). These data were not available for the Tapajós region. The variables used in the analyses are detailed in Table S2.

## 2.5 | Data Analysis

We visualised the multivariate patterns of bird community composition using Principal Coordinates Analyses (PCoA), based on a site-by-species matrix with relative abundance data and the Bray–Curtis dissimilarity index. We also tested presence/absence data (Figure S1), but chose to present the abundance-based

results in the main text as they revealed clearer and more pronounced patterns of community differentiation. To examine the importance of taxonomic resolution in our results, we performed ordinations at the genus, species and subspecies levels. We tested if dissimilarities between bird communities on opposite sides of the river were larger than those between communities on the same side using PERMANOVA (Anderson and Walsh 2013).

To evaluate the relative importance of the predictor variables in determining community structure, we generated multivariate regression trees for each river basin separately and for both basins combined. In these analyses, the response variables were the first two PCoA axes, which captured most of the variation in bird community composition. The predictor variables included proxies of environmental factors such as soil base concentration, Landsat bands and elevation.

To assess if the degree of dissimilarity in bird species composition was correlated with the degree of difference in the environmental variables and/or geographical distances, we used Mantel and partial Mantel tests (McCune and Grace 2002). Compositional dissimilarity was measured with the Bray–Curtis index and environmental difference with the Euclidean distance. We analysed all bird species together as well as various species subsets separately to assess if the correlations varied according to species traits.

All statistical analyses were performed within the R statistical environment, v.4.4.2 (R Development Core Team 2025), using the packages *vegan* (Oksanen et al. 2022), *ggplot* (Wickham 2016) and *rpart* (Therneau et al. 2025).

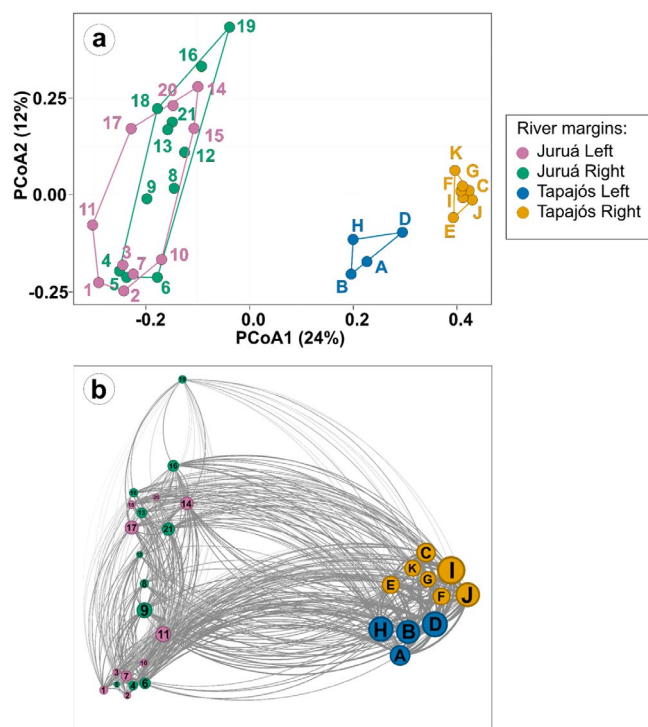
## 3 | Results

A total of 7830 individual birds belonging to 275 species and 46 families (21 non-Passeriformes and 25 Passeriformes) were captured. A total of 5390 captures representing 190 species were obtained in the central Tapajós River region (Maximiano et al. 2020), whereas 2440 captures representing 187 species were obtained along the Juruá River. The high diversity found in both basins is consistent with previous surveys using mist nets: 138 *terra firme* species in the Juruá (Del-Rio et al. 2021) and 134 species in the Tapajós (Wunderle et al. 2006).

The two river basins shared 102 species (~37%; Figure 2b), most of which are widely distributed across Amazonia (e.g., *Myrmotherula axillaris*), while others are only known to occur south of the Amazon River (e.g., *Phlegopsis nigromaculata*). However, each basin also hosted a unique set of species. A total of 85 species (31%) were recorded only at Juruá, such as *Rhegmatorhina melanosticta*, which is found only west of the Madeira River; and 88 species (32%) were recorded only at Tapajós such as *Willisornis vidua*, a species found only east of the Tapajós river.

### 3.1 | Patterns of Community Composition

Differences in species composition between the two river basins are evident in the PCoA plot, where their sites are clearly



**FIGURE 2** | (a) Principal coordinates analysis (PCoA) ordinations of bird communities within sites (sampled with understorey net-lines) in two Amazonian river basins (Juruá and Tapajós). Dissimilarities in bird species composition were calculated using the Bray–Curtis dissimilarity based on relative abundance data. The percentage of variation explained is shown for each axis. (b) Visualisation of bird assemblages found in the two regions sampled. The diagram was generated with Gephi, in which nodes represent sampled sites and edges (grey lines) represent bird species. Lines connecting plots represent species shared between sampling sites. Circle size represents species richness. Plot numeric codes and letters refer to those listed in Table S1.

separated into opposite ends of the first ordination axis (Figure 2a), despite a large number of shared species (Figure 2b). Differences within basins can be seen along the second PCoA axis. Overall heterogeneity among plots is clearly larger in the Juruá basin compared to the Tapajós basin, but their internal structures are different. The Tapajós plots are clearly divided into two groups corresponding to the two margins of the river, whereas the Juruá plots form a longer gradient along the river with no obvious separation between the two margins (Figure 2). The PCoA ordination along the first two axes explained 36% of the variation in species composition (PCoA 1 = 24%; PCoA 2 = 12%), and differences in species composition between basins were marginally statistically significant (PERMANOVA  $F = 1.43$ ,  $p = 0.05$ ).

The regression trees for both basins analysed together indicated that ‘basin’ identity was the most important factor explaining variation in species composition along PCoA axis 1 (importance = 0.39), while soil base cation concentration (soil 2019) was the primary driver for axis 2 (importance = 0.30). At the basin level, in the Juruá, the most influential variable for axis 1 was soil base cation concentration (soil 2023) (0.24), whereas Band 7 was the most important for axis 2 (0.25). In contrast, for the Tapajós, the river acting as a barrier played

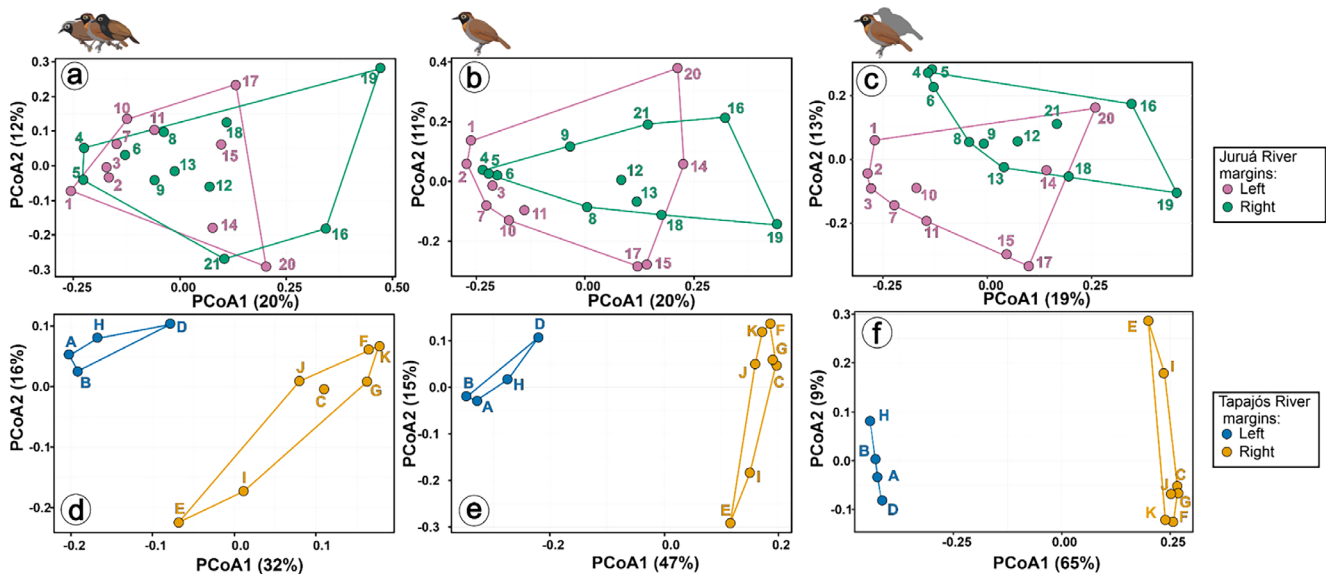
the most significant role on axis 1 (0.12), followed by Band 3 on axis 2 (0.05).

We found no clear differences in bird species composition between the opposite margins of the Juruá River at either the genus or species level. Instead, the first ordination axis reflected a compositional gradient along the length of the river (Figure 3a–c). The PCoA ordination explained 31% of the variation in composition at the genus level (PCoA1 = 20%; PCoA2 = 11%) and 32% at the species level (PCoA1 = 20%; PCoA2 = 12%). There was a weak decay in compositional similarity between sites that were increasingly farther apart, and differences between plots on opposite margins of the river were no greater than those within the same margin, confirming a general lack of differentiation across the river at broader taxonomic levels (PERMANOVA: genus  $F = 0.92$ ,  $p = 0.5$ ; species  $F = 1.24$ ,  $p = 0.2$ ). However, when we analysed community composition at the subspecies level, we detected a statistically significant difference between river margins (PERMANOVA:  $F = 2.15$ ,  $p = 0.003$ ), with river margin explaining about 10% of the variation in community composition. Although modest, this effect suggests that the Juruá River may act as a partial barrier to dispersal at finer taxonomic resolutions, whereby more recent or incipient divergence processes may be detectable.

In contrast, plots on opposite margins of the Tapajós River were clearly separated in the PCoA ordination at all taxonomic levels (Figure 3d–f). The genus-level PCoA ordination along the first two axes explained 48% of the variation in species composition (PCoA1 = 32%; PCoA2 = 16%), and 62% of the variation at the species level (PCoA1 = 47%; PCoA2 = 15%). Differences between plots were significantly larger across the river than within the same margin, both at the genus level (PERMANOVA  $F = 3.45$ ,  $p = 0.004$ ) and especially at the species level (PERMANOVA  $F = 7.63$ ,  $p = 0.002$ ). This pattern was further supported when considering a reduced model for subspecies-level composition, which revealed a strong and significant difference between opposite margins (PERMANOVA  $F = 16.26$ ,  $p = 0.003$ ), with river margin explaining 74% of the observed variation.

### 3.2 | Determinants of Community Dissimilarity

Within the Juruá basin, dissimilarities in species composition were significantly correlated with geographic distance for the entire bird community and most diet- and size-based subsets (Table 1), suggesting a strong spatial structure in community turnover. Soil base cation concentration also showed strong and significant correlations with bird community composition across multiple groups, including insectivores, frugivores, nectarivores, omnivores and small- and medium-bodied birds. Elevation and Landsat bands 4 and 5 were significantly correlated with some groups, particularly omnivores and small-bodied birds. However, when controlling for geographic distance using partial Mantel tests, the strength and significance of these correlations were generally reduced, indicating spatial autocorrelation in environmental variables. The main compositional gradients of palms and ferns did not show significant partial correlations with any bird group, while



**FIGURE 3** | Principal coordinates analysis (PCoA) ordination plots for bird composition and relative abundance data (Bray–Curtis index) within the Juruá (top) and Tapajós (bottom) basins at genus (a, d), species (b, e), and subspecies (c, f) levels. The percentage of variation explained by each PCoA axis is shown for all axes.

melastomes composition remained significantly correlated with frugivores and nectarivores, even after controlling for spatial distance.

Based on the Mantel and partial Mantel results for the Tapajós dataset (Table 2), river margin identity was the strongest factor influencing bird community composition, with significant correlations across all species and multiple subgroups (Mantel  $r=0.64$ – $0.89$ ,  $p<0.01$ ). In particular, small- and medium-bodied insectivorous birds showed significant correlations with river margin and also with variation in Landsat Band 3, suggesting that local vegetation structure may contribute to shaping their assemblages.

In summary, the primary correlates of bird community turnover in the Juruá River basin were geographic distance and soil heterogeneity, reflecting the spatial distribution of habitats. In contrast, in the Tapajós River basin, river margin identity was the strongest correlate, suggesting that the river itself plays a more prominent role as a barrier to dispersal and community differentiation.

## 4 | Discussion

Our results reveal that two major southern tributaries of the Amazon River have very distinct effects on *terra firme* bird assemblages within their basins. Although both the Juruá and the Tapajós rivers are first-order tributaries of the Amazon, they run through very distinct geological terrains and have contrasting evolutionary histories. While several studies have focused on the comparative effects of large Amazonian rivers in structuring vertebrate assemblages, most of them emphasise river width and streamflow (Fordham et al. 2020; Mourthé et al. 2022), whereas few studies consider historical landscape factors when assessing the role of Amazonian (Moncrieff et al. 2020; Musher et al. 2023) and non-Amazonian river systems (Kopuchian et al. 2020) as geographic barriers. Here, we show that examining only the

current landscape does not comprehensively explain species distribution patterns, as current patterns of diversity are also a legacy of past landscapes. Considering past events driven by distinct geological processes can thus contribute to a more accurate and complete narrative about biotic evolution.

### 4.1 | Assemblage-Wide Patterns of Species Composition

The PCoA analysis indicates that the two basins, Tapajós and Juruá, harbour distinct bird assemblages. Although they share a considerable number of species, each basin hosts a unique set of species that drives clear dissimilarities between them. This distinction is evident in the two clusters formed in the PCoA plot in which the Tapajós sites were clearly separated from those in the Juruá basin.

The influence of major rivers as biogeographic barriers is a well-recognised Amazonian pattern, with many studies highlighting their role in shaping the geographic distribution of different vertebrates (Peres et al. 1996; Ribas et al. 2012; Naka et al. 2012; Boubli et al. 2015; Moraes et al. 2016; Silva et al. 2019; Mourthé et al. 2022), and plant taxa (Nazareno et al. 2019). This congruence in patterns of distributions has led to the identification of major areas of endemism across the region (Cracraft 1985), which has been particularly well documented for upland forest birds and primates. Although some studies using publicly available bird distribution datasets failed to recover this pattern (Oliveira et al. 2017; Santorelli et al. 2018; Fluck et al. 2020), a recent thorough review of bird occurrence data for Amazonia corroborates that the prevailing regionalization of Amazonian avifauna is related to the current configuration of large rivers (Rego et al. 2024).

Using a robust and accurate database including more than 600,000 records, Rego et al. (2024) found 10 zoogeographical



**TABLE 2** | Correlation (*r*) between bird species compositional dissimilarities based on diet and geographic distances, river margins and environmental variables, given by the results of Mantel (M) and partial Mantel (PM) tests, for the Tapajós data.

Variable	All species												Trophic guild											
	Community		Insectivores		Frugivores		Nectarivores		Omnivores		Vertivores		Granivores		Small		Medium		Large					
	M	PM	M	PM	M	PM	M	PM	M	PM	M	PM	M	PM	M	PM	M	PM	M	PM				
Dist.geo	0.24		0.29		0.06		0.06		0.18		0.20		0.26		0.25		0.16		0.15					
River	0.89**	0.89**	0.85**	0.86**	0.70**	0.70**	0.91**	0.91**	0.21	0.19	0.23	0.21	0.13	0.11	0.87**	0.87***	0.64**	0.64**	0.10	0.08				
SRTM	0.18	0.10	0.19	0.10	-0.04	-0.06	0.09	0.07	0.51**	0.48**	0.06	-0.02	0.06	-0.04	0.21	0.13	0.12	0.06	-0.15	-0.23				
Band 2	0.13	0.09	0.12	0.07	0.08	0.08	-0.03	-0.05	0.07	0.03	-0.18	-0.22	0.29	0.25	0.14	0.09	-0.06	-0.09	0.23	0.21				
Band 3	0.31*	0.29*	0.33*	0.32*	0.06	0.05	0.32*	0.31*	0.43*	0.42*	-0.07	-0.09	0.05	0.03	0.29*	0.28*	0.20	0.19	-0.14	-0.16				
Band 4	-0.06	-0.14	-0.03	-0.12	-0.24	-0.27	-0.23	-0.26	0.12	0.08	0.03	-0.03	0.19	0.13	-0.06	-0.14	0.06	0.02	0.22	0.19				
Band 5	0.07	0.07	0.09	0.09	-0.03	-0.03	0.05	0.05	-0.11	-0.11	0.52**	0.53**	0.03	0.03	0.07	0.08	0.10	0.11	0.04	0.04				
Band 7	0.07	0.07	0.09	0.09	-0.03	-0.03	0.05	0.05	-0.11	-0.11	0.52***	0.53***	0.03	0.03	0.07	0.08	0.10	0.11	0.04	0.04				
Soil 2019	0.12	0.08	0.07	0.01	0.38**	0.38**	0.12	0.11	-0.09	-0.13	0.14	0.11	0.57***	0.55**	0.13	0.09	-0.04	-0.07	0.15	0.13				
Soil 2023	0.07	0.04	0.09	0.05	-0.09	-0.10	0.03	0.02	0.14	0.12	-0.01	-0.04	-0.15	-0.19	0.07	0.04	0.04	0.02	-0.27	-0.30				

Note: Significance codes (*p*): \* < 0.05; \*\* < 0.01; \*\*\* < 0.001. The number of species and individuals considered within each subgroup can be found in Table S3.

regions, most of which are delimited by major rivers and are largely congruent with previously identified areas of endemism. In their most supported scheme of 10 clusters, the Tapajós marked the limit between two adjacent zoogeographic regions, highlighting its important role as a biogeographic barrier. Zoogeographic regions in the Juruá River basin only became apparent when they considered 20 clusters, but the separation then was between the upper and lower courses of the river rather than between the opposite banks (Rego et al. 2024, Figure S2), corresponding to the geological delimitation highlighted in floristic studies (Tuomisto et al. 2016; Zuquim et al. 2021).

Our results show in more detail how community composition varies along and across these two rivers. The Tapajós and Juruá sub-basins have different geological histories, with different factors shaping the structure of their biota. Western Amazonia experienced greater instability in the establishment of *terra firme* forest habitats, with large portions of upland *terra firme* substrates being formed in the Upper Pleistocene (Bicudo et al. 2019; Pupim et al. 2019). In contrast, the *terra firme* environments of eastern Amazonia, where the Tapajós River basin is embedded, overlay ancient Cretaceous shield rocks whose geomorphology has been more stable (Bicudo et al. 2019). These differences in the temporal dynamics of *terra firme* habitats have likely influenced the establishment of local bird assemblages, resulting in divergent histories and species compositions.

Another important factor contributing to the differences between these two river basins is the environmental heterogeneity at the survey sites. The two basins traverse very different geological formations, leading to variation in soil characteristics and, consequently, associated vegetation types (Tuomisto, Poulsen, Ruokolainen, et al. 2003; Tuomisto, Ruokolainen, Aguilar, et al. 2003; Tuomisto et al. 2016, 2019; Salovaara et al. 2005; Higgins et al. 2011). Birds, especially those inhabiting the understorey of *terra firme* forests, are closely tied to vegetation structure and composition, in terms of their food, shelter and nesting requirements (Terborgh et al. 1990). Each vegetation type therefore sustains a specific associated avifauna (Pomara et al. 2012).

Intrinsic species traits, such as body size, also play a crucial role in determining the ability of bird species to disperse across barriers and traverse open-habitat gaps. Our results indicate that small- and medium-bodied birds exhibit a stronger 'river barrier' signal compared to larger-bodied species, particularly in the Tapajós basin. This is likely due to their lower flight capacity, although this is not a general rule across all lineages (Sutherland et al. 2000). Previous studies have shown that smaller birds, particularly those in the Furnariidae, Thamnophilidae and Dendrocolaptidae families, are less likely to cross open areas such as rivers and deforestation clearings (Moore et al. 2008; Lees and Peres 2009). This pattern reinforces the idea that river barriers exert a species-specific effect, disproportionately impacting smaller-bodied birds and further structuring avian assemblages in Amazonian landscapes.

Our PCoA analyses revealed that the Tapajós acts as a strong biogeographic barrier, structuring bird species distributions along its eastern and western margins. Even at the genus level, compositional differences between the banks were evident,

albeit less pronounced than those at the species and subspecies levels. Differences in subspecies composition between the Tapajós river margins were so pronounced that they were difficult to fully illustrate in the ordination plot, as the first PCoA axis alone explains more than half of the variation between the analysed groups, highlighting a strong separation pattern. Previous studies have documented the Tapajós as an important geographic barrier for birds (Bates 2000; Weir et al. 2015; Maximiano et al. 2020), as well as amphibians and reptiles (Moraes et al. 2016).

Although the Tapajós drains older terrains, recent intraspecific lineage structuring (Silva et al. 2019) suggests that Pleistocene climatic changes affected the barrier effect of this and other Brazilian Shield rivers due to water level fluctuations, as shown for amphibians and lizards (Moraes et al. 2020). Despite these fluctuations, the Tapajós barrier effect has remained consistent over time. This river courses through geologically stable archaic terrains, with few river channel changes throughout its long history (Lundberg et al. 1998).

In contrast, the PCoA analyses did not reveal strong differences in bird genus and species composition between the opposite banks of the Juruá River. However, when using subspecies-level data, a subtle but consistent differentiation between river margins became apparent, suggesting that finer taxonomic resolution can reveal patterns not evident at the higher taxonomic levels. In addition to this western–eastern pattern, we also observed longitudinal compositional changes along the river course, particularly between its middle and upper reaches. These results indicate that the Juruá does not act as a strong barrier to forest bird communities. Instead, variation in community composition along the river may be more strongly influenced by previously documented environmental and floristic gradients (Tuomisto et al. 2016; Zuquim et al. 2021).

Positive correlations between the dissimilarity in bird species and riverbanks were specifically observed among bird taxa characterised by limited dispersal capacities. These groups include understorey birds, insectivores, small frugivores (mainly piprids) and nectarivores (mainly *Phaetornis* spp.). Many of these species may be physically capable of flying long distances, but choose not to fly over water, something known as 'fear of flying' (Diamond 1981), which is quite common in the Furnariidae, Thamnophilidae, Formicariidae, Dendrocolaptidae and Ramphastidae families (Naka et al. 2022). This highlights the heightened impact of riverine barriers on these bird taxa (Naka et al. 2022).

Another interesting relationship found was the positive correlation between changes in the composition of frugivorous birds and Melastomataceae plants. Melastomes produce small, nutritious fruits that mainly attract manakins and tanagers, favouring their effective seed dispersal agents (Snow 1981; Silva et al. 2016), which may have co-evolved (Stiles and Rosselli 1993). Previous work has documented breaks in gene flow and species composition differences between the middle and upper sections of the Juruá River, reflecting environmental and geological variation along its course (Gascon et al. 1998; Patton et al. 2000; Tuomisto et al. 2016; Zuquim et al. 2021). The biological community structure along the Juruá, including birds, seems to be

associated with environmental gradients rather than a barrier effect between opposite banks.

Western Amazonian rivers flow over Pleistocene alluvial terrains and thus are more susceptible to lateral channel migration and avulsion than rivers in more stable cratonic areas (Ribas et al. 2025). In addition, the relative extent of floodplains and uplands has varied during the Pleistocene in this region due to cycles of sediment deposition and erosion (Pupim et al. 2019), making this whole region geomorphologically dynamic (Bicudo et al. 2019).

This geomorphological instability provides a plausible explanation for the lack of significant differences in bird species composition between opposite banks of the Juruá River. Pupim et al. (2019) document that some currently non-inundated terraces in western Amazonia were part of the floodplain in the upper Pleistocene, suggesting retraction of floodplains and expansion of *terra firme* habitat toward the rivers. On the other hand, Ruokolainen et al. (2019) and Rossetti et al. (2021) describe channel shifts during the Quaternary, in which river avulsions shifted entire river floodplains over considerable land sections to new locations, potentially causing both flora and fauna to become associated with a different side of the floodplain than they were before.

However, although lateral channel migration related to river meandering may be more common during the recent history of the Juruá, these events affect mostly the floodplains, covered by *várzeas*. *Várzea* and *terra firme* forests host distinct bird communities, with minimal overlap (Remsen and Parker 1983; Rowedder et al. 2021). When the river-floodplain complex is considered as a barrier to upland *terra firme* birds, the effective width of this barrier can exceed 25 km along the Juruá. Thus, the current lack of strong compositional differences between *terra firme* bird communities on opposite banks of the Juruá may reflect the dynamic nature of the whole regional landscape. Pupim et al. (2019) show that terraces currently covered by upland forest in western Amazonia were part of the floodplain, covered by *várzea* vegetation, in the upper Pleistocene. This suggests that upper Pleistocene retraction of floodplains could have allowed *terra firme* forests and their associated bird communities to expand toward the rivers, enabling recent distribution changes, community restructuring and cross-river dispersal that reduce present-day community dissimilarity.

In addition to the geomorphological processes discussed above, long-term differences in climatic history across Amazonia may have also played an important role in structuring bird communities. Despite the more dynamic and recent geomorphological history, western Amazonia (including the Juruá region) has experienced more stable and humid climatic conditions throughout the Quaternary (Cheng et al. 2013; Wang et al. 2017), which may have facilitated the long-term persistence of forest-dependent species and greater compositional homogenization across sites (Silva et al. 2019). In contrast, southeastern Amazonia (including the Tapajós area), although more stable geomorphologically, has been periodically drier and more climatically unstable (Cheng et al. 2013; Wang et al. 2017), conditions that may have promoted local extinctions and greater heterogeneity in community structure (Silva et al. 2019). These climatic patterns likely interacted

with river dynamics, potentially modulating the strength of biogeographic boundaries imposed by rivers. This perspective adds an additional layer of interpretation to the observed dissimilarities in community composition across Amazonia.

## 4.2 | Drivers of Dissimilarities in Juruá Bird Assemblages

While no genus and species composition differences were found on opposite banks of the Juruá river, a moderate effect of the river as a biogeographic barrier was observed at the subspecies level, primarily evidenced by the replacement, on opposite riverbanks, of subspecies of species such as *Lepidothrix coronata*, *Myrmoborus myotherinus*, *Willisornis poecilinotus* and *Thamnophilus aethiops*. Additionally, slight differentiation can be detected between the upper and lower stretches of the river, highlighted by subspecies turnover in *Thalaurania furcata*, *Malacoptila rufa*, *Automolus infuscatus*, *Hylophylax naevius*, among others. In contrast, the Tapajós River presents a more pronounced barrier effect, with species turnover apparent even at the genus level. This pattern is particularly evident in emblematic taxa such as *Cyphorhinus* spp., *Regmatorhina* spp. and *Phlegopsis* spp., at the species level, and *Glyphorhynchus spirurus*, *Thamnomanes caesius*, *Hypocnemis striata*, *Phaethornis superciliosus*, among others, at the subspecies level, which exhibit mutually exclusive distributions on opposite riverbanks.

Differences in soil base cation concentration and geographic distances showed the strongest correlations with bird community divergence along the Juruá. These factors likely drive ecological gradients that structure communities. Soil properties strongly influence vegetation characteristics, which, in turn, affect bird distributions. Furthermore, dispersal capacity varies among bird species, some of which exhibit broader ranges while others are more restricted, which is inherently linked to geographic distance between sites. Geographic distance particularly influences insectivorous understory birds, which tend to occupy smaller territories and avoid open areas within forests (Jirinec et al. 2022).

Environmental heterogeneity was higher across sites in the Juruá basin compared to those at Tapajós, which can partly be attributed to greater sampling distances, spanning a wider diversity of habitats. The Juruá headwaters in Acre feature nutrient-rich soils and unique vegetation, including bamboo forests, with flooding regimes differing significantly from the middle and lower courses. While no significant compositional differences between Juruá banks were found, recent studies report possible breaks in gene flow between opposite banks (Del-Rio et al. 2021), highlighting the need for further research into the genetic structuring of the avifauna.

## 5 | Conclusion

Our findings are consistent with the notion that geomorphological history and fluviomorphic stability can influence the strength of Amazonian rivers as biogeographic barriers. Although our study is limited to only two major tributaries of the Amazon, the contrasting patterns observed provide clear comparative

insights and generate testable hypotheses for future studies that may eventually include wider river-level replication across the Amazon basin. Our findings are also the first to dispute sweeping claims that seek to generalise the effectiveness of major Amazonian rivers as geographic barriers, often treating very distinct riverine barriers as analogues.

Our results support the notion that the magnitude of the river barrier effect varies widely across the large Amazonian rivers. Although this effect is related to several river and species characteristics, such as river width, length, discharge and the dispersal capacity of individual species, our work highlights the importance of the origin and history of the rivers themselves, which depend on their geological context. As predicted by our hypothesis, the Tapajós plays an important role in shaping *terra firme* bird assemblages, in contrast to the Juruá; despite the large combined river channel floodplain width, it does not play a pronounced role in shaping upland bird assemblages. Differences in bird composition along the Juruá basin were instead more strongly associated with the gradient of soil nutrient concentration along the river. The dynamics of habitat change and headwater-to-lowland river continuum during the Pleistocene have been controlled by both climate and geology, and in turn have shaped upland bird communities. Comparative analyses can clearly benefit from considering not only the contemporary setting of the large Amazonian rivers but also their history.

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#### Conflicts of Interest

The authors declare no conflicts of interest.

#### Data Availability Statement

Most of the environmental descriptors used are available in the methods section. The floristic predictions of ferns, palms, and melatomes for the Juruá region are available at <https://doi.org/10.23729/29caa>

858-9d73-489b-8646-e3eed68d0f7. The Landsat TM/ETM+ composite is available at <http://urn.fi/urn:nbn:fi:att:71ba2590-7112-4669-a4b3-a427c85c7a86>. Bird data are available at <https://doi.org/10.5061/dryad.b5mkkwhq6>.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Localities sampled with mist nets, showing the corresponding basin, geographic coordinates and river margin location. **Table S2:** Description of the predictor variables used in the analysis. **Table S3:** Number of species and individuals included in each category for the Juruá and Tapajós data. **Figure S1:** Principal coordinates analysis (PCoA) ordinations of bird communities within sites (sampled with understorey net-lines) in two river basins (Juruá and Tapajós). **Figure S2:** Specimens of common scale-backed antbird (*Willisornis poecilinotus*) collected from netline sites sampled on opposite banks of the Juruá River, illustrating the phenotypic variation and geographic distribution of this species. **Figure S3:** Specimens of blue-capped manakin (*Lepidothrix coronata*) collected from netline sites sampled on opposite banks of the Juruá River, illustrating the phenotypic variation and geographic distribution of this species. **Figure S4:** Specimens of black-faced Antbird (*Myrmobors myotherinus*) collected from netline sites sampled on opposite banks of the Juruá River, illustrating the phenotypic variation and geographic distribution of this species.