Variation in the spatial structure of communities in terms of species composition (beta diversity) is affected by different ecological processes, such as environmental filtering and dispersal limitation. Large rivers are known as barriers for species dispersal (riverine hypothesis) in tropical regions. However, when organisms are not dispersal limited by geographic barriers, other factors, such as climatic conditions and geographic distance per se, may affect species distribution. In order to investigate the relative contribution of major rivers, climate and geographic distance on Passeriformes beta diversity, we divided Amazonia into 549 grid cells (1° of latitude and longitude) and obtained data of species occurrence, climate and geographic position for each cell. Beta diversity was measured using taxonomic, phylogenetic and functional metrics of composition. The influence of climatic variables, geographic distance and rivers on these metrics was tested using regression analyses. Passerine beta diversity is characterized mainly by the change in species taxonomic identity and in phylogenetic lineages across climatic gradients and over geographic distance. However, species with similar traits are found throughout the entire Amazonia. The size of rivers was proportional to their effect on species composition. However, climate and geographic distance are relatively more important than rivers for Amazonian taxonomic and phylogenetic species composition.

Keywords: dispersal limitation, environmental gradient, geographic barrier, riverine-barrier-hypothesis, species composition, variance partitioning

Introduction

Species composition can be affected by several factors such as geographic barriers, climatic factors and geographic distance, creating different spatial patterns of species distribution (Qian and Ricklefs 2012). Although the effects of rivers, climate and geographic distance on species distribution have been extensively explored for several taxa (Buckley and Jetz 2008, Naka and Brumfield 2018), the relative importance of these processes is not well understood.

In tropical regions, large rivers might act as barriers to species dispersal leading to differences in community composition across river margins (Cracraft 1985, Hayes and Sewlal 2004, Pomara et al. 2014, Naka and Brumfield 2018, Silva et al. 2019).
dispersal can promote allopatric speciation (Ribas et al. 2012) or prevent secondary contact of extant species (Naka and Brumfield 2018). Wide and old rivers, such as the Amazon, could lead to allopatric speciation by preventing gene flow between populations on opposite river margins (Ribas et al. 2012, Boubli et al. 2015). In contrast, more recent-formed rivers such as Negro and Branco (Hooorn et al. 2010) possibly maintain diversity by avoiding secondary contact between taxa that diverged elsewhere (Naka and Brumfield 2018). Despite the potential to create differences in species composition, rivers might be semi-permeable barriers for many taxa (Moraes et al. 2016), permitting gene flow between populations and exchanging of species across margins in the headwaters (Weir et al. 2015). This challenges the hypothesis that rivers, as a whole, are the single and most important factor affecting the diversification and distribution of species in Amazonia (riverine hypothesis; Cracraft 1985).

In addition to rivers, dispersal might be limited by geographical distance per se (Dambros et al. 2017) and distinct environments lead to differences in species composition due to species habitat specialization (Tuomisto et al. 2003, Qian and Ricklefs 2012). As all species are limited by distance at some spatial scale, geographic distance might act as a barrier promoting allopatric speciation at broad scales (Warren et al. 2014). Moreover, the environment can be strongly associated with the distribution of plants (Tuomisto et al. 2003) and vertebrates (Buckley and Jetz 2008). This occurs because each species occupies a specific niche along climatic and edaphic gradients (Zuquim et al. 2012), and environmental gradients promote speciation (Schluter 2000) and differentiation of morphological traits (Luzuriaga-Aveiga and Weir 2019).

Current species distribution in Amazonia likely results from complex interactions of historical geological events and environmental factors (Silva et al. 2019). The distribution of birds in Amazonia has been historically associated with endemism areas delimited by rivers (Cracraft 1985). However, the effect of rivers on vertebrates is controversial – new studies suggest that rivers do not delimitate endemism areas (Oliveira et al. 2017) and have a weak association to the distribution of birds and other vertebrates at the broader scales of Amazonia (Oliveira et al. 2017, Santorelli et al. 2018). Although the environment and geographic distance have also been associated to the distribution of vertebrates (Hubbell 2001, Buckley and Jetz 2008, Silva et al. 2019), plants (Tuomisto et al. 2003) and insects (Dambros et al. 2017), the relative contribution of climate, geographic distance and rivers is still debated.

To assess the relative contribution of climate, geographic distance and rivers in shaping Amazonian diversity, we quantified differences in passerine species composition along climatic gradients, geographical barriers and space. We used metrics of composition that incorporate species taxonomic identity, phylogeny and functional traits. Although most studies of Amazonian biogeography have used a taxonomic approach, phylogenetic information provides insights about the evolutionary processes associated with changes in species composition (Leprieur et al. 2012). In addition, functional information allows identifying how species traits (and adaptations) are associated with changes in species composition along gradients (Villéger et al. 2011).

Specifically, we hypothesized that 1) larger Amazonian rivers (e.g. Amazon river) affect the structure of passerine communities more than smaller tributaries (e.g. Branco river); 2) due to the wide range of climatic conditions and large geographic distances separating areas in Amazonia, these predictors will be at least as important as rivers for the composition of birds; 3) if historical evolutionary processes (e.g. allopatric speciation across rivers) are the main cause of species distribution, the turnover of phylogenetic lineages across these barriers will be stronger than the taxonomic turnover (Hattab et al. 2015); and 4) because traits are associated to species responses to the environment, changes in species traits (functional composition) will occur along broad environmental gradients. Indices of beta diversity can be decomposed in two components: one that is related to species replacement (turnover) without the influence of species richness differences, the other that is related to the influence of nestedness (i.e. species loss or gain between sites; Baselga 2012). By controlling for species richness gradients, we tested the relative importance of rivers, climate and geographic distance in shaping patterns of species taxonomic, phylogenetic and functional true turnover demonstrating how different ecological and evolutionary processes shaped the replacement of species in Amazonia.

Material and methods

Study area

The Amazonian forest is the largest remaining tropical rainforest in the world and covers nine countries in South America, totaling an area of six million square kilometers (Da Silva et al. 2005). Its climate is predominantly warm (approximately 25°C) and with an average precipitation of approximately 2300 mm yr⁻¹ (Fisch et al. 1998). The vegetation is relatively heterogeneous and the main vegetation formations are divided into two groups: terra-firme forests and flooded forests (igapó forest and floodplain forest; Pires and Prance 1985). The Amazonian basin is divided by several large rivers, such as the Amazon, Negro, Madeira, Xingu, Tapajós and Branco (Cracraft 1985, Oliveira et al. 2017).

Data collection

We obtained the list of South American cataloged birds (September 2015 version), which is organized by the South American Classification Committee (<http://datazone.birdlife.org/species/requestdis>). The spatial distribution of Passeriformes species was obtained from the Birdlife database (<http://datazone.birdlife.org/species/requestdis>) and the range maps of species were superimposed on the Amazonian map. The range maps of birds are constructed primarily based on occurrence data and map polygons are created at a finer scale than used here (IUCN 2013). Although methods to produce these species range maps can bias the results
by providing false presences (i.e. species occurrence where it is actually absent; Brooks et al. 2019), these range maps are extensively used in macroecological analyses (Rodrigues and Diniz-Filho 2017, Rangel et al. 2018) and reliable results are achieved using a grid resolution between 1 and 2 degrees (Hurlbert and Jetz 2007).

Considering the limitation of range maps, we divided the entire region into 549 grid cells of $1^{\circ} \times 1^{\circ}$ of latitude and longitude and we obtained the presence and absence data of individual species for each cell (site). The data included 1164 species of Passeriformes, 457 of Passer suborder and 707 of Tyranni suborder, including migratory and excluding exotic species. Phylogenetic data were compiled from <http://birdtree.org/> (Jetz et al. 2012). Only eight recently described species had to be added to the phylogeny. We added these species to the most recent node by inserting a branch at the base of the genera tree. Functional data on diet, foraging strata and body mass, key attributes defining species function in communities, were obtained from Wilman et al. (2014). Data on foraging strata for each species were represented as the percentage of use for each of eight categories: 1) below the water surface, 2) on or just (< 5 inches) below water surface, 3) ground, 4) understory, 5) mid-high, 6) canopy, 7) aerial and 8) pelagic specialist. Similarly, diet was quantified as the frequency of consumption in 10 categories: 1) invertebrates, 2) mammals or birds, 3) reptiles and amphibians, 4) fishes, 5) vertebrates-general or unknown, 6) scavenger and similar, 7) fruits, 8) nectar 9) seed plants and 10) plants and similar.

We extracted environmental variables for each cell with a resolution of 10 m ($\sim$340 km$^2$) from the WorldClim (<www.worldclim.org>) and The Atlas of the Biosphere (<https://nelson.wisc.edu>) platform. We chose variables that are usually highly correlated to the distribution of species (Buckley and Jetz 2008, Qian and Ricklefs 2012): mean annual temperature (bio1), mean annual precipitation (bio12) and altitude. In addition, latitude and longitude data were extracted from the centroid of each cell. All variables were standardized before analyses.

Rivers data were obtained from <www.ore-hybam.org>. Using the Quantum GIS program 2.14.2 (<www.qgis.org/>), we extracted vectorized data only for the main Amazonian rivers suggested as barriers for species dispersal (Cracraft 1985, Ribas et al. 2012): Amazon, Negro, Madeira, Xingu, Tapajós and Branco.

### Data analysis

To summarize species traits that are correlated to each other, to reduce trait dimensionality and to include categorical traits in functional metrics, we calculated the trait distance between each pair of species by generalizing the Gower’s distance using the method proposed by Pavoine et al. (2009). This method allows calculating pairwise distances between species in the trait space using both quantitative (body mass) and qualitative (foraging strata and diet) data (Pavoine et al. 2009). The matrix representing the trait distance between all pairs of species was summarized into ordination axes using a principal coordinates analysis (PCoA). The first two PCoA axes of trait similarity were used as species traits. These axes explained 55% of the variability in the original matrix of species traits, which is relatively high compared to other studies using qualitative traits (Pavoine et al. 2009). We have not used additional PCoA axes due to the high computational demand that the estimation of functional similarity in three dimensional morphospace would require considering the large number of species and communities in our study. Nevertheless, it is likely that using two or three axes would produce qualitatively similar results. Using a random sample of 20 sites, the correlation between the functional similarities obtained using two and three axes was 0.7 (Supplementary material Appendix 1 Fig. A1). We used a correlation test to quantify the contribution of individual traits to the PCoA axes.

In order to determine the effect of climatic variables, isolation by distance and isolation by rivers on species beta diversity, we calculated the dissimilarity in species composition between pairs of sites and associated this measure to differences in climate, geographic distance and separation by rivers. To quantify the taxonomic, phylogenetic and functional beta diversity, we used the Jaccard dissimilarity index, which is the most frequently used index for tests involving binary data, such as species presences and absences (Qian and Ricklefs 2012). This is a paired measure between two communities defined as $'a/(a+b+c)'$, where 'a' is the number of species present in both cells, 'b' is the number of unique species in the first cell and 'c' is the number of species unique to the second cell (Legendre and Legendre 2012).

The Jaccard dissimilarity index can be partitioned into different components: turnover and nestedness (Baselga 2012). The turnover component represents the substitution of species between cells (Baselga 2010), whereas nestedness represents the contribution of differences in species richness between cells to the dissimilarity index (Baselga 2010, 2012). This partitioning can also be applied for phylogenetic (Leprieur et al. 2012) and functional diversity (Villéger et al. 2011). Phylogenetic turnover reflects the evolutionary distinctiveness of lineages between sites, whereas phylogenetic nestedness represents the sharing of species evolutionary history between sites (Leprieur et al. 2012). Functional turnover measures the functional space not shared between sites, whereas functional nestedness quantifies the contribution of differences in species richness on the functional dissimilarity between sites (i.e. sites with high nestedness are functionally similar because one site has a subset of the functions present in the other site; Villéger et al. 2011). Both the original Jaccard dissimilarity index and the turnover and nestedness components of the index were calculated for all sites (multiple site measure) for taxonomic and phylogenetic, and for each pair of sites individually (pair-wise measure) for taxonomic, phylogenetic and functional diversities (Baselga 2010, Villéger et al. 2011, Leprieur et al. 2012). Considering the large number of species and communities, we have not measured multiple site dissimilarity for functional diversity.
due to the high computational demand. Only turnover values from pairwise analyses were used as response variables because the turnover component was much more influential on beta diversity metrics than the nestedness component (see below). In addition, the turnover component is the most affected by evolutionary (e.g. allopatric speciation) and ecological processes (e.g. environmental filtering) at broad scales (Menegotto et al. 2019).

As each pair of sites had a value of taxonomic, phylogenetic and functional turnover (i.e. dissimilarity values), we performed a principal coordinates analysis (PCoA) for each of these dissimilarity matrices, generating ordination scores for each $1^\circ \times 1^\circ$ cell. Cells with similar values in the PCoA axes have similar taxonomic, phylogenetic or functional composition (Tuomisto and Ruokolainen 2006). This allowed the graphical representation of the spatial dissimilarity of species throughout Amazonia.

Distance matrices were created for each predictor variable (temperature, precipitation, altitude and geographic distance) by calculating the difference between the values of these variables obtained from the centroid of each cell (Euclidean distance). We also created distance matrices for each Amazonian river using the geographic position of each pair of cells separated by the river. On cases in which rivers crossed a cell, cell centroid was used as reference.

We acknowledge that rivers do not completely divide all Amazonian regions because river extension is shorter than region extent. For example, cells in southern (A in Fig. 1) and northern Amazonia (B in Fig. 1) are separated by the Amazon River (Fig. 1). However, these individual cells (A–B in Fig. 1) are not separated from other cells by the same river in the Andes region (C in Fig. 1). Hence, by drawing a straight line between two cells, we were able to ascertain whether cells were separated by the river (score 1 for presence) or not (score 0 for absence) and create a distance matrix for each river. Differently from previous approaches that categorize Amazonia based on all rivers (biogeographic regions; Cracraft 1985, Ribas et al. 2012), we were able to determine the individual and combined influence of each river on species beta diversity.

In order to avoid collinearity between predictor variables, we used a Pearson correlation test with a threshold of 0.7 (Dormann et al. 2013). A strong correlation was found between temperature and altitude ($r = 0.96$), and results on their effects on species turnover were also similar (Supplementary material Appendix 1 Table A1) and therefore only temperature was included in subsequent analyses (Buckley and Jetz 2008, Dambros et al. 2015, 2017).

Regression analysis was performed to test the association between the distance matrices representing each Amazonian river (Amazon, Negro, Madeira, Xingu, Tapajós and Branco) and the pairwise dissimilarity in taxonomic, phylogenetic and functional composition. Using the same analysis, we sequentially regressed the matrices of geographic distance, differences in temperature and differences in precipitation against the matrices of species dissimilarity. Although the regression analysis was conducted using each river separately, the variance explained ($R^2$) by all rivers was combined to represent the maximum variance in taxonomic, phylogenetic and functional composition that could be explained by all Amazonian rivers. Similarly, we combined temperature and precipitation to represent the climatic predictor.

![Figure 1. Map of the study area and diagram representing the method used to create connectivity matrices for each main Amazonian river. By drawing a line between two cells, we were able to determine whether cells were separated by the river or not. The process was performed for each pair of cells and separated matrices were created for each Amazonian river. Letters A, B and C represent cells located in central Amazonia (A), northern Amazonia (B) and the Andes region (C).](image)
We used variance partitioning to separate the variance explained exclusively by each predictor variable and the variance that could be explained by all the variables combined (shared).

All analyses and data processing were performed in the R program (R Development Core Team) using the raster (Hijmans and Etten 2012), betapart (Baselga et al. 2017), ecodist (Goslee and Urban 2007), rgdal (Bivand et al. 2011), ade4 (Dray and Dufour 2007) and vegan (Oksanen et al. 2010) packages. The R scripts necessary to replicate all our results are available in the Supplementary material Appendix 1 and all data used are available in the Figshare repository (doi: 10.6084/m9.figshare.6955091) under the CC-BY 4.0 license (free to use and distribute).

**Results**

Changes in taxonomic and phylogenetic composition of species was mostly associated to the replacement (turnover) of species between sites (turnover = 0.99; nestedness = 0.001; total dissimilarity = 0.99).

The taxonomic and phylogenetic turnover (Fig. 2a–b) were explained by the differences in temperature, geographic distance and presence of rivers (Supplementary material Appendix 1 Table A1). However, the variation in taxonomic and phylogenetic turnover was more strongly associated with the differences in temperature (33.2% and 40%, respectively) and the geographic distance separating regions (41.5% and 32.7%, respectively) than to rivers (Supplementary material Appendix 1 Table A1). Different from taxonomic and phylogenetic turnover, functional turnover was homogeneous throughout Amazonia and mostly related to foraging strata (Fig. 2c; Supplementary material Appendix 1 Table A2). Functional turnover was weakly associated with differences in temperature ($R^2 = 2\%$) and geographic distance ($R^2 = 10\%$) separating sites (Supplementary material Appendix 1 Table A1).

![Spatial variation in bird taxonomic (a), phylogenetic (b) and functional (c) composition in the Amazonian Forest. Changes in composition are represented by ordering scores (indicated by numbers from −0.3 to 0.2; colors). Ordering scores were obtained from a principal coordinates analysis (PCoA) using the turnover component of the Jaccard dissimilarity index between pairs of cells. As variability in functional diversity was mostly associated to foraging strata (Supplementary material Appendix 1 Table A2), bird foraging strata is shown for two distinct Amazonian regions with extreme values of functional composition along the first PCoA axis (c).](image-url)
In spite of the importance of temperature and geographic distance, all rivers combined explained 14.2% of the variation in taxonomic turnover, 9% in phylogenetic turnover and 11% in functional turnover between sites (Supplementary material Appendix 1 Table A1). Results using total beta diversity (raw Jaccard dissimilarity) were very similar to results using only the turnover component (Supplementary material Appendix 1 Table A3).

As predicted based on river size (Supplementary material Appendix 1 Table A4), the Amazon River was the most important river to beta diversity of species in Amazonia, followed by Negro, Madeira, Xingu, Tapajós and Branco, respectively (Supplementary material Appendix 1 Table A4; Fig. 3, grey bar; correlation between riverbed extension and river effect on species turnover \( r = 0.87 \)). When the effect of other rivers was removed from the data, the Amazon River was still the river with the largest explained variance for taxonomic and phylogenetic dissimilarity (Supplementary material Appendix 1 Table A4; Fig. 3, black bar).

When the effect of climate and geographic distance was removed from the data, rivers explained less than 4% of the variation on species taxonomic, phylogenetic and functional turnover. On the other hand, when we removed the effect of rivers and geographic distance from data, climate still explained 23% and 30% of the variation in taxonomic and phylogenetic dissimilarity. Taxonomic and phylogenetic dissimilarities were also associated with geographic distance (\( R^2 = 16\% \) and 12%) when the effect of other variables was removed from the data. (Fig. 3 insets).

**Discussion**

Patterns of taxonomic and phylogenetic beta diversity in Amazonia were strongly congruent, indicating that relatively recent evolutionary and/or ecological processes are more important for the structure of bird communities in Amazonia than old evolutionary processes (i.e. diversification at the base of the phylogeny; Hattab et al. 2015, Silva et al. 2019). These processes are likely associated with the presence of dispersal barriers and environmental filters, even though Passeriformes have an evident ability to disperse longer distances than other terrestrial vertebrates. Contrary to hypothesized (hypothesis 4; Fig. 2c), results from taxonomic and phylogenetic analyses suggest that species distribution is affected by current climate, geographic distance and rivers.

Among the climatic variables tested, temperature had the strongest association with species taxonomic and phylogenetic beta diversity. Although the tropics have a relatively uniform temperature (Janzen 1967), the climate abruptly changes along elevation gradients (Giarla and Jansa 2014). Discrepant conditions on the opposite extremes of the temperature gradient could prevent species adapted to survive in narrow temperature ranges from occurring along the entire region, creating a compositional turnover (Janzen 1967). In addition, differences in environmental conditions might prevent the exchange of individuals with distinct adaptations and promote speciation (ecological speciation; Schluter 2000). We have not found species functional traits to be strongly associated with environmental variables (Fig. 3c). However, the functional measures used in our study (e.g. foraging) are likely to determine species occurrences at smaller spatial scales and traits associated with species reproduction might be more important for ecological speciation (Luzuriaga-Aveiga and Weir 2019).

In addition to the strong association with the temperature gradient, differences in taxonomic and phylogenetic composition were also associated with geographic distance. Geographic distance is usually correlated to differences in environmental variables, which are responsible for the turnover in species composition (Buckley and Jetz 2008). Spatial patterns in soil conditions created during the Andean uplift separates the Andes and the Central-Amazonia regions, and these differences in soils are associated with the turnover of plant species (Higgins et al. 2011). Nevertheless, geographic distance was associated with changes in species composition even after controlling for differences in the environment (Fig. 3 insets). Variation in species composition in isolated areas is likely to result from dispersal limitation caused by distance per se (Dambros et al. 2017), highlighting a key influence of neutral processes in structuring communities (Hubbell 2001, Warren et al. 2014) in addition to the direct effect of the environment.

Although climate and geographic distance were relatively more important than rivers for passerine composition, large Amazonian rivers were also associated with species distribution (Fig. 3 insets and Supplementary material Appendix 1 Table A1). The large Amazonian rivers, especially the Amazon, might prevent the exchange or dispersal of individuals between populations on the opposite margins, leading to differences in species composition due to ecological or evolutionary processes (Hayes and Sewlal 2004, Pomara et al. 2014, Weir et al. 2015). The lack of gene flow between populations in opposite margins promotes allopatric speciation and limited dispersal between margins difficult secondary contact between taxa originated elsewhere (Naka and Brumfield 2018). In Amazonia, rivers have long been proposed to be barriers to species distribution (Wallace 1854), promoting diversification (Ribas et al. 2012, Boublí et al. 2015) and creating endemism zones (Cracraft 1985). However, our results suggest that the diversification process occurs mostly along the relatively wider and older Amazon River and that other processes (e.g. ecological specialization and isolation by distance) are more important. Although previous studies show the effect of geographic distance, climate and rivers on the spatial turnover of several taxa, our study is the first to compare the relative contribution of these factors on species distribution from fine to broad geographic scales. We evidenced that temperature and geographic distance are the main drivers of species turnover in Amazonia. As demonstrated in previous studies with birds (Cracraft 1985, Hayes and Sewlal 2004, Ribas et al. 2012, Pomara et al. 2014, Naka and Brumfield 2018) and other animal groups
Figure 3. Variance in bird taxonomic (a), phylogenetic (b) and functional (c) composition explained by the main Amazonian rivers (barplot and blue circle in Venn diagram), geographic distance and climate. The variance explained by rivers was decomposed into variance exclusively explained by each individual river (i.e. could not be attributed to the presence of other rivers; black bars) and total variance explained by each individual river (shared with other rivers; grey bars). The results were obtained from multiple and partial regression analyses using distance matrices (geographic, climatic and the presence of each individual river separating cells) as predictor variables and the pairwise matrix representing the turnover component of the Jaccard dissimilarity as response variable. Although climate, geographic distance and rivers exclusively explained a significant portion of the variance (p < 0.05 for all individual components in the diagram), climatic variables were the most important predictor of bird species composition in Amazonia.
(Wallace 1854, Boublí et al. 2015), rivers do influence species composition. However, this effect is likely to be of less importance at broad geographic scales where species may face large climatic differences and limiting geographic distances.

**Data availability statement**

The R scripts necessary to replicate all our results are available in the Supplementary material Appendix 1 and all data used are available on the Figshare repository (https://doi.org/10.6084/M9.FIGSHARE.6955091.V1) (Fluck et al. 2019) under the CC-BY 4.0 license (free to use and distribute).

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Supplementary material (available online as Appendix ecog-04753 at <www.ecography.org/appendix/ecog-04753>). Appendix 1.