



RESEARCH ARTICLE

Elevation drives taxonomic, functional and phylogenetic β -diversity of phyllostomid bats in the Amazon biome

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Abstract

Aim: We evaluated the relative importance of geographical and environment variables for taxonomic, phylogenetic and functional β -diversity of phyllostomid bats along the entire Amazon biome and specifically in the lowlands.

Location: Amazon biome.

Taxon: Chiroptera.

Methods: We carried out a bibliographic review and compiled a wide and unprecedented database of 106 phyllostomid bat species at 102 sites throughout the Amazon biome. For all possible pairs of sites in both datasets, we estimated the Jaccard pairwise dissimilarity, that is, β -diversity, considering its three dimensions—taxonomic, phylogenetic and functional—for its two components—turnover (substitution of species) and differences in species richness. The association between dissimilarity measurements and geographical and environment variables was assessed using multiple regressions on distance matrices (MRM).

Results: We found that turnover and differences in species richness had similar contributions to the taxonomic β -diversity. However, for phylogenetic and functional β -diversity, lineages and functions richness differences contribute slightly more than

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turnover for total β -diversity. In the lowlands, species, lineages and functions richness differences were slightly higher than turnover for all diversity dimensions. When accounting for all the sites, elevation was the main predictor of phyllostomid bats' taxonomic, phylogenetic and functional turnover. For lowland sites, ecoregions was the main (but relatively weak) predictor associated with all β -diversity dimensions.

Main conclusions: Analysis of filtering sites according to elevation revealed that species in the Amazonian lowlands are taxonomically and phylogenetically different from species in the Andes, and present taxonomic, phylogenetic and functional redundancy between assemblages. When accounting for the whole range of distribution of bats, results showed the predominant effect of elevation over other geographical and environmental predictors. This indicates that the diversity of good dispersers such as bats is more affected by specialisation along environment and climatic gradients than by geographical barriers throughout the Amazon biome.

KEYWORDS

Amazonia, biogeographical regions, Chiroptera, dispersal capacity, geographical barrier, Neotropics, riverine barrier-hypothesis, species distribution

1 | INTRODUCTION

Species distributions can be structured by environmental (e.g. terrain elevation, ecoregions and climate) and geographical features (e.g. rivers and mountains—Dambros et al., 2020; Quian & Ricklefs, 2012). Differences in climate or the presence of geographical barriers can sort species depending on their adaptations, and influence dispersal and cladogenesis, promoting turnover and the loss and gain of species across sites (nestedness) (Baselga, 2012; Silva et al., 2022; Varzinczak et al., 2017). Owing to the high levels of biodiversity and the broad range of environmental and geographical conditions, the Neotropics are frequently used to study the mechanisms underlying species distribution. For example, spatial compositional dissimilarity has been associated with geographical variables such as large rivers in Amazon (Cracraft, 1985; Silva et al., 2019).

Large Amazonian rivers have long been regarded as potential dispersal barriers for terrestrial species and, therefore, promote species turnover by vicariant speciation (Ribas et al., 2012). This allopatric speciation has been historically associated with endemism areas delimited by rivers (Lynch Alfaro et al., 2015; Wiley, 1988). Although studies have already highlighted this for different taxa (Cracraft, 1985; Moraes et al., 2016; Mourthé et al., 2022), large rivers seem to act differently according to the taxon's dispersal capacity (Dambros et al., 2020). Whereas the turnover of taxa with limited dispersal capacities (e.g. some terrestrial birds and plants with larger seeds) is more related to the presence of rivers, taxa with greater dispersal capacity (e.g. bats, flying insects and most birds) tend to be more associated with environmental and climatic variables, making them relevant factors for Amazonian biogeography (Aguirre et al., 2016; Fluck et al., 2020; Moraes et al., 2016; Nazareno et al., 2017; Ribas et al., 2012).

In addition to rivers, terrain elevation, vegetation structure (i.e. ecoregions), soil properties and climate have also been identified as predictors of species distribution on a large scale along the Amazon biome (Aguirre et al., 2016; Fluck et al., 2020; Tavares et al., 2017). Differences in terrain elevation promote changes in temperature and composition of plant species, producing a replacement of structurally distinct types of vegetation along the temperature gradient (Patterson et al., 1998). In the Amazon, this is more noticeable in large mountain ranges such as the Andes and the Pantepui (Cisneros et al., 2014; Patterson et al., 1998). However, low variation in terrain elevation has also been suggested as a predictor of species replacement, associated with soil nutrient and texture gradients (Capaverde Jr. et al., 2018; Dambros et al., 2020).

Ecoregions delimit vegetation types that can filter species and influence turnover between regions due to habitat specialisation (Morrone, 2014). Species which are sensitive to severe weather conditions can also have their distributions restricted by temperature and precipitation—northwestern Amazonia can experience more than 3500 mm of annual rainfall, while the foothills of the Andes on the eastern margin are dry with <100 mm of annual rainfall (Maeda et al., 2017). In addition, geographical distance per se can also lead to differences in species composition due to variation in vegetation type, climatic conditions and the intersection of geographical barriers such as rivers and mountain ranges, promoting allopatric speciation on large scales (Dambros et al., 2020; Fluck et al., 2020; Tuomisto et al., 2003). Many ecoregions in the Amazon are also delimited by rivers (Olson et al., 2001), indicating a correspondence level between predictors. However, although the role of the environment should be stronger for taxa with high dispersal capacity, such as bats, the relative effect of geographical barriers versus environmental variables on the distribution of these species has not



been properly investigated on a broader scale within Amazon region (e.g. Santos et al., 2019; Silva et al., 2022; Tavares et al., 2017).

Bats are highly diverse in terms of both species' richness and ecology. They are highly sensitive to natural or man-made environmental changes and play a key role in maintaining ecosystem functioning (Carvalho, Mustin, et al., 2021; Kunz et al., 2011; Martins et al., 2017). Therefore, these flying mammals with high dispersal capacity are an excellent group for studying patterns of distribution and community assembling or different diversity dimensions (e.g. Carvalho, Mustin, et al., 2021; Cisneros et al., 2014). The Amazon biome is a hotspot of bat diversity, with more than 200 species currently recognised (López-Baucells et al., 2018). In addition, the Andean Amazon is within one of the main areas of bat endemism in South America (López-Aguirre et al., 2018). Although bats seem less affected by rivers than other taxa (Santorelli Jr. et al., 2018), their association with vegetation structure and plant composition is strong in different regions at both micro- and meso-scales (Aguirre et al., 2016; Capaverde Jr. et al., 2018; Carvalho, Mustin, et al., 2021). However, because of limited data available in previous macroscale studies, it is possible that important environmental gradients affecting the distribution of bats have not been captured (Dambros et al., 2020). Studies have indicated that biogeographical regions and recent history of formation of the Amazonian terrestrial ecosystems have an influence on bat distributions (Lim & Tavares, 2012; Santos et al., 2019; Silva et al., 2022; Tavares et al., 2017). However, the results in the Amazon have been contradictory. Low variation in terrain elevation is known to be among the main drivers of phyllostomid bat species diversity at the micro- and meso-scales (Aguirre et al., 2016; Bobrowiec & Tavares, 2017; Capaverde Jr. et al., 2018). On a broad scale, there is a weak relationship between the diversity of this group and any predictor variable, including elevation and climate (Dambros et al., 2020). One possible cause for the differences between studies is that current knowledge about the broad-scale distribution of bats in Amazon is concentrated in the lowlands—regions with low variation in climate and elevation (Dambros et al., 2020).

Most studies that have aimed to show which environmental variables drive bat diversity (e.g. Capaverde Jr. et al., 2018; Dambros et al., 2020), and how areas of endemism influence species distribution (e.g. Santos et al., 2019; Tavares et al., 2017) have used only the taxonomic dimension of diversity throughout the Amazon biome (but see Silva et al., 2022 for phylogenetic diversity). The combination of taxonomic with functional and phylogenetic dimensions allows for more robust conclusions regarding the evolutionary processes involved, and for a description of the causes of the variation in function and lineage distributions over time and space (Freitas & Mantovani, 2018; Tucker et al., 2017). However, despite the recent development of tools for estimating these dimensions of diversity and their components (Mammola et al., 2021; Moreno et al., 2018), there is still a lack of studies that integrate these indices. Taxonomic, phylogenetic and functional diversities can be incorporated in analysis of β -diversity partitioning to understand which diversity aspects respond to large-scale environmental gradients and geographical barriers. The use of β -diversity has become a key approach to better

understanding the large-scale variation in bat species composition between different Neotropical habitats (e.g. Batista et al., 2021; Carvalho, Mustin, et al., 2021; Varzinczak et al., 2019). Partitioning the community composition variation in components of species replacement (or turnover) and richness difference (or nestedness) provides relevant information on communities structure and underlying processes (Legendre & De Cáceres, 2013). Communities structured by species replacement reflect the substitution of species along an ecological gradient according to species niche breadth, while the difference in richness among communities can be caused by the disappearance or gain of species associated with environmental conditions (Legendre, 2014; Legendre & De Cáceres, 2013).

Our objective is to evaluate the relative contribution of geographical (rivers, areas of endemism and geographical distance between locations) and environment (ecoregions, soil nutrients, elevation and climate—temperature and precipitation) variables on the taxonomic, phylogenetic and functional β -diversity components (turnover and richness difference) of phyllostomid bats first within the entire Amazon biome and also within the Amazonian lowlands (sites equal or below 300 m a.s.l.). In addition, we aim to disentangle the role of species adaptations (traits) and evolutionary history (lineages) on their distribution. In contrast to previous studies conducted on large scales (Aguirre et al., 2016; Lim & Tavares, 2012; Santos et al., 2019; Silva et al., 2022; Tavares et al., 2017), we use an extensive dataset compiled from a large set of previously published studies in the Amazon biome. For both, entire Amazon biome and Amazonian lowlands, we expect species, functional and lineage turnover to be more important than richness difference in driving taxonomic, phylogenetic and functional β -diversity, due to environmental sorting, as this has been found for bats in other studies carried out in Neotropical forests (e.g. Batista et al., 2021; Carvalho, Mustin, et al., 2021; Dambros et al., 2020; Silva et al., 2022; Varzinczak et al., 2019). Due to the high dispersal capacity of bats (Esbérard et al., 2017), we expect that the presence of rivers will have low explanatory power for taxonomic, phylogenetic and functional turnover in the entire Amazon biome and in the Amazonian lowlands, as has been found for other taxa with high dispersal capacity such as birds (e.g. Fluck et al., 2020). For both datasets analysed, we also expect areas of endemism to have low predictive power for species turnover as they are often delimited by large rivers (Dambros et al., 2020). As ecoregions are considered subsets of large biomes (Olson et al., 2001), being analogous to the biogeographical regions considered for Amazonian bats (Santos et al., 2019; Tavares et al., 2017), we expect their explanatory power to be low for the two datasets analysed. We also expect geographical distance between locations to have a high explanatory power, as has already been observed for birds in the Amazon biome (Fluck et al., 2020), as more distant locations tend to have greater differences in their environmental characteristics. Finally, we expect that elevation and climate will have strong explanatory power, mainly when consider the entire Amazon biome for the differences between species turnover, as they can affect bats regardless of their physical ability to disperse, niche partitioning and interspecific competition along gradients

(Aguirre et al., 2016; Carvalho, Martins, Esbérard, et al., 2019; Fluck et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area comprises the Amazon biome, located in the northern part of South America and covering an area of approximately 6.8 million km² (Figure 1—Wittmann & Junk, 2016). The Amazon biome extends over nine South American countries (Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname and Venezuela), with 60% of the total extent in Brazil. The Amazon biome harbours four of the ten largest rivers on Earth in terms of water discharge and drainage area, and includes different types of ecosystems, such as wetlands, terra-firme forest (non-flooded), seasonally flooded forests (igapó and várzea), savannahs and white-sand ecosystems, as well as montane forests (Adeney et al., 2016; Carvalho & Mustin, 2017; Pires & Prance, 1985). The biome has a widely varying climate, with average annual rainfall and temperatures ranging from ~100 mm and ~15°C in the Andes to ~3500 mm and ~25°C in the lowlands (Casimiro et al., 2013; Fisch et al., 1998; Maeda et al., 2017). The elevational gradient in the Amazon biome is also very wide, with elevations ranging from sea level to more than 6000 m a.s.l. in the Andes. However, most of the Amazon biome is below 250 m a.s.l. and the principal humid zones, with a predominantly warm climate, are located below 100 m a.s.l. (Goulding et al., 2003).

2.2 | Species data collection

We searched for previous studies on bats in the Scientific Electronic Library Online—SciELO (<http://www.scielo.org>), Web of Science

database—WoS (<http://www.webofknowledge.com>) and Google Scholar (<https://scholar.google.com.br/>), using a combination of the following keywords: bat, bats, morcego, morcegos, murciélagos, murciélagos, Amazon, Amazonia, Amazônia, Amazonian, Amazônica, Amazônica, Bolivia, Brazil, Colombia, Ecuador, French Guiana, French Guiana, Guyana, Guyana, Peru, Suriname and Venezuela. These searches returned a total of 203 studies, which were then filtered in two steps. First, we removed those studies that did not contain data on the Phyllostomidae family, as bats in this family are best sampled by mist nets (Kunz & Parsons, 2009), which is the most used method in bat studies in the Amazon biome (Appel et al., 2021). We only included studies that presented a species list with the intention of sampling the local species composition. Second, we merged the data from studies that were carried out within 20 km of each other, based on the geographical coordinate of the centroid of the sampling sites (e.g. Rocha et al., 2018). As a result, the data used here represent 102 sites and 94 different studies (Figure 1; data available in <https://doi.org/10.6084/m9.figshare.14701728.v3>).

We then revised the species nomenclature to standardise our database following Wilson and Mittermeier (2019) and Garbino et al. (2020). To validate species identification, we also verified if the species listed in each paper fall within the geographical distribution limits proposed by Gardner (2008), and removed those species recorded outside their known distribution range. We also removed species that are not known to be found in the Amazon biome (e.g. *Vampyressa pusilla* and *Lonchophylla mordax*). In addition, we disregarded all species considered as *conferatum* (cf.) and those which would have problems with species identification within the genus and that have been classified under a specific epithet (e.g. *Lophostoma* sp.). We also considered *Platyrrhinus angustirostris*, *P. fusciventris*, *P. guianensis*, *P. incarum*, *P. infuscus* and *P. helleri* as *Platyrrhinus* spp., because the first five species were recognised as *P. helleri* until 2010 (Velazco et al., 2010; Velazco & Lim, 2014). Given ongoing difficulties associated with the separation of *Carollia*

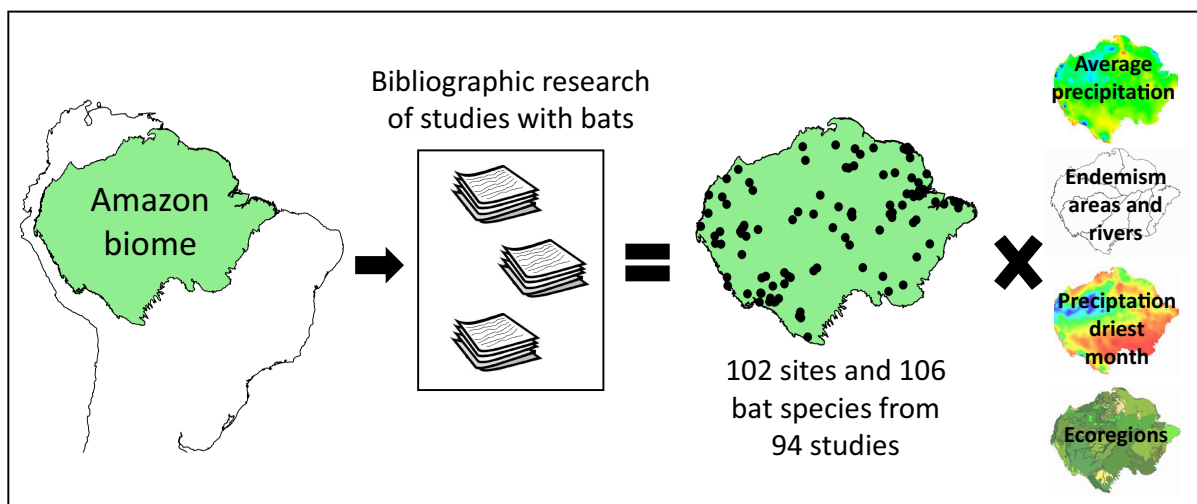


FIGURE 1 Summary of the methods showing the study area (Amazon biome), total studies and bat species compiled, as well as the indication of five predictor variables from a total of eight used in our analyses.



brevicauda, *C. perspicillata* and *C. benkeithi* based on morphological characters alone (Lemos et al., 2020), we also joined records of these three species as *Carollia* spp. Finally, as *Hsunitycteris pattoni* and *H. thomasi* were recently separated into two species, and have similar morphological characteristics (Velazco et al., 2017), we chose to consider them as *Hsunitycteris* spp. Thus, we considered a total of 106 species out of 140 initially compiled (Figure 1; data available in <https://doi.org/10.6084/m9.figshare.14701728.v3>).

2.3 | Predictor variables

The predictor variables selected are known to positively or negatively influence the richness and diversity of phyllostomid bats (Aguirre et al., 2016; Carvalho, Martins, Esbérard, et al., 2019; Tavares et al., 2017) and were obtained through databases already available in the literature. Climatic variables important for the distribution of species, including average temperature (bio 1), average precipitation (bio 12), precipitation of the driest month (bio 14) and elevation were extracted directly from WorldClim (<https://www.worldclim.org>) with a resolution of 2.5 minutes of a degree. Soil base-cation concentration was extracted from a digital map modelled using direct and plant-derived soil data with spatial resolution of 6 arcmin (Zuquim et al., 2019). The information on Amazon rivers was taken from a vectorized dataset of the Amazon hydrographic basin available at www.ore-hybam.org with the use of the Quantum GIS program 3.16.5 (www.qgis.org/). Only rivers previously identified as important for vertebrate diversity in the Amazon were considered (Amazon, Negro, Madeira, Xingu, Tapajós and Branco—Cracraft, 1985; Ribas et al., 2012). Based on these rivers, a vectorised dataset of the areas of endemism was assembled following Cracraft (1985), Ribas et al. (2012), Borges and Silva (2012) and Naka (2011)—Guyana, Pantepui, Napo, Inambari, Rondônia, Tapajós and Xingu. We measured the Euclidean distance to obtain geographical distance values between pairs of sites' centroids. Finally, we considered ecoregions outlined by Olson et al. (2001), which are derived from vegetation structure and composition of several biotic groups. A vectorised dataset with the delimitation of the ecoregions was downloaded from: <https://ecoregions2017.appspot.com/>.

2.4 | Species functional traits and phylogeny

To calculate functional β -diversity, we selected five functional traits of Neotropical bats commonly used in studies in the Neotropical region (Bogoni et al., 2021; Carvalho, Lourenço, et al., 2021): body mass, forearm size, trophic level, diet and habitat breadth (data available in <https://doi.org/10.6084/m9.figshare.14701728.v3>).

Body mass—There is a higher abundance of larger species, which have greater energy requirements (Castillo-Figueroa & Pérez-Torres, 2021), in more complex habitats, as these have higher food availability (Carvalho, Mustin, et al., 2021). Amazonian areas with nutrient-rich soils, higher temperatures and rainfall (climate

promote greater forest productivity (Toledo et al., 2010). Thus, we used the body mass of bats as a functional trait that may be a response to these environmental characteristics. We used body mass values in Gardner (2008), Reis et al. (2013), and Wilson and Mittermeier (2019). Logarithmic transformations were performed on body mass to normalise the values.

Forearm length—Forearm length is a proxy for dispersal ability, with bats that have longer forearms travelling longer distances (Jakobsson et al., 2020; Trevelin et al., 2013). Thus, this functional trait can help us to assess how rivers, ecoregions, areas of endemism and geographical distance influence the functional β -diversity of bat assemblages. We used forearm size from data from the literature and from individuals collected by us in the field.

Diet and trophic level—Diet and trophic level are closely associated with habitat use by bats, with carnivorous or animalivorous bats being strongly associated with more productive and complex habitats (Carvalho, Mustin, et al., 2021). Thus, diet and trophic level can help us see how soils, higher temperatures and rainfall (climate) influence the functional composition of bat assemblages. Diet was based on the main food item consumed by each species (carnivores, frugivores, insectivores, nectarivores, omnivores or sanguinivores; Alroy, 2017). Species that are not present in the Alroy database (2017—<http://ecoregister.org/>) were classified according to the closest congener (e.g. *Anoura fistulata* was placed together with the other species of *Anoura*). For trophic levels, the bats were classified as animalivores or phytophages (Giannini & Kalko, 2004).

Habitat breadth—This trait represents the level of habitat specialisation of a bat species (Bogoni et al., 2021) and is based on the number of habitat types in which a species occurs. We used the ecoregions delimited by Olson et al. (2001) as habitat types. The trait ranged from 1 (ecologically specialised species) to 25 (generalist species).

Phylogeny—For phylogenetic estimates, we used the most recent and complete species-level phylogeny of bats (<http://vertlife.org/phylosubsets>—Upham et al., 2019) as it covered most of the species in our database. For *Carollia* spp. and *Hsunitycteris* spp., we considered the phylogenetic data of the subfamilies, Carollinae and Lonchophyllinae, respectively, as this represents the most basal division within the branch of these genera. For *Platyrrhinus* spp., we considered the phylogenetic data for *Platyrrhinus brachycephalus*, one of the most basal species within that genus (Velazco & Lim, 2014).

2.5 | Data analysis

We performed all analyses first considering the entire Amazon biome, then considering only the Amazonian lowlands (sites equal or below 300 m a.s.l.), with the latter excluding the effect of the Amazonian mountain ranges (mainly the Andes). Studies have shown that bat richness and diversity decrease more markedly above 400–500 m a.s.l. along the mountain ranges of the South American rainforests, including the Andes (Bogoni et al., 2021; Carvalho, Martins, Esbérard, et al., 2019; Cisneros et al., 2014; Patterson et al., 1996).

To estimate β -diversity and its components, we followed the framework developed by Podani and Schmera (2011) and Carvalho et al. (2012). Therefore, to calculate the dissimilarity between bat assemblages, considering the entire Amazon biome and the Amazonian lowlands, we decomposed the taxonomic, phylogenetic and functional β -diversities into turnover (species/lineages/functions replacement or substitution) and species/lineages/function richness difference (owing to loss or gain of bat species/lineages/functions/), using Jaccard dissimilarity. The estimation and decomposition of β -diversity were conducted using the beta function of the R package 'BAT' (Cardoso et al., 2015). The β -diversity components were computed using rarefaction (1000 runs). For estimated functional traits matrices, Gower's distance can produce a multi-trait dissimilarity with a disproportionate contribution of certain traits, especially categorical and correlated traits (de Bello et al., 2021). To solve this, and obtain similar contributions of individual traits, we used the function *gawdis* from package 'gawdis' (de Bello et al., 2021). This function balances the different traits when computing multi-trait dissimilarities, finding weights that minimise the differences in the correlation between the dissimilarity of each single trait and the multi-trait one. Subsequently, the *gawdis*-based functional distance matrix was transformed into a functional tree to estimate the functional β -diversity (i.e. based on the distance between the terminal tips of the tree), just as the phylogenetic β -diversity is also based on a phylogenetic tree (Cardoso et al., 2014; Cardoso et al., 2015).

Before performing the regression analysis, we created Euclidean distance matrices for each predictor variable between pairs of sites and tested the correlation between the predictor variables to avoid collinearity. We applied the Pearson correlation test with a threshold of 0.7, because values above 0.7 indicate a weakened ability of the analysis to identify relevant factors (Tabachnick & Fidell, 1996). Only temperature and elevation presented correlations above 0.7, so we did not use temperature in further analyses. In our study area, the temperature varies in relation to the elevation, mainly in the high-altitude elevation of the Andean Amazon, and is not influenced by latitude (Casimiro et al., 2013). In the lowland areas (≤ 300 m a.s.l.) of the Amazon, the terrain elevation is also related to soil edaphic characteristics such as granulometry and soil nutrients (Schiatti et al., 2014). Therefore, elevation is the more appropriate variable to include in the analysis, as there is not much variation in temperature in the Amazonian lowlands.

To investigate the association of each predictor variable with taxonomic, phylogenetic and functional turnover and richness difference (components of β -diversity) of phyllostomid bats across the entire Amazon biome and in the Amazonian lowlands, we performed multiple regression on distance matrices (MRM). Additionally, we used hierarchical partitioning to calculate the independent contributions of each explanatory variable to taxonomic, phylogenetic and functional turnover. We only used turnover because it was the only β -diversity component that showed explanatory power with different significant predictor variables (see Results). Endemism areas and geographical distance and rivers were combined to form a 'geographical' predictor, while elevation, ecoregions, average precipitation and precipitation of the driest month were combined to form the

'environment' predictor. All analyses were conducted in programme R (R Core Team, 2021) using the 'rgdal' (Bivand et al., 2021), 'raster' (Hijmans, 2020), 'rgeos' (Bivand & Rundel, 2020), 'ecodist' (Goslee & Urban, 2020), 'vegan' (Oksanen et al., 2020) and 'FD' (Laliberté et al., 2014) packages. The R scripts are available in .share repository (<https://doi.org/10.6084/m9.figshare.14701728.v3>) under the CC-BY 4.0 license (free to use and distribute).

3 | RESULTS

At the level of the entire Amazon (considering all sites), taxonomic turnover (0.31 ± 0.19) and species richness difference (0.32 ± 0.21) had similar contributions to the value of taxonomic β -diversity (β -total = 0.64 ± 0.14 ; Figure 2). However, function and lineage richness difference contributed slightly more than turnover to functional (β -total = 0.40 ± 0.14 , turnover = 0.17 ± 0.12 , function richness difference = 0.23 ± 0.17) and phylogenetic β -diversity (β -total = 0.41 ± 0.14 , turnover = 0.17 ± 0.12 , lineages richness difference = 0.24 ± 0.17 —Figure 2). When we considered only those sites ≤ 300 m a.s.l., species richness difference (0.34 ± 0.22) contributed slightly more than turnover (0.27 ± 0.17) to the value of taxonomic β -diversity (β -total = 0.61 ± 0.14). The same relationship was found for phylogenetic β -diversity (β -total = 0.40 ± 0.15 , turnover = 0.15 ± 0.13 , lineage richness difference = 0.24 ± 0.17) and functional β -diversity (β -total = 0.38 ± 0.14 , turnover = 0.14 ± 0.11 , function richness difference = 0.24 ± 0.17 ; Figure 2).

At the level of the entire Amazon biome, only elevation was significantly related and had the higher explanatory power for taxonomic (10%) and functional (8%) turnover (Table 1; Figures 3 and 4). Average precipitation, geographical distance, areas of endemism and ecoregions were significantly related to taxonomic and functional turnover, but with low explanatory power (<2%) on the turnover of any of the three dimensions evaluated (Table 1). Phylogenetic turnover was significantly related to the same variables, except endemism, also with low explanatory power (<2%). Variables of precipitation of the driest month, soil nutrients and rivers were not significantly related to any dimension of the β -diversity (Table 1). When we removed the largest Amazonian mountain ranges, using only sites at elevations ≤ 300 m a.s.l., geographical distance, areas of endemism and ecoregions were significantly related to functional turnover, whereas only ecoregions were related to taxonomic, phylogenetic and functional turnover. However, all these predictors' variables had low explanatory power (<1%; Table 1).

Only geographical distance and areas of endemism were significantly related to species and function richness difference at the level of the entire Amazon biome, respectively (Table 2). At elevations ≤ 300 m a.s.l., geographical distance and areas of endemism were significantly related to species richness difference of the three dimensions of the β -diversity (taxonomic, phylogenetic and functional) (Table 2). However, all these predictors' variables, to the entire Amazon biome and at elevations ≤ 300 m a.s.l., had low explanatory power (<1%—Table 2 and Figure S1).

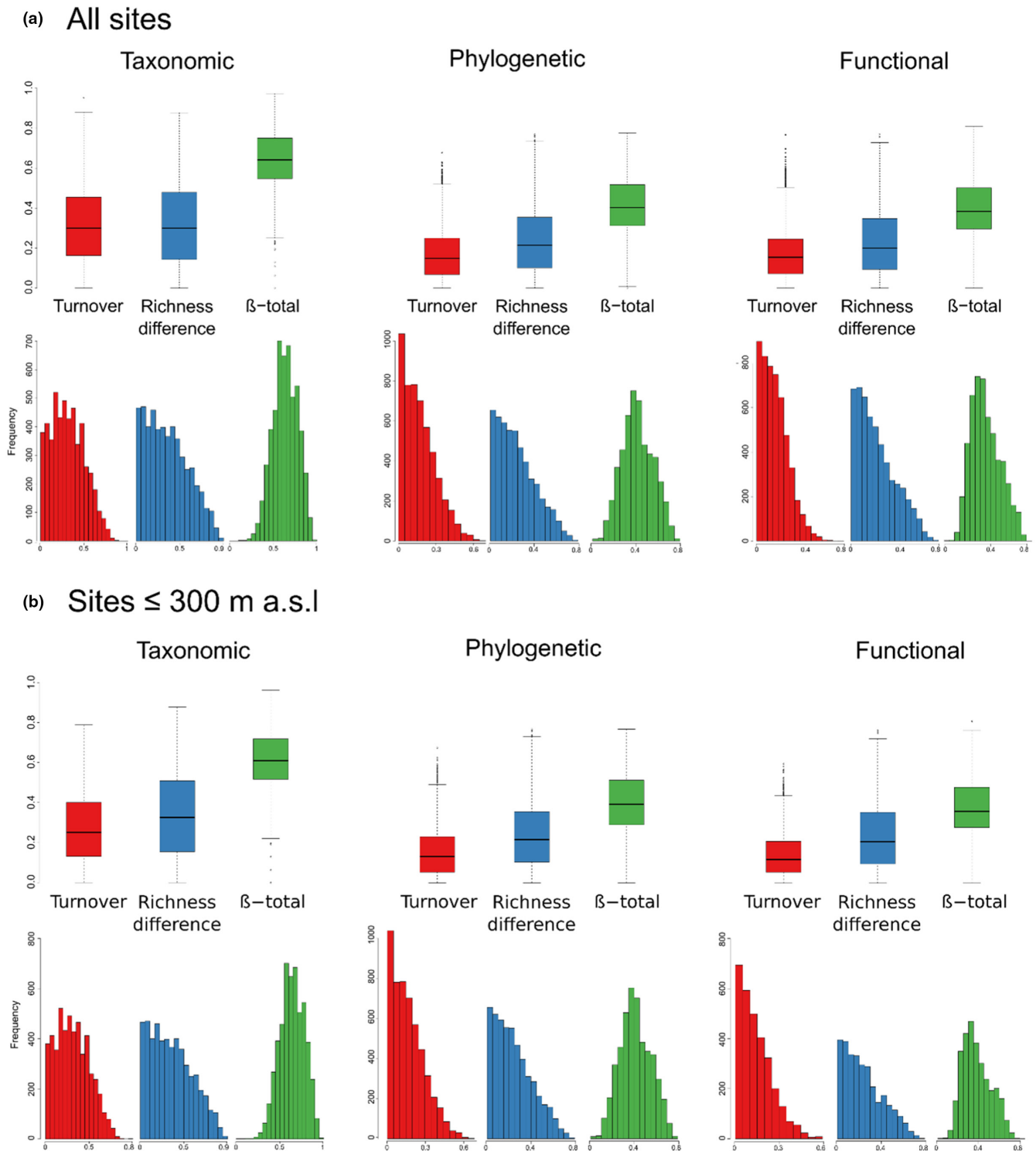


FIGURE 2 Boxplots and histograms representing relative values of turnover, richness difference and total β -diversity (β -total) pairwise values for taxonomic, phylogenetic and functional diversities considering bats in the entire Amazon biome (a) and for sites at ≤ 300 m a.s.l. (b). Boxplots represent the relative percentages among turnover, richness difference and total β -diversity; histograms represent the number of pairs of sites (Y-axis) for each value of turnover, richness difference and total β -diversity (X-axis).

Hierarchical partitioning showed that the isolated effect of the environment on taxonomic, phylogenetic and functional turnover is greater than the effect of variables related to dispersal limitation. Whereas the environment explained 9%, 3% and 7% of taxonomic, phylogenetic and functional turnover, the

dispersal limitation explained 1% of taxonomic, phylogenetic and functional turnover. The groups of variables (environment and dispersal limitation) shared 2%, 1% and 2% of explanation in taxonomic, phylogenetic and functional turnover, respectively (Table S1).

TABLE 1 Explanatory power (R^2) of the relationship between taxonomic, functional and phylogenetic turnover component of β -diversity, and predictor variables using multiple regression on distance matrices (MRM) analysis

Predictor variables	All sites			Sites $\leq 300\text{m}$ elevation		
	Taxonomic R^2	Functional R^2	Phylogenetic R^2	Taxonomic R^2	Functional R^2	Phylogenetic R^2
Average precipitation (bio12)	(+) 0.02**	(+) 0.01*	(+) 0.01*	0.007	0.0008	0.008
Precipitation of the driest month (bio14)	0.0002	<0.0001	0.0006	0.0006	0.001	<0.0001
Elevation	(+) 0.10***	(+) 0.08***	(+) 0.023*	0.004	0.002	0.005
Geographical distance	(+) 0.02***	(+) 0.01***	(+) 0.008***	0.003	(+) 0.004*	0.0006
Soil nutrients	0.002	0.001	<0.0001	0.008	0.003	0.002
Rivers	0.004	0.007	0.006	0.007	0.007	0.01
Areas of endemism	0.002*	0.002*	0.001	0.001	(+) 0.003*	0.0008
Ecoregions	(+) 0.008***	(+) 0.007**	(+) 0.004**	(+) 0.003*	(+) 0.004*	(+) 0.003*
All non-correlated variables	(+) 0.11***	(+) 0.08***	(+) 0.03*	0.013	0.01	0.008

Note: Results for the analysis carried out using all sites (102 sites encompassing 106 species) and only for sites at $\leq 300\text{m}$ a.s.l. (78 sites encompassing 87 species). The sign (-/+) in parentheses represents the direction of the effect of significant relationships. Variables which had correlation value less than 0.7 were included in a unique model. These variables were elevation, geographical distance, soil nutrients, areas of endemism and ecoregions and results are indicated in the last line of the table (All non-correlated variables).

***<0.001; **<0.01; *<0.05.

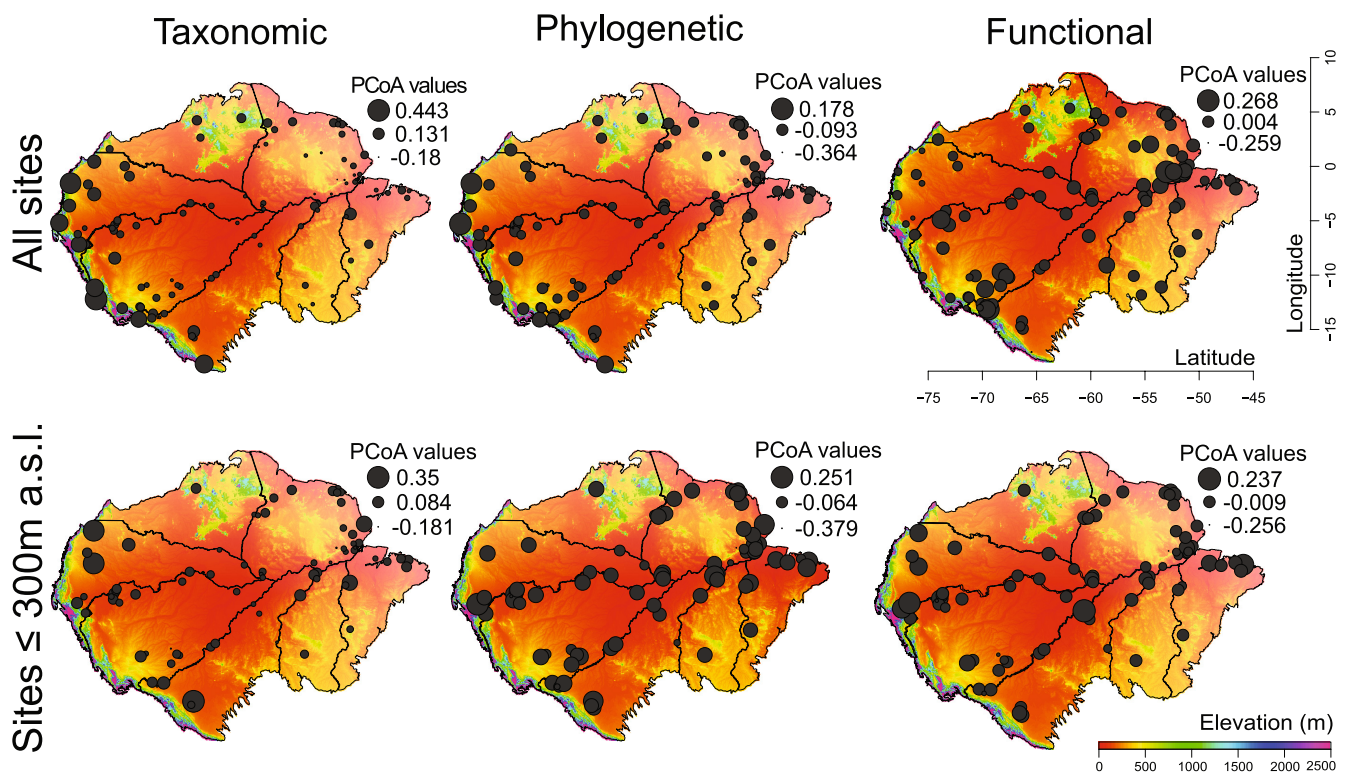


FIGURE 3 β -diversities in the Amazon across the elevational gradient for all sites ($n = 102$) and for sites at $\leq 300\text{m}$ a.s.l. ($n = 78$). To illustrate compositional differences among sites, we calculated the first PCoA axis summarising values of taxonomic, phylogenetic and functional turnover, and sized the circles accordingly. Circles with similar size correspond to sites with similar composition. The axes in the figure of the functional turnover considering the entire Amazon biome represent latitude (Y-axis) and longitude (X-axis).

4 | DISCUSSION

Our results using a wide database for phyllostomid bat assemblages throughout the Amazon biome indicate that turnover and species

richness difference contribute similarly to the total value of the taxonomic β -diversity. On the other hand, for the phylogenetic and functional dimensions, lineages and functions richness difference contributed slightly more than turnover to the total value of the

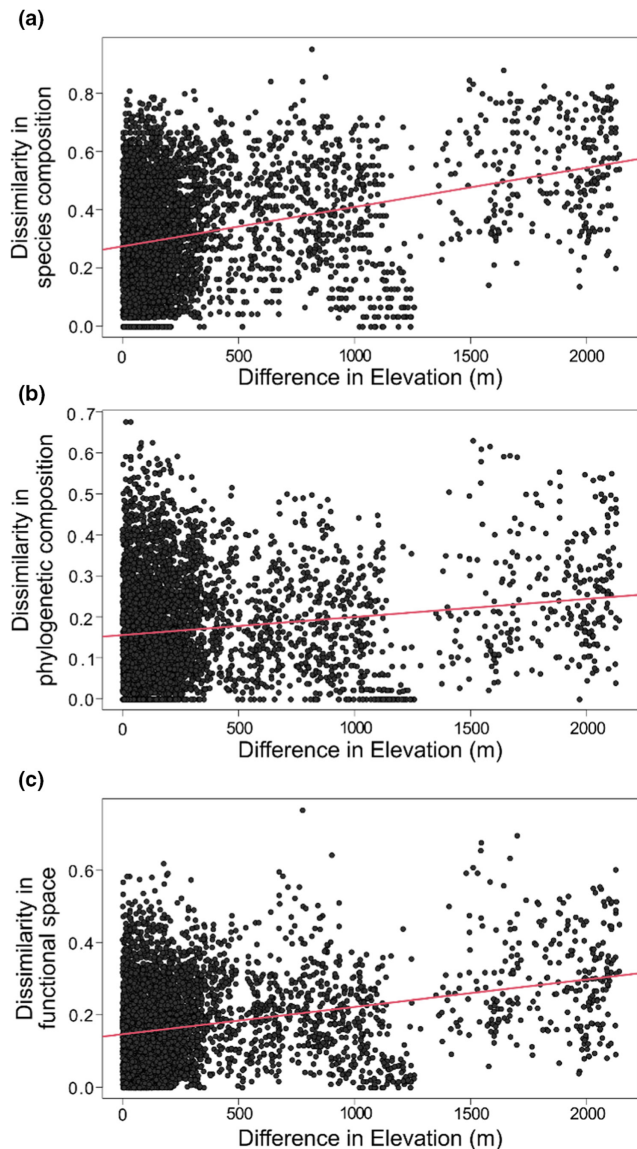


FIGURE 4 Relationship between (a) species, (b) phylogenetic and (c) functional dissimilarities (turnover component of β -diversity) of the bat assemblages in the Amazon in relation to elevation. The red line represents the slope of multiple regression on distance matrices (MRM) models carried out using all sites (102 sites encompassing 106 species): taxonomic: $1.35e-4$ ($p = 0.001$); phylogenetic: $4.41e-05$ ($p = 0.01$); functional: $7.56e-05$ ($p = 0.001$).

β -diversity. Also, when we considered only those sites ≤ 300 m a.s.l., richness difference contributed slightly more to the total value of all dimensions of β -diversity than turnover. For the entire Amazon biome, taxonomic and functional turnover of phyllostomid bats were more strongly related to elevation than to geographical barriers to dispersal (rivers and endemism areas). This result was also congruent when we evaluated the effects of environmental and dispersal limitation predictors, with the environmental predictor group explaining 9% and 7% of the taxonomic and functional turnover, respectively. However, when we only covered the lowlands, all predictors showed low predictive power to explain the dissimilarity of bat assemblage

in all diversity dimensions. This indicates that large mountain ranges impose higher rates of species replacement.

In accordance with our prediction, the highest levels of assemblage dissimilarity occur between sites in the lowlands and sites in the Andes, as taxonomic and functional turnover were driven by elevation. Some previous studies have highlighted the importance of elevation as an environmental filter for Neotropical bats (Batista et al., 2021; Carvalho, Martins, Esbérard, et al., 2019; Cisneros et al., 2014; Patterson et al., 1996; Stevens, 2013). At higher elevations, species that are more adapted to low temperatures replace other species that cannot reach higher elevations (species turnover), as they will have their own functional traits, such as optional torpor, longer and denser fur, greater capacity to use natural cavities and vertical migration (Carvalho, Martins, Dias, et al., 2019; Carvalho, Martins, Esbérard, et al., 2019; Espinoza, 2006; Soriano et al., 2002). Therefore, despite the occurrence of some cold-tolerant species in both the higher regions of the Andean Amazon and in lower areas (e.g. *Sturnira lillium* and *Anoura geoffroyi*—Audet & Thomas, 1997; Espinoza, 2006), the Andean Amazon tends to have an endemic bat fauna specialised to colder climates. As an indirect effect of temperature, vegetation species composition and structure changes with increasing elevation (Asner et al., 2014), which requires different flight abilities and presents different availability of resting sites and food for phyllostomid bats (Carvalho, Martins, Esbérard, et al., 2019). Furthermore, elevation also changes the relative abundance of bat food resources (Larsen et al., 2011; Quitián et al., 2018), which will also influence which species will occur in different elevation strata. Therefore, this greater occurrence of endemic species makes these bat assemblages different from those that occur in the Amazonian lowlands, driving the relationship we found between taxonomic turnover and elevation.

In contrast to taxonomic and functional turnover, phylogenetic turnover was poorly related to elevation, suggesting that a species replacement occurs between closely related species. For example, species adapted to low temperatures, such as *Sturnira bidens*, *Sturnira erythromos* and *Anoura latidens* (Espinoza, 2006; Soriano et al., 2002), are found only along mountains in the west and north of the Amazon biome. These species are replaced by close relatives (congenerics) in the warm lowlands (e.g. *Sturnira lillium* and *Anoura caudifer*). As with taxonomic turnover, we also did detect functional dissimilarity along the elevational gradient. This can be explained by the same mechanism of phylogenetic turnover—replacement of congeneric species with the same traits between the Andean Amazon (e.g. nectarivores—*Anoura latidens*) and the Amazonian lowlands (e.g. nectarivores—*Anoura caudifer*). In addition, the substitution of similar traits can also be found between genera. For example, frugivorous bats of the genus *Artibeus*, common in the lowlands, are replaced in the Andean Amazon by frugivorous species of the genus *Sturnira*. However, this functional redundancy throughout the Amazon biome may also be biased by the functional traits used in our analysis. The selected functional traits are widely distributed in Neotropical forests and are not specific to any type of environment. Other functional traits, such as vertical stratification, wing

TABLE 2 Explanatory power (R^2) of the relationship between species, functions and lineages richness difference component of β -diversity, and predictor variables using multiple regression on distance matrices (MRM) analysis

Predictor variables	All sites			Sites ≤ 300 m elevation		
	Taxonomic R^2	Functional R^2	Phylogenetic R^2	Taxonomic R^2	Functional R^2	Phylogenetic R^2
Average precipitation (bio12)	0.0007	~0	0.0001	~0	0.001	0.0004
Precipitation of the driest month (bio14)	~0	0.0001	0.0003	0.0003	~0	0.001
Elevation	0.003	0.002	0.0009	~0	~0	~0
Geographical distance	0.0003	(+) 0.0025*	0.001	(+) 0.004*	(+) 0.007**	(+) 0.004*
Soil nutrients	0.0001	0.0003	0.003	0.0002	~0	0.008
Rivers	0.002	0.005	0.0021	0.008	0.0116	0.01
Areas of endemism	(+) 0.002*	0.0017	0.001	(+) 0.005**	(+) 0.005*	(+) 0.005*
Ecoregions	0.0001	0.0003	0.0006	0.0004	~0	0.0001
All non-correlated variables	0.005	0.006	0.007	0.008	0.011	0.011

Note: Results for the analysis carried out using all sites (102 sites encompassing 106 species) and only for sites at ≤ 300 m a.s.l. (78 sites encompassing 87 species). The sign (-/+) in parentheses represents the direction of the effect of significant relationships. Variables which had correlation value less than 0.7 were included in a unique model. These variables were elevation, geographical distance, soil nutrients, areas of endemism and ecoregions and results are indicated in the last line of the table (All non-correlated variables).

** <0.01 ; * <0.05 .

morphology, echolocation call structure or metabolic characteristics, could indicate functional patterns associated with vegetation type (e.g. Aguirre et al., 2016), but were not feasible to measure in this study because we consider a very wide range of species that do not yet have other quantified functional traits. We suggest that future studies should focus on building a database including a diverse range of functional traits for bats, including traits of continuous values, and that can be constantly updated, especially for newly described species.

Rivers were significantly related to the β -diversity dimensions and components. However, this relationship received low support, indicating that only some interfluves differ from each other, possibly between distant interfluves as indicated by the positive relationship between turnover of all dimensions and geographical distance. The rearrangement of some tributaries of major Amazonian rivers in the late Pleistocene and Holocene suggests that these rivers were connected in the past (Ruokolainen et al., 2019). Possibly this will be repeated in the future because of the movement of tectonic plates. This connection, mainly in the extension between the Negro and Madeira rivers (Ruokolainen et al., 2019), may have allowed not only the dispersion of bat species through the tributary channel, but also the insects and plants that these bats consume. Therefore, our results contradict the theory that species distributions are strongly delimited by the great rivers, and areas of endemism delimited by rivers, in the Amazon (Wallace, 1854) and go against results from studies corroborating this theory using primates (Boubli et al., 2015; Fordham et al., 2020; Mourthé et al., 2022), terrestrial birds (Braga et al., 2022; Ribas et al., 2012; Silva et al., 2019) and bats (Silva et al., 2022). Bats have a high capacity of movement and displacement, and as a result these flying mammals relatively homogeneously occupy all of the Amazonian lowlands (Esbérard et al., 2017). Therefore, our results confirm that rivers are unlikely to delimit the distributions of animals with high dispersal capacity. Furthermore, considering that we used

an approach similar to Fluck et al. (2020), our results also suggest that the greater the dispersal capacity, the lesser the effect of rivers on species distribution along the Amazon biome. However, studies focusing on gene flow and historical processes of diversification must be carried out to better understand the importance of rivers in the evolutionary process of Chiroptera in the Amazon.

Contrary to what we expected, ecoregions had low predictive power for the β -diversity dimensions and components of phyllostomid bats. The low predictiveness of ecoregions indicates that different types of vegetation do not prevent the movement (Esbérard et al., 2017) nor promote environmental specialisation (Tuomisto et al., 2003) of these highly mobile mammals. Indeed, we have records of bats travelling over 100 km in less than 12 months across contrasting Amazonian habitats (between savannah and *terra firme* forest, in the state of Amapá, Brazil—unpublished data). In addition to ecoregions, areas of endemism also had low relative influence on taxonomic, functional and phylogenetic turnover. Thus, our results contradict other studies that used different data and scales and considered different ecoregions from those we considered here. For example, Tavares et al. (2017), Santos et al. (2019) and Silva et al. (2022) did not include many studies carried out in the Andes, and also used much larger scales to verify the differences and similarities between areas of endemism. Tavares et al. (2017) suggest another geographical pattern of Amazonian bats, with three major ecoregions (western Amazon, eastern Amazon and Guyana Shield), being later supported by other studies (see Santos et al., 2019; Silva et al., 2022). In addition, the lack of association with areas of endemism found here compared with previous studies may also reflect the inclusion of other Chiroptera families besides Phyllostomidae in their analyses (see Lim & Tavares, 2012; Santos et al., 2019; Tavares et al., 2017). Our result for areas of endemism may be linked to the difference in diversification between Chiroptera families throughout South America. The most distinguished centre of endemism in South



America is the Andes, mainly for the Vespertilionidae family (López-Aguirre et al., 2018; Patterson et al., 1996; Patterson et al., 2012). In addition, it has been suggested that the Phyllostomidae have a tropical origin around the Equator, with most species not presenting functional adaptations to the extremely low temperatures that occur in the high elevations of the Andes and higher latitudes (Ramos Pereira & Palmeirim, 2013). Future studies should focus on surveying Molossididae and Vespertilionidae data to test whether these biogeographical patterns are divergent or convergent within the Chiroptera.

When accounting for all sites, there was a positive effect, although weak, of the average precipitation on turnover of all β -diversity dimensions, but we found no support for the effect of precipitation of the driest month. However, neither average precipitation nor precipitation of the driest month had statistically significant effects on turnover in the lowlands. This can be explained by the availability of water in permanent water bodies throughout this continental biome which meets the water needs of bats. However, sites with high precipitation rates (>3000mm/year) can limit the bat flight and make thermoregulation difficult, acting as a filter for species. Many of these areas are located in humid altitude forests in Colombia. Water availability is expected to affect the presence and establishment of all organisms directly and indirectly (Hawkins et al., 2003). In fact, a seasonal (wet and dry season) effect on bat abundance, richness and diversity has been previously found throughout the natural habitats in the Amazon (Bobrowiec et al., 2014; Carvalho et al., 2018). However, it is possible that our two environmental variables related to the precipitation are not strong enough predictors of seasonality to determine the composition of bat communities at the scale we used. At this Amazonian scale, we were unable to assess the presence of permanent water bodies, which can only be assessed on a fine scale. For bats, it has been shown that water availability and permanent lakes are important for maintaining local diversity and foraging areas (Martins et al., 2022; Torrent et al., 2018), especially in the dry season (Torrent et al., 2018). Precipitation patterns may also affect the bat assemblage indirectly, through its effect on vegetation (Wang et al., 2011). However, changes in the vegetation may have been represented by other variables, such as elevation, soil nutrients, ecoregions and geographical distance.

Geographical distance had low predictive power for β -diversity dimensions and components for phyllostomid bats. In contrast to our results, Varzinczak et al. (2017) and Batista et al. (2021) showed that geographical distance is the main driver of taxonomic and phylogenetic diversity among bat assemblages in South America. However, these studies considered regions with greater latitudinal variation: the Neotropics (Varzinczak et al., 2017) and the Atlantic Forest (Batista et al., 2021). Latitude has a large influence on the similarities between bat assemblages, mainly due to the increase in climatic heterogeneity (temperature and precipitation—Stevens, 2013; Batista et al., 2021). Nevertheless, Dambros et al. (2020) corroborate our results for the Amazon biome and also found a low association between geographical distance and the composition of bat species. In the Amazon, climate (mainly temperature) differs in the east-west

direction at large scales, mainly in the extreme west in the Andes (Casimiro et al., 2013). Therefore, the low influence of isolation by geographical distance on phyllostomid bats in Amazon may be associated with the low latitudinal variation, which leads to low north-south climatic variation.

Our results indicate that the Andes are home to more species that are taxonomically and phylogenetically different from the lowlands of the Amazon. In addition, the Amazonian lowlands are taxonomically, functionally and phylogenetically homogeneous, that is, there is taxonomic, functional and phylogenetic redundancy between bat assemblages in these lowlands. However, this result should be cautiously interpreted: bats have a fundamental role in seed dispersal, pollination and insect population suppression, and the loss of species and functions may have irreversible consequences for the maintenance of ecosystems (Bobrowiec et al., 2022; Carvalho et al., 2020; Laurindo et al., 2019). The Amazon biome has suffered different human impacts such as increased deforestation, mining and infrastructure development, and this has increased in recent years in different countries (e.g. Carvalho, Mustin, Hilário, et al., 2019; Clerici et al., 2020). These impacts have already been widely studied on a local scale for bats along the Amazon biome (Bobrowiec et al., 2022; Bobrowiec & Tavares, 2017; Carvalho et al., 2020; Klingbeil & Willig, 2009; Martins et al., 2017; Rocha et al., 2018). Thus, our results indicating the low dissimilarity among bat assemblages in the lowlands at large scales does not mean that the loss of species due to anthropogenic threats is not harmful to the biome. Despite the sample gaps in the Amazon, even for the Phyllostomid family, which is the best sampled family of Chiroptera (Delgado-Jaramillo et al., 2020), our results are based on a wide and unprecedented database built from an extensive bibliographic review on the occurrence of phyllostomid bats in the Amazon biome. Here we show that species turnover and richness difference are components with similar contribution to total β -diversity among bat assemblages in the Amazon biome. Meanwhile, lineage and function richness differences are the most important components for the phylogenetic and functional dimensions of the total β -diversity. Beyond showing low influence of rivers, ecoregions, geographical distance and precipitation on species composition, we highlight that among several factors, elevation is the main determinant of taxonomic and functional turnover of phyllostomid bats when we consider the entire Amazon biome. These results might indicate that, for good dispersers, species specialisation along elevational/climatic gradients impacts species distribution more strongly than the presence of geographical barriers.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study (occurrence data, environmental and spatial variables and the R script) are openly available in 'figshare' at <https://doi.org/10.6084/m9.figshare.14701728.v3>.

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BIOSKETCH

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SUPPORTING INFORMATION

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