Journal of Animal Ecology

DR JULIANO ANDRÉ BOGONI (Orcid ID : 0000-0002-8541-0556)

DR VÍTOR CARVALHO-ROCHA (Orcid ID : 0000-0002-4747-1219)

Interacting elevational and latitudinal gradients determine bat diversity and distribution across the Neotropics

Juliano A. Bogoni[a,b], Vítor Carvalho-Rocha[a,c], Katia M. P. M. B. Ferraz[b], Carlos A. Peres[a]

[a] School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, Norwich, United Kingdom.
[b] Universidade de São Paulo (USP), Escola Superior de Agricultura "Luiz de Queiroz" (ESALQ), Departamento de Ciências Florestais, Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Piracicaba, SP 13418-900, Brazil.
[c] Programa de Pós-Graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil.
* Corresponding author: bogoni@usp.br

Abstract

New World bats are heavily affected by the biophysical setting shaped by elevation and latitude. This study seeks to understand the patterns of bat species diversity across elevational, latitudinal and vegetation height gradients throughout the Neotropics. Systematically gathered putative and empirical data on bat species distribution across the entire Neotropics were examined using descriptive statistics, spatial interpolation of bat taxonomic, functional and phylogenetic diversity, generalized linear models, generalized linear mixed models, and phylogenetic generalized least squares. We uncoupled the effects of elevation, latitude, and vegetation height to predict Neotropical bat diversity, showing that dietary level, home range, and habitat breadth were the most important ecological traits determining coarse-scale bat distributions. Latitude was largely responsible for sorting the regional species pool, whereas elevation appears to apply an additional local filter to this regional pool wherever tropical mountains are present, thereby shaping the structure of montane assemblages. Bats provide multiple ecosystem services and our results can help pinpoint priority areas for bat research and conservation across all Neotropics, elucidate the thresholds of species distributions, and highlight bat diversity hotspots at multiple scales.

Keywords: Chiroptera, diversity patterns, continental-scale, mammals, species distribution, tropical forest.

Introduction

A central tenet in ecology states that biodiversity distribution on Earth is neither uniform nor random (Soria-Carrasco & Castresana, 2012). Variation in latitude and elevation are widely recognized biogeographic gradients that profoundly influence multilevel patterns of species diversity worldwide (Willig & Bloch, 2006). Latitudinal influences on species diversity range from taxonomic components to functional traits and phylogeny (Buckley et al., 2010). Species diversity increase from polar to tropical regions (Willig et al., 2003; Hillebrand, 2004). To explain the high levels of tropical diversity, three main hypotheses have been posed: (1) the "Cradle hypothesis": the premise that there has been much higher diversification rates in tropical organisms; (2) the "Museum hypothesis": indicating low extinction rates near the Equator (i.e. the tropics tends to harbour "old" species); and (3) the "Destination hypothesis": the tropics has received high immigration rates, acting as a realm in which species originated elsewhere will eventually invade and accumulate (Stenseth, 1984; Rohde,

1992). Some of these explanations are circular, and high diversity across the tropics can be further attributed to higher energy input that virtually precludes an upper diversity limit (Rohde, 1992).

Several other leading hypotheses have been proposed to explain the latitudinal and elevational effects on species diversity and distribution, including the Rapoport's rule and Stevens' extension. Rapoport's rule describes the tendency of species geographic ranges to expand away from the equator, allowing more species to coexist at lower latitudes (Rapoport, 1975). Stevens' extension describes how so many species can coexist in the tropics and provides an analogous extension of the latitudinal Rapoport's rule to elevational gradients (Stevens, 1989; 1992). Further, habitat type and vegetation structure change across elevational and latitudinal gradients, inducing a nested influence on species composition that impose high turnovers for several taxonomic groups (Terborgh, 1977). Given that elevational gradients induce dramatic changes in abiotic factors, differences in elevational zones are also reflected in species trait evolution, persistence and phylogenetic histories (Brown, 2001).

The Neotropics hosts the most species-rich mammal fauna on Earth (Hershkovitz, 1958) and Neotropical bats (Mammalia: Chiroptera) are one of the most diverse groups of homeotherms in local vertebrate assemblages. The Chiroptera first appeared in the Eocene when they were already distinctive in the evolution of true flight (Jepsen, 1970), radiating widely into the Paleotropics and the Neotropics, where they comprise the second-largest order of mammals (Brosset, 1966). As many as 82 sympatric bat species can coexist at a single site (Patterson et al., 1996), with estimates of up to 117 sympatric bat species in some Brazilian regions (Delgado-Jaramillo et al., 2020). Earlier studies have shown that local Neotropical bat diversity is highest at low-elevation zones (e.g., Patterson et al. 1996; Stevens & Tello 2018), even if local assemblages exhibit high species turnover regionally (Batista et al. 2020), whereas continental to global bat diversity patterns are highest at low to mid-latitudinal regions (Stevens & Tello 2018).

Microchiropterans are the most species-rich mammalian suborder, representing over 18% of all extant mammal species (Simmons et al. 2005), and bats are the most ecologically radiated mammal taxon, making a disproportionally high contribution to local mammal species richness (Wilson, 1974). This reflects the fact that bat species occupy the vast majority of functional groups of all vertebrates, from hypercarnivores to strictly hematophagous (blood-feeding) species, and even

folivores (Eisenberg, 1981; Duque-Márquez et al. 2019). The widespread bat adaptive radiation directly reflects their ecomorphological functional traits, which can lead to high functional diversity within this group. Functional diversity is undoubtedly an important component of biodiversity, as it represents the difference in functional traits between organisms. However, measures of functional diversity depend on which life-history traits are considered (Tilman, 2001). Ecomorphological traits in bats are therefore associated with several ecosystem services (Kunz et al., 2011), and determine the guild structure of local assemblages across sharp environmental gradients, such as those in steep montains (Patterson et al. 1996).

The Neotropical realm encompasses a large proportion of bat diversity worldwide, since this biogeographic region hosts a myriad of habitat types, elevational zones, and a large latitudinal gradient, spanning 64° degrees (Feeley & Stroud 2018), generating dozens of biomes and hundreds of ecoregions (Olson et al. 2011). The Neotropics also contains the largest latitudinal cordillera on Earth: the Andes, and the tropical forest biome with the longest latitudinal gradient: the Atlantic Forest of South America. Although highly modified by human activity, the Atlantic Forest is an ideal biome in which to understand the distribution of bat diversity given that it is relatively well studied, including several data papers on mammal distribution (e.g., Muylaert et al. 2017). The Atlantic Forest biome encompasses a mix of lowland forest, montane kniferidges, (semi)deciduous plateaus, and highlands spanning some 40° of latitude, throughout which the bat fauna attains high levels of beta-diversity (Batista et al. 2020). However, the Atlantic Forest is one of the most threatened biomes in South America. The Atlantic Forest has been encroached by agricultural frontiers since early colonial times. This chronic and widespread primary habitat conversion has been historically overwhelming (Dean 1996). Once spanning over 1.1 million km^2, this tropical forest domain succumbed to the highest conversion rates in the highly agricultural semi-deciduous plateaus of interior regions and urbanized coastal areas, where forest cover is now restricted to only 28% (Rezende et al. 2018; for further details see Supporting Information S1). Despite this widespread habitat loss, both the Neotropical realm and the Atlantic Forest biome encompass a wide variation in forest and non-forest vegetation height, which conforms to ecoregion types, and serves as a proxy of aboveground phytomass, structural complexity, vertical stratification, available niche space and productivity. These are also correlated with both the biotic and functional diversity of ecosystems (Potapov et al. 2020).

Although several studies indicate an elevational-latitudinal (and consequently vegetational) driver of bat diversity and distribution, no study to date has explored this three-dimensional relationship at broad continental and biome scales. Thus, our goal here is to understand the main geoecological drivers of bat macrodistribution across the entire Neotropics. Specifically, we (1) depict and map the patterns of bat diversity (i.e., taxonomic, functional, phylogenetic, and assemblage-wide traits) across the Neotropics and the Atlantic Forest based on theoretical and empirical data on bat distributions; (2) evaluate if assemblage-wide average bat dietary modes track the patterns of environmental stress induced by elevational, latitudinal and vegetational gradients; (3) understand the patterns of bat species distribution — and consequently taxonomic diversity — across elevational and latitudinal gradients associated with vegetation height and their interactions at two broad spatial scales (i.e., continental and biome), while constraining bat distributions by ecomorphological traits and phylogeny; and (4) both map and explain the macroecological patterns of bat assemblage-wide metrics, such as mean body size.

We hypothesize that all measures of bat diversity follow both elevational and latitudinal gradient pattern across the Neotropics and the Atlantic Forest. However, bat species occupancy (consequently taxonomic diversity) across the elevational and latitudinal gradients depends on species dietary level, body size, wingspan, and home range size. For example, trophic level and body size are likely higher in more hostile conditions, whereas wingspan and home range size are likely greater in lowland areas at mid-latitudes. Bat distribution across the most extreme portions of the gradients depends on dietary modes that are typically depauperate, but on average energetically higher, at high elevations and latitudes. Basal metabolic rate (BMR) allometrically scaled to body size may enable the use of more hostile environments, and daily rates of dispersal ability (proxied by wingspan and home range size) may ensure movements across more heterogeneous landscapes. The decay in taxonomic diversity across elevational and latitudinal bands depends on these four ecomorphological traits, which are themselves driven by phylogeny.

Methods
Bat distribution

We systematically explored all assemblage-wide local bat studies across the Neotropics using search engines (e.g., Web of Science). This literature review was based on the grouping of several keywords such as: "bats (or Chiroptera, or volant-(flying-) mammals)" AND "distribution (or richness, or inventory)" AND/OR "assemblage(s) (or community(ies))". However, these studies were too patchy and insufficient in that few could be described as exhaustive inventories of local bat faunas. We therefore extracted 1,000 random putative bat assemblages within the Neotropics using IUCN polygons (IUCN 2018) to overcome this data limitation. Simple IUCN polygons generally overestimate species occupancy by assuming a 100% range filling, thereby overinflating local richness. However, severe Wallacean gaps in biodiversity knowledge can introduce a larger bias than the overfilling of IUCN polygons, given that most studies are undertaken at short distances (<12.5 km) from main roads and urban centers (Oliveira et al. 2017) thereby overinflating pseudo-absences. Thus, data on mammal occurrence derived from IUCN polygons have been widely used in conservation ecology studies (e.g., Schipper et al., 2008), and are appropriate for well-studied taxa such as mammals (Herkt et al. 2017). IUCN polygons also comprise the only available datasets with which putative assemblages can be constructed at continental to global scales (e.g., González-Maya et al. 2017).

We then organized the assemblage-level species-by-row data according to the contrast between presences and absences. For example, a species that is present at 300 of 1,000 sites should have 700 rows indicating local putative absences. This approach resulted in a 242,000-row dataframe for the entire Neotropics, once 242 species were present across any 1,000 random sites. For each row in the dataframe, the corresponding site was tagged for further trait co-variables and data analysis. We performed all data compilations using our purpose-made R script (R Core Team, 2021). We refer to this dataset as Neotropical putative-site-based dataset (hereafter, NPS). For the Atlantic Forest, we used the only empirical dataset available for any Neotropical biome (sourced from Muylaert et al., 2017), which consists of 205 sites sampled from 1991 to 2016, and gathers information on >90,000 captured individuals of 99 bat species. However, we again binarized the dataset and organized the data as species-by-rows, resulting in a 20,295-row data frame of empirical occurrences. We refer to this dataset as Atlantic Forest empirical-site-based dataset (hereafter, AFS).

Additionally — to avoid any pseudo-absences or pseudo-presences — we created a third dataset for the entire Neotropics based on a hexagonal grid system with cell size of 5,000-km^2 (43.87-km side; Earth equal-area projection), which we refer to as the Neotropical hex–cell grid (hereafter, NHG). This resulted in a computationally feasible number of 4,602 hex-cells. We then estimated the bat assemblage for each cell by superimposing IUCN polygons and considering any species as present if they intersected that hex-cell. We also estimated bat species richness as the species count at each hex-cell. Bat assemblages and richness were estimated using the R package *letsR* (Vilela & Villalobos, 2015).

Bat traits and phylogeny

For each bat species in our three datasets, we obtained four traits sourced from Jones et al., (2009) and Wilman et al., (2014): (1) adult body mass (g); (2) home range size (ha); (3) trophic level, weighting the proportion of each major dietary mode of any given species according to Bogoni et al., (2020); and (4) habitat breadth (sum of habitat layers). Moreover, we obtained a 5th trait (i.e., species wingspan [m]) via allometry of body size by functional groups or guilds (i.e. insectivores, frugivores, Molossidae and/or Vespertilionidae bats; see Norberg (1981) for equations). Missing information on species traits was completed with either the mode or average of the nearest taxonomic level, based on synapomorphy. The bat phylogeny was based on Jones et al., (2002) because this is the largest species list compared to other available phylogenies. We were forced to prune the original phylogeny to include only those species compatible with the alpha taxonomic nomenclature in each dataset.

Spatial co-variables

For each sites (NPS and AFS), we obtained detailed information on (1) geographic coordinates (longitude and latitude; decimal degrees); and (2) elevation (meters above sea level [masl]) derived from ASTER-GDEM (https://asterweb.jpl.nasa.gov/gdem.asp). In addition, we used GEDI-Landsat data (Potapov et al. 2020) and extracted the average vegetation height (m) at each site using a radial-buffer of 1.06-km for all sites across the Neotropics, and a radial-buffer of 2.03-km for sites across Atlantic Forest. These values represents the mean species home range size. We used Google Earth's Engine platform (code.earthengine.google.com) to extract the geographic coordinates (latlong

centroid), mean elevation, elevational range, and mean and standard deviation vegetation height of each hex-cell (NHG). We used the same elevation and vegetation height data as used for the sites-based.

Data analysis

For each scale of analysis (i.e., Neotropics and Atlantic Forest) and datasets (i.e., NPS, AFS and NHG), we explored the data according to classic diversity descriptors, such as taxonomic diversity (T_{Div}; richness) and variations thereof, including bivariate plots of T_{Div} per bat family in relation to elevation, latitude, and vegetation height. We also tested the hypothesis — based on the NPS and AFS datasets — that more hostile conditions are associated with a decrease in assemblage-wide trophic energy levels (e.g. high elevations and high latitudes derived in classes [e.g. 10° latitude and 1000 masl elevation]) using a Kruskal-Wallis test (Kruskal & Wallis 1952). We calculated the functional dispersion (F_{Dis}) as a proxy of functional diversity to represent and quantify the occurrence-weighted average dispersion of species from the occurrence-weighted center of gravity of all bat species in the overall multidimensional trait space (Fichaux et al., 2019). We derived the bat phylogenetic diversity (P_{Div}) for each site at both spatial scales. P_{Div} was obtained through an unrooted measure for sets of tips on the phylogeny sourced from Jones et al., (2002). This metric serves as a descriptor of evolutionary similarity between species (Huelsenbeck & Rannala, 1997). To develop these analyses, we used the R program (R Core Team, 2021) and the packages *FD* (Laliberté et al. 2014) and *PhyloMeasures* (Tsirogiannis & Sandel, 2017).

Given that we identified a spatial autocorrelation in these three levels of diversity [$M_{obs(TDiv)} = 0.11$; $M_{exp(TDiv)} = -0.01$; $p < 0.001$; $M_{obs(FDis)} = 0.09$; $M_{exp(FDis)} = -0.01$; $p < 0.001$; $M_{obs(PDiv)} = 0.13$; $M_{exp(PDiv)} = -0.01$; $p < 0.001$; and $M_{obs(TDiv)} = 0.10$; $M_{exp(TDiv)} = -0.01$; $p < 0.001$; $M_{obs(FDis)} = 0.10$; $M_{exp(FDis)} = -0.01$; $p < 0.001$; $M_{obs(PDiv)} = 0.11$; $M_{exp(PDiv)} = -0.01$; $p < 0.001$; for the NPS and AFS, respectively], we used a kriging interpolation approach (Cressie 1993) to derive a map of diversity indices across the Neotropics and the Atlantic Forest. For these datasets, we also predicted the number of bat species, F_{Dis}, and P_{Div} across the elevational-latitudinal contrast using 3D and bivariate plots. For predictions of bat T_{Div} from the NPS, we used a generalized regression model with a Poisson error on the variance (Chatterje et al. 2000). For the NPG dataset, we mapped the bat T_{Div}, F_{Dis}, and P_{Div} per

hex-cell, which were contrasted with the elevation and vegetation height maps. We also derived a map of assemblage-wide averages (and *sd*) of the five species traits across the Neotropics.

For the NPS and AFS, under a binomial distribution, we performed an *a priori* generalized linear mixed model **(**GLMM; Zuur et al. 2009) to obtain the intercepts for each bat species distribution according to the elevation, latitude and vegetation height gradients, using species as a random variable. Latitude geocoordinates are analysed as absolute latitude. Thus, we used the following models for both geographic scales: (1) presence/absence ~ elevation + (1 | species); (2) presence/absence ~ abs(latitude) + (1 | species); (3) presence/absence ~ vegetation height + (1 | species); and (4) presence/absence ~ elevation × abs(latitude) + vegetation height + (1 | species). We then used the intercepts of each bat species in a *post hoc* phylogenetic generalized least squares (PGLS) approach (Martins & Hansen 1997) given that the intercepts were the result of elevational, latitudinal and vegetational influences on each species derived from GLMM. The PGLS aimed to understand the trait effects constrained by species phylogeny on bat distributional responses. PGLS models consisted of: bat species intercept ~ traits (i.e. the five aforementioned traits, standardizing for data asymmetry through the *decostand* of the *vegan* R package [Oksanen et al. 2013]) + compatible phylogeny (previously pruned to 169 species (69.8%) for the NPS and 74 species (74.8%) for the AFS. For the NPS, we also re-run the PGLS analysis while removing home range size from the model to avoid any circularity. We performed these analyses in R version 4.0.2 (R Core Team 2021) based on the packages *lmer* (Bates et al. 2015) and *caper* (Orme et al. 2018).

For the NPG, we used multiple generalized linear models (GLM; Dobson 1990) to predict the variation on bat diversity metrics (T_{Div}, F_{Dis}, and P_{Div}) as a function of elevation, latitude, and vegetation height. To further improve our understanding on bat ecological variation across the Neotropics, GLM models were used to predict the hex-cell scale assemblage-wide averages of the five species traits. For both analyses, the model is defined as follows: response variable (e.g., T_{Div}) ~ average elevation + abs(latitude) + average vegetation height. To minimize spatial autocorrelation effects among the hex-cells, we performed each GLM 1,000-times by selecting at random set of 1,500 (*ca.* 1/3) of the 4,602 cells. The results therefore are presented as the average of 1,000-GLMs, focused on model intercepts and $R^2\text{-}_{adj}$ values. We performed these analyses in R, under a Poisson distribution for T_{Div} and used a Gaussian distribution for all other $\log_{10}$-transformed response variables, using the

lmer package (Bates et al. 2015). We also derived bivariate plots between assemblage-level metrics *vs.* latitude constrained by elevational bands (e.g., 0–1,000 masl, 1,001–2,000 masl) to uncover the distribution patterns of bat diversity and traits. For bat traits, we also derived bivariate plots between trait *sd* vs. latitude and elevation bands. Finally, we plotted all response variables *vs.* all predictors at the hex-cell in a correlation panel, using absolute latlong values and corrected all data asymmetry using $\log_{10} x + 1$.

Results

Patterns of bat diversity

Site-based approaches

Based on NPS (242 species across 1,000 sites), local bat T_{Div} was on average 37.67 ($\pm$ 23.41) species, ranging from 0 to 81 sympatric species. This level of diversity was widely distributed across the central plateaus and northwestern South America, as well as the central portion of Mesoamerica, but always declining in species richness farther away from the equator (Supporting Information S2A). Over three-quarters (78.5%) of all bat species were represented by phyllostomids and vespertilionids. F_{Dis} ($F_{Dis} = 0.126 \pm 0.04$) based on five ecomorphological traits showed less variability, and — similarly to P_{Div} ($P_{Div} = 87.35 \pm 48.9$) — was higher across the lowland Amazon (Supporting Information S2). Across the Atlantic Forest, T_{Div} was on average 12.25 ($\pm$ 7.73), ranging from 1 to 53 species, most of which concentrated in the southeast and northeast mesoregions (Supporting Information S2). Patterns of F_{Dis} and P_{Div} were similar to that of T_{Div}, sharing similar geographic patterns across the Atlantic Forest (Supporting Information S2). Point T_{Div} across the Neotropics broken down by bat family decreased in a similar pattern at increasingly higher elevations, except for verspertilionids.

Across the Atlantic Forest (99 bat species at 205 sites), the distribution of T_{Div} decomposed by bat family in relation to elevation, latitude, and vegetation height was highly variable, especially for phyllostomids and vespertilionids (Supporting Information S3). Average dietary level per local assemblage across the Neotropics was reduced at increasingly higher elevation bands and extreme latitudes, but increased in higher-stature vegetation (Supporting Information S4). These overall

patterns are significantly different for all three of these gradients [elevation: Kruskal-Wallis = 17.1; df: 4, p < 0.01; latitude: KW = 664.4; df = 6; p < 0.001; vegetation height: KW = 92.8; df: 2, p < 0.001]. These patterns were similar in the Atlantic Forest, but with more subtle changes in average dietary level retained per assemblage. There were statistical differences in average assemblage-wide trophic level across the Atlantic Forest elevation [KW = 16.7; df: 4, p = 0.02], latitude [KW = 42.7; df = 4; p < 0.001] and vegetation height [KW = 16.9; df: 2, p < 0.01].

Gridded patterns of diversity

Based on the NPG dataset (386 bat species at 4,602 hex-cells), the mean species richness (T_{Div}) was 57.8 (± 36.1), ranging from 0 to 130 species. Mean F_{Dis} was 0.133 (± 0.04) and the mean P_{Div} was 132.6 (± 68.8). These diversity metrics across the Neotropics were congruent with those obtained from the site-based approach, and following a latitudinal trend, with the highest diversity metrics at low elevations and more stratified vegetation. The northwestern region of South America, as well as Mesoamerica were the most megadiverse macroregions, but bat diversity declined monotonically away from the equator and at higher elevations (Fig. 1). Assemblage-wide mean (and *sd*) species trait maps revealed a clear decline further south than 30°S in all metrics, except for trophic level which showed an inverse pattern (i.e. increasing towards higher latitudes; Fig. 2).

Drivers of bat distribution across environmental gradients
Site-based approaches

For both the NPS and AFS, our GLMMs showed that bat species distributions are negatively affected by elevation [Neotropics: z-value = –40.40; p < 0.001; Atlantic Forest: z-value = –6.95; p < 0.001], and therefore the local species packing that defines alpha diversity. Our predictions revealed that an elevation range up to 1,000 masl on average encompasses between 6% and 10% of all species (from 14.5 to 24.2 species of all 242; Fig. 3A). Bat species distribution across the elevational gradients further declined from 2% to 0% (from 4.8 to 0 species) in elevation ranges above 4,500 m.a.s.l. (Fig. 3A). Across the ~2,000 masl Atlantic Forest elevation gradient, we observed similar effects on species richness (Fig. 3D). The overall effect of latitude on bat species distribution was also

negative [Neotropics: z-value = –22.14; Atlantic Forest: p < 0.001; z-value = 3.50; p < 0.001]. Peak latitudinal diversity was observed at the equator, on average encompassing up to 29 (12%) of all species, but gradually declining at either side of the equator to 20°S and 20°N, to an average of 4.8 (~2%) species (Fig. 3B). The AFS also revealed this latitudinal effect, but with a wider confidence interval, reaching a diversity peak of 6.4 bat species at ~30°S (i.e., on average 6.3% of the 99 species; Fig. 3E). Vegetation height had an overall positive effect on the species distribution across both the Neotropics [z-value = 62.62; p < 0.001] and the Atlantic Forest [z-value = 4.80; p < 0.001], with higher species diversity increasingly taller vegetation across both geographic scales (Fig. 3C and Fig. 3F). Models based on the joint elevational-latitudinal gradient revealed that elevation was more important than latitude in determining any measure of local bat diversity (Supporting Information S5), with an overall effect on T_{Div} of 0.728, compared to an effect size of 0.299 for latitude (Supporting Information S6). Our modelled results showed that T_{Div} at 54°S declined by 63.2% at very high elevations (i.e., projected to 4,900 m.a.sl.), compared to the same latitude at sea level. This reduction in species richness at the equator (44.8% of all species; $S_{sea\ level}$ = 46.1; $S_{upper\ elevation}$ = 23.1 species) was comparable with that at 30°N (49.9% of all species; $S_{sea\ level}$ = 51.3; $S_{upper\ elevation}$ = 28.4; Supporting Information S7).

GLMM predictions based on the combination of fixed effects revealed weaker effects on species distribution and diversity across the Neotropics than any single fixed effect [z-value$_{(interaction)}$ = –12.50; p < 0.001; z-value$_{(vegetation)}$ = –7.5; p < 0.001], indicating the pivotal effect of latitude [z-value$_{(latitude)}$ = –87.12; p < 0.001] and the absence of a continental-wide elevation effect [z-value$_{(elevation)}$ = –0.22; p = 0.82]. Species random effects were also widely variable (Supporting Information S8). Based on the AFS, the combined effect of elevation and latitude was stronger than either one of these two variables in isolation [z-value$_{(interaction)}$ = –12.50; p < 0.001; z-value$_{(elevation)}$ = 10.27; p < 0.001; z-value$_{(latitude)}$ = 8.87; p < 0.001; z-value$_{(elevation)}$ = 4.89; p < 0.001], while random effects on species also varied widely, with phyllostomids and vespertilionids comprising 75% of the top 20 most-influential species (Supporting Information S9). The *post hoc* PGLS examining species intercepts across the Neotropics indicated that bat home range size and habitat breadth — controlled for species phylogeny — significantly predicted the random effects on species derived from elevation, latitude, the interaction between elevation and latitude, and vegetation height (Fig. 4; Supporting

Information S10). When removing species home range size, we found that trophic level significantly explained the species intercepts [t = 2.63; p = 0.02; t = 2.62; p = 0.02; t = 2.61; p = 0.02; and t = 2.62; p = 0.02; for elevation, latitude, vegetation height, and the interactive model, respectively]. Home range size, habitat breadth and trophic level had positive influences on species distribution across the elevation ranges (maximum minus minimum), latitude and vegetation height gradients (Supporting Information S11). Considering only the Atlantic Forest, we were unable to identify any ecomorphological trait that could meaningfully predict the effects of predictors and their interaction on distribution and diversity (Supporting Information S10).

Hex–grid approach

Consistent with occurrences at the site scale, diversity mapped at the ~5,000-km^2 scale showed that elevation, latitude and vegetation height affected almost all assemblage-wide metrics. GLMs showed a wide range in explanatory power in terms of T_{Div} [R^2-$_{adj(average\ over\ 1,000\ GLMs)}$ = 0.722], F_{Dis} [R^2-$_{adj(average)}$ = 0.466], P_{Div} [R^2-adj$_{(average)}$ = 0.659], average body mass [R^2-$_{adj(average)}$ = 0.253], home range size [R^2-$_{adj(average)}$ = 0.142], trophic level [R^2-$_{adj(average)}$ = 0.02], wingspan [R^2-$_{adj(average)}$ = 0.100], and habitat breadth [R^2-$_{adj(average)}$ = 0.154]. The intercepts of all three predictive variables had significant influences on the variation in bat diversity (typically at p < 0.001 and showed negative trends; Fig. 5). Bivariate plots evidenced the non-linear trends of these relationships, especially between T_{Div}, F_{Dis}, P_{Div} and assemblage-wide mean home range size in relation to latitudinal bands constrained by elevational bands. There was also a more rapid decline in bat diversity at elevations higher than 3,000 masl and latitudes lower than 20°S (Fig. 6). The influence of latitude constrained by elevational bands was more evident in the assemblage-wide standard deviation of bat traits (Supporting Information S12). A correlation panel evidenced all residual effects on bat diversity and trait metrics, given that we also detected an additional negative relationship between mean home range size and elevation range, and a positive relationship between P_{Div} and vegetation height *sd* (Supporting Information S13).

Discussion

Understanding and disaggregating the causal effects of elevation and latitude on the geography of biological diversity is a central challenge in macroecology and biogeography. A few studies have shown the pivotal role of elevation gradients in determining bat diversity, including divergent effects on different bat guilds (Patterson et al., 1996), as seen in other homeotherm vertebrate taxa (Presley et al. 2011). While the upper distribution boundaries of individual bat species are determined by environmental tolerance (Presley et al. 2011), a global meta-analysis found both a decreasing pattern and mid-elevation peaks in bat diversity (McCain, 2007). By stressing the relationships between the combined elevation and latitude effects on bat faunas at continental and biome scales based on multiple datasets, we showed that terrain-elevation along Neotropical latitudinal bands was far more important than latitude *per se* in determining any measure of bat diversity. However, the latitudinal gradient was the main determinant of overall bat distribution, occupancy and mean assemblage-wide trait profiles.

These relationships depend primarily on where montane areas and elevational gradients are located across the latitudinal zones. For instance, the NPS revealed that low-latitude bat species richness at high elevations (i.e. 10° S and 3,000–4,000 m.a.s.l.) was twice as high as at the same elevational range at 30° S. Likewise, in low to mid elevation areas (<2000 m.a.s.l.) at 30° S latitude, bat richness was three times greater than high elevation areas (>2000 m.a.s.l.) at a comparable latitude. Meanwhile, geographic effects on species distributions at any lowland site (<1000 masl) could either increase or decrease by 40.1%, depending on latitudinal position. Thus, latitude was largely responsible for sorting the regional species pool, whereas elevation appears to apply an additional local filter to this regional pool wherever tropical mountains are present, thereby shaping the structure of montane assemblages. Subtropical to temperate species pools at latitudes higher than 30° N or S is ~60% smaller than that near the equator. Elevational effects on diversity at mid to high latitudes is apparently more severe. This may be partly explained by the existence of already a depauperate regional species pool, which contains fewer species traits that predispose high tolerance for, among other things, climatic extremes induced by the double-whammy of high latitude and high elevation. These conditions may also be amplified by vegetation structure, herein typically comprised of shrublands and grasslands that can restrict the spectrum and availability of critical resources, such as roosting sites and food.

These site-scale patterns are reinforced by the NHG. Bat taxonomic diversity declined by ~50% from –10°S to –20°S at average elevations above 3,000 masl compared to the same elevation near the equator, whereas the same reduction of ~50% were observed at–35°S when average elevations were below 2,000 m.a.s.l. (see Fig. 1 and Fig. 6A). Similar patterns were found for bat phylogenetic diversity (Fig. 6B), which were not influenced by elevational effects *per se* (Fig. 5), whereas bat functional dispersion increased at higher elevations (Fig. 6C), due to (i) lower species richness, and (ii) higher trait divergence between species pools (Fig. 2). Assemblage-wide trait means, on the other hand, showed a more subtle change (Fig. 6), been influenced by both latitude and vegetation, but not elevation (Fig. 5). These results indicate that latitude is an important determinant of trait profiles, but given the wide variation in elevation within hex-cells (which ranged from 0 to 6,276 m), the overall effects of elevation on bat assemblages can only be captured at site-scale. Our results further confirm the importance of elevation, given that the variances in assemblage metrics were clearly congruent at high elevations (Fig. 2), inducing higher functional dispersion (Fig. 6B).

Site-based assemblage-wide average dietary energy levels in Neotropics and Atlantic Forest bat faunas changed according to elevational, latitudinal and vegetation structure gradients. Once phylogeny was constrained, the main ecomorphological traits that are apparently sensitive to the triple effects of elevation-latitude-vegetation were species habitat breadth and home range size. The distribution of taxonomic diversity grouped by family also manifested a similar pattern. One exception was the Vespertilionidae, which are mainly comprised of low-flying insectivores (Patterson et al. 1996) that reach their species richness peak at higher elevations and higher latitudes than all other bat families. Whereas, leaf-nose bats (Phyllostomidae), the most diverse family of volant or nonvolant mammals in terms of dietary guilds (Patterson et al. 1996), showed a reverse pattern of richness across the Atlantic Forest compared to Vespertilionidae. The two most speciose Neotropical bat families thus illustrate a key dissimilarity in continental-scale distributions; while vespertilionids persist as important components of bat assemblages even in highly stressful environments, phyllostomids are more strictly restricted to lower elevations and/or latitudes.

Putative occurrences of bat species across these major environmental gradients were further explained by habitat breadth and home range size, indicating that geographic occupancy is filtered by both habitat specificity and spatial requirements across the landscape. Our results showed that species

distribution ranges across all three environmental gradients was positively related with greater habitat breadth constrained by phylogeny. Habitat breadth represents the spectrum of habitat types that any species can occupy across the wider geographic range (Jones et al., 2009), indicating the degree to which species specialize on habitats and resources, and the functional influence of any given species on different habitats (Cooke et al. 2019). This is an important ecological descriptor, given that provides a measure of how ecologically specialized or generalized any species is, and may reflect its evolutionary longevity, speciation rates, and long-term range expansion and contraction (Simpson 1953). Although the number of species and functional guilds became increasingly reduced in high-latitude regions (cf. Stevens 2004), our results show a disproportionate influence of elevation, latitude, and vegetation stature on the dominant bat families.

The Neotropical latitudinal gradient encompasses a vast continental landmass characterized by a wide variety of macro-, meso- and micro-habitat types, and this also applies to elevational ranges in montane areas. Therefore, satellite imagery-derived vegetation height is an excellent proxy of vegetation structure across all biomes — from evergreen rainforests to dry deserts — that contain the most species-rich terrestrial vertebrate fauna on Earth (Olson et al. 2011; Feeley & Stroud 2018). On the other hand, home range size is a strong proxy of spatial requirements that is related to wing morphology, and hence the dispersal capacity of different species (Tello & Stevens 2010; Luo et al. 2019). Rates of species-specific site occupancy largely covary with geographic range size, which are affected by dispersal limitations in moving between different habitats (Gaston 2003). In bats, this is strongly related to aerodynamics, patterns of flight locomotion, and foraging behaviour (Norberg 1981). At the continental scale, larger home ranges were positively related to the spectrum of latitude, elevation and vegetation height a species could occupy in all three scales of analysis. Further, hex-grid cells revealed a latitudinal effect on virtually all community-averaged bat traits. Yet we failed to identify any trait-based determinant of bat occupancy across the Atlantic Forest. This could be explained by the more limited extent of this biome, and the fact that only a small fraction of local bat faunas currently persists in the Atlantic Forest, given that bats are highly sensitive to high rates of environmental degradation (Jones et al. 2003). Further, bat assemblages operate under four dimensions of rarity, from locally abundant and widespread to locally scarce and range-restricted

species (see Arita 1993). This is relevant to the Atlantic Forest scale where local bat inventories presumably missed many rare species.

Contrary to our expectations, we largely failed to reveal a direct and explicit relationship between wingspan and species distribution across the geoecological gradients examined here. The large confidence interval found around the higher estimate compared to other traits (see Fig. 4) may be more strongly related to families or functional groups, given that there is strong phylogenetic conservatism in some traits (Norberg 1981). This is despite the non-significant effect of diet on the metabolism of phyllostomid bats (Cruz-Neto et al. 2001). Yet there was a significant negative effect of latitude and vegetation stature on community-averaged wingspan. We also expected an overall effect of body size on latitudinal and altitudinal distribution, given that body mass is related to BMR in mammals, even if constrained by phylogeny (Cruz-Neto & Jones 2006). Although body size was not a decisive predictor of species distribution in the site-scale analysis, there was a clear spatial pattern of increasing trophic levels and smaller mean body size in high-latitude and/or high-elevation and habitats. We expect that bats feeding on flying insects are more likely to persist at high latitudes or high elevations, given that the full spectrum of bat prey will be more restricted at hostile climatic and habitat conditions (Stevens et al. 2003). For instance, bird species richness declines much faster at increasingly higher elevations in the Peruvian Andes in generalist and specialist insectivores than in frugivores of comparable sizes (Terborgh 1977). Our hex-cell maps indicate that bat assemblages at higher latitudes or high elevations were smaller-bodied and operated at higher trophic levels, indicating that these challenging environments are associated with species with faster metabolism.

Furthermore, the spectrum and amount of available trophic resources are important determinants of local species richness (Stevens 2004). Species traits can predict species-specific persistence and tolerance to unfavourable habitat conditions, particularly in Neotropical microchiropterans, given their wide diversification in ecomorphological and physiological traits. We showed that dietary profiles of bat assemblages varied predictably with elevation, but we cannot confirm whether the metabolic pace of low-latitude lowland bat faunas is on average slower than in birds (Wiersma et al. 2007). However, average trophic-energy levels of lowland assemblages at <1000 m.a.s.l. was only 3.6% lower than those at higher altitudes (>1000 m.a.s.l.), whereas assemblage-averaged energy levels peaked between 30°S and 30°N, increasing at similar rates at

greater distances north and south of the equator. This is apparently congruent with forest birds for which metabolic expenditure does not differ along a 2,600-m elevation gradient in the Peruvian Andes (Londoño et al. 2014). Compared to assemblages at higher elevations, are trends in trait profiles of lowland bat faunas primarily driven by intrinsically lower thermoregulatory costs, reduced fecundity due to more intense competitive and/or predation arenas, or lower requirements for seasonal altitudinal migrations? Although we cannot resolve these questions here, food resource types, including flying and non-flying insects and lower-energy food items, such as fruit pulp and nectar, are available all year-round at lowland sites, but decline in diversity and abundance with increasing elevation, particularly above a certain threshold (Stevens et al. 2003).

A similar pattern occurs in relation to vegetation height. Vegetation height is a good proxy of vertical stratification and habitat heterogeneity, and our results show that high-stature vegetation sites host assemblages exploiting resources at higher trophic levels. However, these patterns were unapparent in the Atlantic Forest biome. One explanation could be due to insufficient community-wide composition data because of severely incomplete inventories, habitat degradation, or both. The Atlantic Forest is one of the most severely altered tropical biomes, with only ~12% of its original vegetation cover remaining, most of which isolated in fragments smaller than 50 ha (Ribeiro et al. 2009). This is further reflected in high levels of regional-scale mammal defaunation (Bogoni et al. 2018). By the 1980s, only two South American bat assemblages — in the Caatinga and edaphic Cerrado of northeast Brazil — had been intensively studied (Willig 1986). Local bat faunas in the Amazon and semi-arid Caatinga-Atlantic Forest transition are now known to be very species-rich (e.g., Faria et al. 2006), and could pack as many as 100 sympatric species (Delgado-Jaramillo et al. 2020). However, there is an inherent sampling artefact related to vegetation height in that forest canopy and aerial bats are often poorly sampled in forest sites, whereas many more species are feasibly captured in low-stature vegetation of open-habitat biomes. Thus, a strong comparative analysis at site-scale of bat community ecology still await additional quasi-exhaustive studies (Willig 1986).

The patterns of cross-scale diversity examined here show progressively fewer species occurring at both higher elevations and higher latitudes right across the Neotropics. Globally, local bat species richness declines rapidly above a certain elevation threshold, and this threshold increases

monotonically from the tropics to the temperate zone (McCain, 2007). Overall, the spatial distribution of bat diversity metrics was congruent between the entire Neotropics and the Atlantic Forest, with the highest diversity concentrated in the northwest Amazon (a high priority macroregion for inventories; see Aguiar et al. 2020) and the southeast and northeast mesoregions of the Atlantic Forest, which coincide with bat endemism centers. However, patterns of beta-diversity change with the scale of analysis. For example, climatic factors in the Atlantic Forest have a strong influence on the distributional pattern of bats, and changes in precipitation and temperature alter the configuration of beta-diversity components across this biome (Batista et al. 2020). These patterns could be affected by stochastic or deterministic species assembly processes from available species pools (Willig 1986), such as amount and quality of food (Stevens et al. 2003), and this depends on the spatial grain along the latitudinal gradient (Sreekar et al. 2018).

To further explain bat distribution and community assembly, data deficiency on species physiological and behavioural traits should also be addressed. Explaining these macrodistributional patterns should also take into account shelter and roost requirements, which become particularly important for microchiropterans under stressful hypothermic conditions. New World bats often have very species-specific roosting requirements that cannot be violated, which clearly determine marginal (micro)habitat tolerances. For instance, some Amazonian bats only roost inside arboreal termite nests or large leaves (e.g. tent-making bats; Voss et al. 2016), and thereby depend on specific co-occurrences with plants and social insects. Lateral or long-range migrations are also an underlining factor in bat habitat occupancy (Fleming & Eby 2003; Arnone et al. 2016), as many species expand and contract their latitudinal and altitudinal ranges seasonally. Lateral and altitudinal migration is apparently more common in bats than previously thought (see McGuire & Boyle 2013), but unfortunately these idiosyncrasies cannot be captured by existing macroecological data.

Our understanding of the primary drivers of continental-scale variation in tropical bat diversity and distribution remains at best patchy. Whereas latitudinal patterns for some bat clades are clear (e.g. Noctilionoidea; see Stevens and Tello 2018), the evidence on elevational effects remains concentrated into a few landscapes (e.g. Patterson et al. 1996). Our results identify coarse-scale geographic thresholds of elevation and latitude in explaining both the diversity and distribution of Neotropical bats, including the ecomorphological and phylogenetic constraints that lead to observed patterns.

These insights are based on both putative and empirical data obtained by different approaches across two distinct, but vast geographic scales across the Neotropics. This enabled us to conclude that latitude is a key determinant of the regional species pool, whereas elevation applies an additional local filter onto the available regional biota wherever montane areas occur. This also determines the local to geographic distribution of individual species, given that the combined elevation-latitude-vegetation filters are sensitive to species life-history traits and evolutionary history. Given that bats provide multiple ecosystem functions (e.g. pollination, seed dispersal, and nutrient transport) and services (e.g. insect pest suppression) (Bogoni et al. 2020), our results can usefully pinpoint priority areas for bat conservation. Our insights further indicate that bat distribution and diversity patterns are multifactorial and highly dependent on the geography of environmental stressors.

Conflict of interest

The author(s) declare no competing interests.

Data Availability Statement

Data used here are available from IUCN range polygon (https://www.iucnredlist.org/resources/spatial-data-download) and a data paper (Muylaert et al. 2017; https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2007). Data analysis scripts are available as Supporting Information (see Supporting Information S14).

Authors' contributions statement

JAB: conceptualization, data acquisition, data analysis, writing & revising the original draft; VC-R: data acquisition & revising the original draft; KMPMBF: revising the original draft; CAP: conceptualization, revision & major editing.

References

Aguiar, L.M.S., Pereira, M.J.R., Zortéa, M., & Machado, R.B. (2020). Where are the bats? An environmental complementarity analysis in a megadiverse country. *Diversity and Distributions, 26*, 1510–1522.

Arita, H.T. (1993). Rarity in Neotropical Bats: Correlations with Phylogeny, Diet, and Body Mass. *Ecological Applications, 3(3)*, 506–517.

Arnone, I.S., Trajano, E., Pulchério-Leite, A., & Passos, F.C. (2016). Long-distance movement by a great fruit-eating bat, *Artibeus lituratus* (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica, 16(1),* e0026.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48.

Batista, C.B., Lima, I.L., & Lima, M.R. (2020). Beta diversity patterns of bats in the Atlantic Forest: How does the scale of analysis affect the importance of spatial and environmental factors? *Journal of Biogeography, 48, 1–10*.

Bogoni, J.A., Pires, J.S.R., Graipel, M.E., Peroni, N., & Peres, C.A. (2018). Wish you were here: How defaunated is the Atlantic Forest biome of its medium- to large bodied mammal fauna? *PLoS ONE,* 13(9), e0204515.

Bogoni, J.A., Peres, C.A., & Ferraz, K.M.P.M.B. (2020). Effects of mammal defaunation on natural ecosystem services and human well being throughout the entire Neotropical realm. *Ecosystem Services*, *45*, 101173.

Brosset, A. (1961). La Biologie des Chiroptères. Masson. Paris.

Brown, J.H. (2001). Mammals on mountainsides: elevational patterns of diversity. *Global Ecology & Biogeography, 10*, 101–109.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B. et al. (2010). Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B*. doi:10.1098/rspb.2010.0179.

Chatterjee, S., Hadi, A.S. & Price, B. (2000). Regression Analysis by Example. 3rd ed., John Wiley & Sons, New York.

Cooke, R.S.C., Bates, A.E., & Eigenbrod, F. (2019). Global trade-offs of functional redundancy and functional dispersion for birds and mammals *Global Ecology and Biogeography, 28,* 484–495. Doi: 10.1111/geb.12869

Cressie, N.A.C. (1993). Statistics for Spatial Data. Revised Edition. John Wiley & Sons, Inc.

Cruz-Neto, A., Garland, T., & Abe, A.S. (2001). Diet, phylogeny, and basal metabolic rate in phyllostomid bats. *Zoology, 104(1)*, 49–58. doi: 10.1078/0944-2006-00006.

Cruz-Neto, A., & Jones, K.E. (2006). Exploring the Evolution of the Basal Metabolic Rate in Bats. In: Zubaid, A., McCracken, G.F., Kunz, T.H. (eds.). Functional and Evolutionary Ecology of Bats. Oxford University Press. pp: 56–89.

Dean, W., 1996. With Broadax and Firebrand: The Destruction of the Brazilian Atlantic Forest. University of California Press, California.

Delgado-Jaramillo, M., Aguiar, L.M.S., Machado, R.B., & Bernard, E. (2020). Assessing the distribution of a species-rich group in a continental-sized megadiverse country: Bats in Brazil. *Diversity and Distributions*, *26*, 632–643.

Dobson, A.J. (1990). An Introduction to Generalized Linear Models. Chapman and Hall.

Duque-Márquez, A., Ruiz-Ramoni, D., Ramoni-Perazzi, P., & Muñoz-Romo, M. (2019). Bat Folivory in Numbers: How Many, How Much, and How Long? *Acta Chiropterologica, 21(1)*, 183–191.

Eisenberg, J.F. (1981). The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behaviour. The Athlone Press Ltd. London, UK.

Faria, D., Laps, R.R., Baumgarten, J., & Cetra, M. (2006). Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. *Biodiversity and Conservation, 15*, 587–612.

Feeley, K.J. & Stroud, J.T. (2018). Where on Earth are the "tropics"? *Frontiers of Biogeography, 10(2),* e38649. doi: 10.21425/F5101-238649.

Fleming, T.H., & Eby, P. (2003). Ecology of bat migration. In: Kunz, T.H., & Fenton, M.B., eds. Bat Ecology. Chicago: University of Chicago Press. pp 156–208.

Fichaux, M., Béchade, B., Donald, J., Weyna, A., Delabie, J.H.C., Murienne, J., Baraloto, C., & Orivel, J. (2019). Habitats shape taxonomic and functional composition of Neotropical ant assemblages. *Oecologia, 189*, 501-513. doi: 10.1007/s00442-019-04341-z.

Fraser, E.E., McGuire, L.P., Eger, J.L., Longstaffe, F.J., & Fenton, M.B. (2012). Evidence of Latitudinal Migration in Tri-colored Bats, Perimyotis subflavus. *PLoS ONE, 7(2)*, e31419. doi:10.1371/journal.pone.0031419.

González-Maya, J.F., Martínez-Meyer, E., Medellín, R. & Ceballos, G. (2017). Distribution of mammal functional diversity in the Neotropical realm: Influence of land-use and exticton risk. *PloS One*, *12(4),* e0175931.

Hershkovitz, P. (1958). A geographic classification of Neotropical mammals. Chicago natural history museum. *Fieldiana Zoology, 36*, 581–620.

Herkt, K.M.B., Skidmore, A.K. & Fahr, J. (2017). Macroecological conclusions based on IUCN expert maps: A call for caution. *Global Ecology and Biogeography, 2017*, 1–12. doi: 10.1111/geb.12601.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist, 163*, 192–211.

Huelsenbeck J.P. & B. Rannala. (1997). Phylogenetic methods come of age: testing hypotheses in an evolutionary context. *Science, 276,* 227–232.

IUCN (2018). Spatial data download: Mammals. Available at: http://www.iucnredlist.org/technicaldocuments/spatial-data#mammals. Accessed: June-11-2018.

Jepsen, G.L. (1970). Bats origins and evolution. In: Biology of bats. Wimsatt, W.A. (ed.) New York Academic Press. pp: 1–64.

Jones, K.E., Purvis, A., MacLarnon, A., Bininda-Emonds, O.R.P., & Simmons, N.B. (2002). A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews of the Cambridge Philosophical Society*, 77, 223–259.

Jones, K.E., Purvis, A., & Gittleman, J.L. (2003). Biological Correlates of Extinction Risk in Bats. *The American Naturalist, 161(4),* 601–614.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., et al. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology, 90(9),* 2648.

Kruskal, W.H., & Wallis, W.A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association, 47,* 583–621 and errata, ibid. 48, 907–911 (1952).

Kunz, T.H., Torrez, E.B., Bauer, D., Lobova, T., & Fleming, T.H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, *1223*, 1–38.

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Londoño, G.A., Chappell, M.A., Castañeda, M.R., Jankowski, J.E., & Robinson, S.K. (2014). Basal metabolism in tropical birds: latitude, altitude, and the 'pace of life'. *Functional Ecology, 29(3)*, 338–346.

Luo, B., Santana, S.E., Pang, Y., Wang, M., Xiao, Y., & Feng, J. (2019). Wing morphology predicts geographic range size in vespertilionid bats. *Scientific Reports, 9*, 4526. https://doi.org/10.1038/s41598-019-41125-0.

Martins, E.P., & Hansen, T.F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist, 149,* 646–667.

McCain, C.M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography, 16,* 1–13.

McGuire, L.P., & Boyle, W.A. (2013). Altitudinal migration in bats: evidence, patterns, and drivers. *Biological Reviews, 88*, 767–786.

Muylaert, R.L., Stevens, R.D., Esbérard, C.E.L., Mello, M.A.R., et al., (2017). Atlantic bats: a dataset of bat communities from the Atlantic Forests of South America. *Ecology, 98(12)*, 3227–3227.

Norberg, U.M. (1981). Allometry of bat wings and legs and comparison with bird wings. *Philosophical Transactions of the Royal Society B, 292,* 359–398.

Oksanen J., Blanchet G., Kindt R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. (2013). Vegan: Community Ecology Package. R package version 2.0-7. http://CRAN.R-project.org/package=vegan.

Oliveira, U., Soares-Filho, B.S., Paglia, A.P., Brescovit, A.D., et al., (2017) Biodiversity conservation gaps in the Brazilian protected areas. *Scientific Reports, 7*, 9141.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., et al. (2011). Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience, 51(11)*, 933–938.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 1.0.1. https://CRAN.R-project.org/package=caper.

Patterson, B.D., Pacheco, V., & Solari, S. (1996). Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology, 240,* 637–658.

Patterson, B.D., Willig, M.R., & Stevens, R.D. (2003). Trophic Strategies, Niche Partitioning, and Patterns of Ecological Organization. In: Kunz, T.H., & Fenton, M.B. Bat Ecology. University of Chicago Press. pp: 536–579.

Potapov, P., Li, X., Hernandez-Serna, A., Tyukavina, A., et al. (2020). Mapping and monitoring global forest canopy height through integration of GEDI and Landsat data. *Remote Sensing of Environment*, 112165. https://doi.org/10.1016/j.rse.2020.112165.

Presley, S.J., Cisneros, L.M., Patterson, B.D., & Willig, M.R. (2011). Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds. *Global Ecology and Biogeography,* 10.1111/j.1466-8238.2011.00738.x.

R Core Team (2021). R: A language and environment for statistical computing: Vienna, Austria: R Foundation for Statistical Computing.

Rapoport, E.H. (1975). Areografía. Estrategias Geográficas de las Especies. Fondo de Cultura Económica, México.

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., et al. 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation*, 16(4): 208-214.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., & Hirota, M.M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation, 142,* 1141–1153.

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for primary cause. *Oikos, 65*, 514–527.

Sreekar, R., Katabuchi, M., Nakamura, A., Corlett, R.T., et al., (2018). Spatial scale changes the relationship between beta diversity, species richness and latitude. *Royal Society Open Science, 5,* 181168. http://dx.doi.org/10.1098/rsos.181168.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., et al. (2008). The Status of the World's Land and Marine Mammals: Diversity, Threat, and Knowledge. *Science, 322*, 225–230.

Simmons, N. B., Wilson, D. & Reeder, D. (2005). Order Chiroptera. In Mammal species of the world (eds Wilson, D. E. & Reeder, D. M.). Smithsonian Institution Press. pp 312–529.

Simpson, G.G. (1953). The major features of evolution. Columbia University Press, New York.

Soria-Carrasco, V., & Castresana, J. (2012). Diversification rates and the latitudinal gradient of diversity in mammals. *Proceedings of the Royal Society B, 279*, 4148–4155. doi:10.1098/rspb.2012.1393.

Stenseth N.C. (1984). The tropics: cradle or museum? *Oikos, 43*, 417–420.

Stevens, G.C. (1989). The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *The American Naturalist, 133*, 240–256.

Stevens, G.C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist, 140(6)*, 893–911.

Stevens, G.C. (1996). Extending Rapoport's rule to pacific marine fishes. *Journal of Biogeography*, 23, 149–154.

Stevens, R.D., Willig, M.R. (1999). Size assortment in New World bat communities. J. Mammal. *80*, 644–658

Stevens, R.D. (2004) Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. *Journal of Biogeography, 31,* 665–674.

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters, 6,* 1099–1108.

Stevens, R.D., Tello, J.S. (2018). A latitudinal gradient in dimensionality of biodiversity. Ecography 41: 2016–2026.

Tello, J.S., Stevens, R.D. (2010). Multiple environmental deter-minants of regional species richness and effects of geographic range sizes. Ecography 33: 796–808.

Terborgh, J. (1977). Birds species diversity on an Andean elevational gradient. *Ecology, 58*, 1007–1019.

Tilman, D. (2001). Functional Diversity. *Encyclopedia of Biodiversity, 3*, 109–121.

Tsirogiannis, C., & Sandel, B. (2017). PhyloMeasures: Fast and Exact Algorithms for Computing Phylogenetic Biodiversity Measures. R package version 2.1. https://CRAN.R-project.org/package=PhyloMeasures.

Vilela, B. & Villalobos, F. (2015) letsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*, 6, 1229-1234.

Voss, R.S., Fleck, D.W., Strauss, R.E., Velazco, P.M., & Simmons, N.B. (2016). Roosting Ecology of Amazonian Bats: Evidence for Guild Structure in Hyperdiverse Mammalian Communities. *American Museum Novitates, (3870),* 1–43.

Wiersma, P., Muñoz-Garcia, A., Wlaker, A., & Williams, J.B. (2007). Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences, 104(22)*, 9340–9345.

Willig, M.R. (1986). Bat community structure in South America: a tenacious chimera. *Revista Chilena de Historia Natural, 59*, 151–168.

Willig, M.R., Kaufman, D.M., & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics, 34*, 273–309.

Willig, M.R., & Bloch, C.P. (2006). Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. *Oikos, 112*, 163–173.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology, 95,* 2027–2027. doi: 10.1890/13-1917.1.

Wilson, J.W. (1974). Analytic zoogeography of North American mammals. *Evolution, 28*, 124–140.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., & Smith, G.M. (2009). Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Figures

Fig. 1. Geographic patterns of bat diversity metrics (A: Taxonomic diversity; B: Functional dispersion; C: Phylogenetic diversity) and their respective predictors (D: Average elevation; E: Elevational range; F: Average vegetation height; G: Standard deviation in vegetation height) examined across 4,602 hexagonal cells (of 5,000-km^2 in area) throughout the Neotropical realm (NHG dataset).

Fig. 2. Geographic patterns of average (A to E) and standard deviation (F to J) values of five bat species traits explored in this study across the Neotropics (NHG approach). Assemblage-wide values are based on bat species defined as present within each of the 4,602 hexagonal cells (5,000-km^2 area) derived from IUCN range maps.

Fig. 3. Effect size derived from generalized linear mixed models (GLMMs) explaining bat species distributions across the (A) elevational, (B) latitudinal, and (C) vegetation height gradients based on 1,000 sites distributed throughout the Neotropics (NPS dataset). Comparable effect sizes of (D) elevation, (E) latitude, and (F) vegetation height on bat species distributions throughout 205 sites across the Atlantic Forest biome (AFS dataset).

Fig. 4. Bat species traits constrained by phylogeny, which was used to explain the beta intercepts derived from the each GLMM model via phylogenetic generalized least squares (PGLS) models based on 1,000 random bat assemblages distributed throughout the Neotropics (NPS dataset).
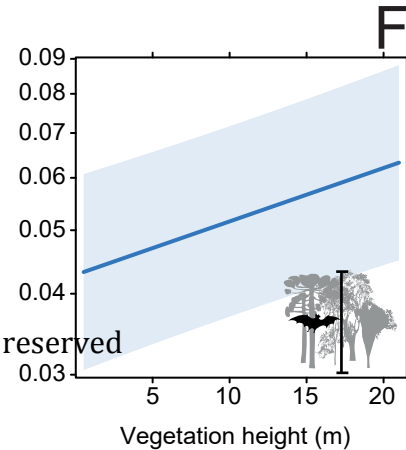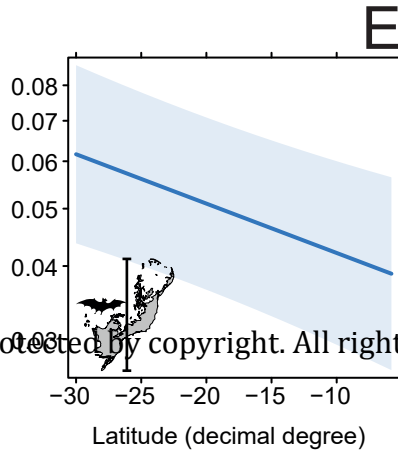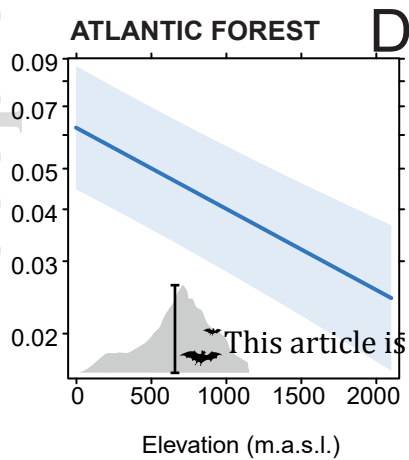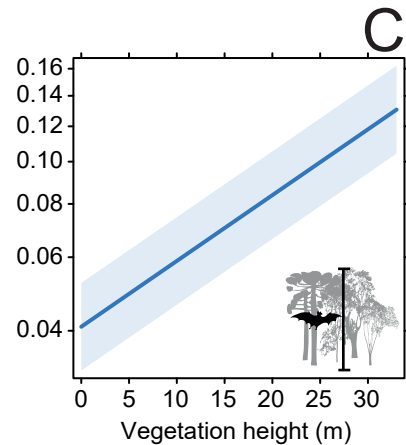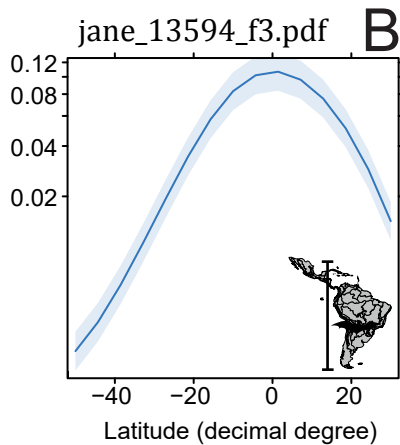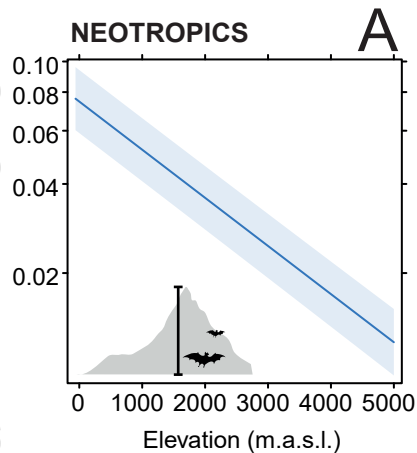
Fig. 5. Assemblage-wide responses in relation to elevation, latitude and vegetation height derived from GLM models based on 4,602 hexagonal cells (5,000-km^2 area) overlapping the entire Neotropical realm (NHG dataset). Significant relationships, for which 95% confidence intervals do not have a null estimate, are highlighted by an asterisk. Mean estimates are colour-coded top to bottom from most positive to the most negative coefficients.

Fig. 6. Bivariate plots between assemblage-wide metrics — taxonomic diversity (T_{Div}; A), functional dispersion (F_{Dis}; B), phylogenetic diversity (P_{Div}; C), assemblage-wide mean body mass (D), mean home range size (E), mean trophic level (F), mean wingspan (G), and mean habitat breadth (H) — and latitude constrained by elevational bands based on 4,602 hexagonal cells (5,000-km^2 area) across the Neotropics (NHG dataset).
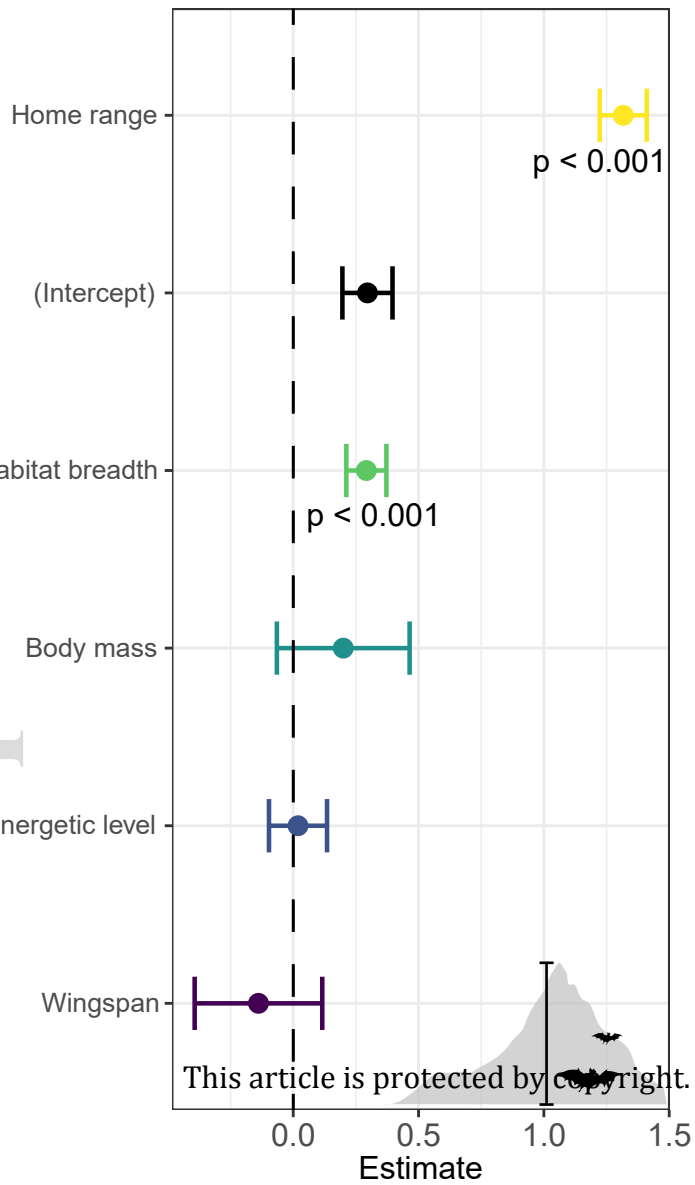
Model: elevation + abs(lat) + vegetation height