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# Traits that allow bats of tropical lowland origin to conquer mountains: Bat assemblages along elevational gradients in the South American Atlantic Forest

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## Abstract

**Aim:** This study aims to contribute to the identification of ecological determinants of tropical moist forest montane biodiversity, analysing changes in the structure of bat assemblages along an elevational gradient and testing the role of species traits shaping those assemblages.

**Location:** Mountain ranges in the Brazilian Atlantic Forest.

**Methods:** We compiled a dataset with the composition of phyllostomid bat assemblages at 32 forested sites, ranging from 60 m to 1,960 m a.s.l. We quantified how abundance and diversity changed along this elevational gradient, and assessed the capacity of each species to be present and abundant at each elevation, identifying traits that may influence that capacity.

**Results:** Abundance and species diversity declined markedly with increasing elevation. Tolerance to low temperatures, low habitat specialization and cave roosting facilitated success at higher elevations. Owing to trait filtering, and to changes in resource availability with elevation, assemblages were progressively dominated by a smaller number of mostly generalist species as elevation increased. Higher elevations harbour only a subset of the species that are present in the lowland forest, with no mountain specialized species.

**Main conclusions:** High mountains harbour phyllostomid assemblages that are impoverished subsets of those at lower elevations. Phyllostomids have a tropical origin and may thus have a low potential to adapt to montane forest environments, which possibly explains the observed climatic trait filtering. Habitat filtering is also important, keeping forest specialists mostly at lowest elevations. Protected areas in the Atlantic Forest are mostly limited to mountains. While these areas are clearly important to protect biodiversity, including phyllostomid assemblages, it is now critical to protect and restore the few remnants of lower elevation Atlantic Forest where higher productivity and resource levels, increased complexity of vertical structure, and fewer climatic constraints favour the success of a wider range of phyllostomid bat species of tropical origin.

## KEYWORDS

Brazil, Chiroptera, elevation, Mantiqueira Mountains, mountain conservation, phyllostomid bats, Serra do Mar Mountains, tropical animal ecology



## 1 | INTRODUCTION

Mountainous regions are very important for the preservation of the world's biodiversity, and indeed many are considered biodiversity hotspots (Körner & Ohsawa, 2005) and conservation priorities (Le Saout et al., 2013). The importance of these regions is likely to increase in the future because habitat destruction is still the main threat to biodiversity (Pereira, Navarro, & Martins, 2012) and steep terrain offers some protection against habitat destruction, as human occupation and use for agriculture are more difficult here (Silva, Metzger, Simões, & Simonetti, 2007). The second most extensive mountain range in South America is the chain of mountains that make up the eastern edge of the Brazilian Highlands. They were once mostly covered by Atlantic Forest, an ecosystem that also dominated the adjacent lowlands, but which has been virtually wiped out (Costa et al., 2009; Joly, Metzger, & Tabarelli, 2014; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Atlantic Forest remnants represent only c. 7.5% of the original extent and are mostly located on mountainous terrain (Costa et al., 2009; Joly et al., 2014; Ribeiro et al., 2009). Despite this dramatic decline, the region still harbours an extremely rich biodiversity, and a recent study included five of its protected areas amongst the sites with the greatest irreplaceability value globally for the conservation of terrestrial vertebrates (Le Saout et al., 2013).

The great conservation value of tropical mountain areas in general, and of those in the Atlantic Forest region in particular, make it important not only to adequately describe how the structure of species assemblages varies along elevational gradients, but also to understand the ecological factors underlying those variations. In fact, this understanding may also shed light on the potential effect of those factors on species assemblages across latitudinal gradients at continental scales.

Bats of the family Phyllostomidae are a good model to study these issues because they are a speciose and often locally abundant group that includes species with a very broad range of life histories (Gardner, 2008; Stevens, 2013). This is well expressed in the great diversity of their diets, which includes nectarivory, frugivory, insectivory, carnivory, piscivory, haematophagy and omnivory (Schnitzler & Kalko, 1998). The family has a Neotropical origin (Teeling et al., 2005) and, together, its more than 200 species range across most of the tropical and subtropical regions of the Americas (Fenton & Simmons, 2015).

A number of studies have described how bat richness and abundance vary along elevational gradients, including some in tropical regions (see McCain, 2007 for a review). These include descriptions and discussions of the changes in the structure of bats assemblages across elevational gradients in the Andes (Cisneros et al., 2014; Graham, 1990; Patterson, Pacheco, & Solari, 1996; Soriano, 2000; Willig & Presley, 2016) and in the Brazilian Highlands (Dias, Esbérard, & Peracchi, 2008; Esbérard, 2004; Martins et al., 2015; Moras, Bernard, & Gregorin, 2013; Nascimento, 2007). Moreover, Cisneros et al. (2014) tested competing theories to explain those elevational

changes in assemblage structure, comparing the level of dispersion in several functional traits across the elevational gradient. They concluded that both competitive exclusion and abiotic filtering are likely to be barriers to species richness in high elevation areas, which suggests that species traits are involved in the shaping of their assemblages. However, to our knowledge no studies have tested the role of individual species traits as determinants of the capacity of bats to persist in high tropical mountain ranges, that is their ability to thrive in the distinct climatic and biological conditions prevailing there. This information on the role of specific traits is critical to understand the mechanisms influencing the patterns of montane biodiversity, but is still surprisingly scarce for most types of organisms (Graham et al., 2014).

The overall objective of this study is thus to contribute to the understanding of the ecological determinants of tropical rainforest montane biodiversity, combining and analysing original and literature data on phyllostomid bat assemblages in mountains within the Atlantic Forest region. We first determined how species composition, richness and abundance changed in assemblages along the elevational gradient and then attempted to identify some of the mechanisms explaining the observed patterns by testing the potential role of several traits as determinants of the capacity of species to persist, and thrive, in montane forest. The evaluated traits include trophic guild, wing shape, wing loading (WL), body mass, use of underground roosts, independence of continuous forest (ICF) and latitudinal range. Finally, the conservation consequences of our results are discussed.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study area is in the moist Atlantic Forest region of South Eastern Brazil, between 21 and 24°S. We limited the selection of sites to this three-degree band to avoid the potentially confounding effects of the changes in environmental conditions along broad latitudinal gradients (Ramos Pereira & Palmeirim, 2013). Remnants of Atlantic Forest patches in this region are mainly located on three coastal ranges—Serra do Mar, Serra da Mantiqueira and Chapada das Perizes. Here, forest usually extends up to c. 2,000 m, above which high-elevation grasslands predominate (Ururahy, Collares, Santos, & Barreto, 1983).

We used capture data from surveys that sampled bat assemblages with mist nets in Atlantic Forest remnants. In addition to our own data, included in the database of Laboratório de Diversidade de Morcegos (LADIM) do Instituto de Biologia da Universidade Federal Rural do Rio de Janeiro (UFRRJ), we searched for surveys in the thesis database of CAPES (<http://www.capes.gov.br/servicos/banco-de-teses>), in the Scientific Electronic Library Online—SciELO (<http://www.scielo.org>) and in the Web of Science database—WoS (<http://www.webofknowledge.com>). Only the family Phyllostomidae was used, not only because it is the most diverse, but also because bats of other families are better at avoiding mist nets and thus tend to

be poorly represented in surveys (Marques, Ramos Pereira, & Palmeirim, 2016).

We compiled surveys with adequate information on location and capture effort for 32 forested sites located from 60 to 1,960 m a.s.l. (Figure 1, Table 1). In the case of studies in which nets were placed in the same area but at multiple sites across a small range of elevations, we used the average of the site elevations. When geographical coordinates of the study sites, but not elevation, were available, we obtained the latter using Google Earth®. For some analyses, we pooled the data in 500 m elevational bands. The number of survey sites per elevational band varied between 7 and 10, and the number of captures between 339 and 3,446 (Tables 1 and 2). We estimated the approximate capture effort at each site by multiplying the number of mist nets used by the number of sampling nights and the numbers of hours during which the nets remained open each night (Table 1).

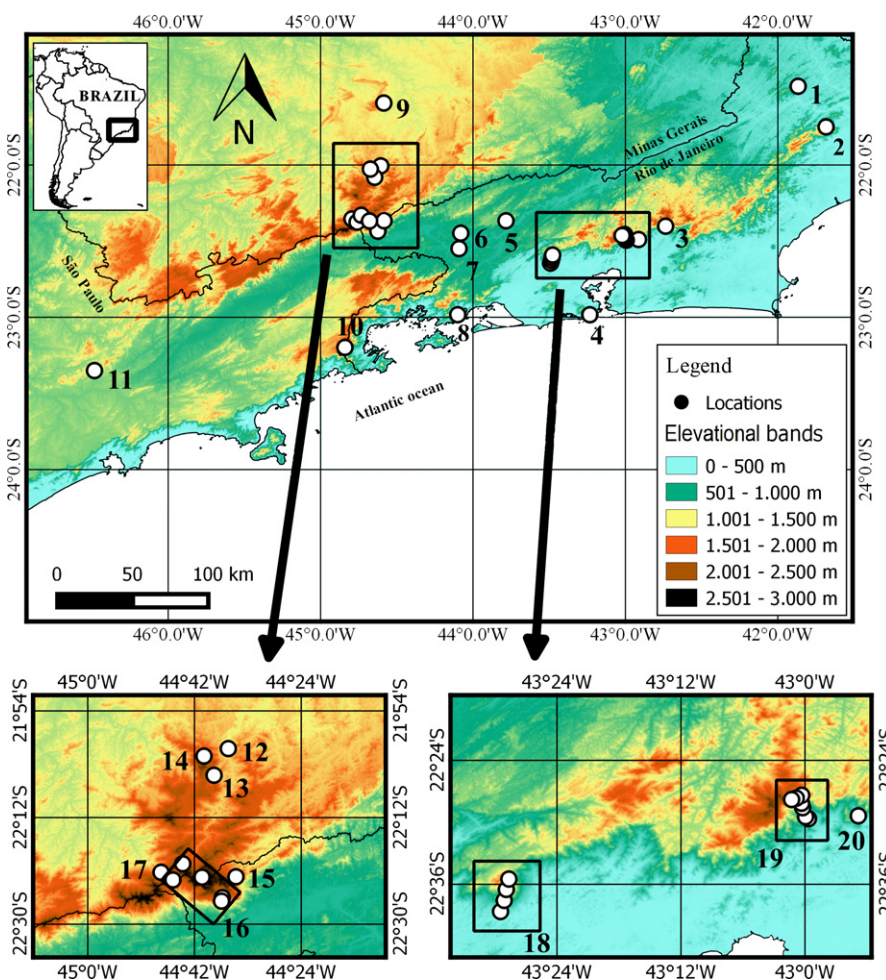
## 2.2 | Influence of elevation on bat abundance and diversity parameters

The captures from all sampled sites were aggregated into the above referred 500 m wide elevational bands. Using narrower elevational bands would have resulted in very unbalanced numbers of sampled

sites and captures in each band and in poor estimates of confidence intervals. These 500 m bands were used in all the analyses described in this section.

We obtained a rough index of bat abundance for each elevational band by dividing the total number of bats captured in the sites within that band by the total capture effort at those sites. The resulting values were multiplied by 100 to avoid using very small values (Table 2). We then used generalized linear models (GLM) with Gaussian errors and an identity link function to test the effect of elevation on the pooled abundance of bats and, separately, on the total abundance of each trophic guild.

Hill numbers were used to compare the taxonomic diversity patterns of bat assemblages across elevational bands (Chao et al., 2014). We estimated the numbers corresponding to the three most widely used species diversity measures: species richness ( $q = 0$ ), Shannon diversity ( $q = 1$ ) and Simpson diversity ( $q = 2$ ), using individual based rarefaction/extrapolation, in the *INEXT* R package (Hsieh, Ma, & Chao, 2016). Comparisons were made for a sample size of 678 individuals, which is twice the sample size of the smallest sample, as recommended by Chao et al. (2014). Since we pooled samples from multiple locations to characterize each elevational band, the calculated statistical parameters refer to the regional (landscape scale) gamma diversity (McCain & Grytnes, 2010).



**FIGURE 1** Map showing the locations of the phyllostomid bat surveys included in this study. All sites are located in an area of Atlantic Forest in south-eastern Brazil. Numbers in the map: References: 1—Albuquerque et al. (2013); 2—Modesto, Pessoa, Enrici, et al. (2008); 3—Santos (2013); 4—Esbérard (2004); 5—Modesto, Pessoa, Jordão-Nogueira, et al. (2008); 6—Pereira et al. (2013); 7, 12, 13, 14, 17 and 20—LADIM; 8—Luz, Costa, Lourenço, and Esbérard (2011); 9—Moras et al. (2013); 10—Delciellos et al. (2012); 11—Bertola et al. (2005); 15—Luz et al. (2013); 16—Martins et al. (2015); 18—Dias et al. (2008) and 19—Nascimento (2007) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**TABLE 1** Elevational bands, locality, total number of captures of phyllostomid bat species, sampling effort and elevation of the 32 sites used in the present study. All sites are located in an area of Atlantic Forest in south-eastern Brazil

Elevational bands (m)	Locality	Total no. captures	Sampling effort	Elevation (m)	Reference (data base)
0–500	Reserva Rio das Pedras (1)	1,208	4,644	60	1
	Estação Ecológica Paraíso (1)	724	2,775	100	2
	Reserva Biológica do Tinguá—Site I (1)	191	312	150	3
	Reserva do Guapiaçu (2)	741	4,320	360	4
	Parque Nacional da Serra dos Órgãos—Site I (1)	8	60	365	5
	ARIE Floresta da Cicuta (2)	474	3,744	422	2
	Parque do Ingá (2)	85	294	430	6
	Parque Nacional da Serra dos Órgãos—Site II (1)	15	60	450	5
501–1,000	Reserva Biológica do Tinguá—Site II (1)	102	312	900	3
	Reserva Biológica do Tinguá—Site III (1)	33	156	600	3
	Parque Estadual da Cantareira (1)	512	1,296	880	7
	Maciço da Tijuca (2)	1,176	5,760	540	2, 8
	Cambuci (2)	111	662	641	9
	SVS Serra da Concórdia (2)	1,185	4,920	650	2, 10
	Parque Nacional da Serra dos Órgãos—Site III (1)	33	300	1,024	5
1,001–1,500	RPPN Cachoeira do Tombo (2)	226	1,620	1,121	2
	Parque Nacional da Serra da Bocaina (1)	24	96	1,121	11
	Parque Nacional do Itatiaia—Site I (1)	41	336	1,150	12
	Parque Nacional do Itatiaia Site II (1)	21	168	1,300	12
	Parque Estadual do Desengano (2)	107	768	1,250	13
	Reserva Biológica do Tinguá—Site IV(1)	13	156	1,270	3
	Parque Nacional da Serra dos Órgãos—Site IV (1)	47	300	1,370	5
	Parque Nacional da Serra dos Órgãos—Site V (1)	3	180	1,100	5
	Cachoeira das Fadas (2)	86	1,200	1,350	2
	RPPN Alto Montana (1)	58	324	1,470	2
1,501–2,000	Chapada do Abanador (2)	87	1,680	1,500	14
	Parque Nacional da Serra dos Órgãos—Site VI (1)	5	180	1,582	5
	Parque Estadual da Pedra Selada (1)	166	441	1,600	15
	Parque Nacional do Itatiaia—Site III (1)	8	168	1,670	12
	Cachoeira dos Garcias (2)	42	480	1,671	2
	Parque Nacional da Serra dos Órgãos—Site VII (1)	1	120	1,900	5
	Parque Nacional do Itatiaia—Site IV (1)	30	672	1,960	12

Locality: 1—Site in undisturbed forest and 2—Site in disturbed forest.

References: 1—Luz et al. (2011), 2—LADIM, 3—Dias et al. (2008), 4—Santos (2013), 5—Nascimento (2007), 6—Pereira et al. (2013), 7—Bertola et al. (2005), 8—Esbérard (2004), 9—Albuquerque et al. (2013), 10—Modesto, Pessoa, Enrici, et al. (2008), 11—Delciellos et al. (2012), 12—Martins et al. (2015), 13—Modesto, Pessoa, Jordão-Nogueira, et al. (2008), 14—Moras et al. (2013) and 15—Luz et al. (2013).

### 2.3 | Quantification of the response of species to elevation

We assumed that where species abundance declines less over elevation, species are better capable of using higher elevation forest. Therefore, we developed a measure of the aptitude of species to use elevated forest based on the proportion of total observations at each of six 300-m-wide elevational bands. This measure reflects the relative, not absolute, decline in abundance. To calculate it we first divided the number of captures in each band (weighted by the

capture effort) by the number of captures in all bands combined. A matrix of species (rows) versus elevational bands (columns) was generated using these proportions. Finally, a Detrended Correspondence Analysis (DCA) was carried out on this matrix, the first axis of which clearly represented how species used the elevational gradient (see Supporting Information Appendix S1). The coordinate of a species along this first axis is henceforth referred to as its *Elevational Abundance Index* (Figure 2) and is determined by the response to elevation, compared to that of other species; species with a higher index value are those with a greater proportion of its total

Taxa	Elevational bands (m)			
	0–500	501–1,000	1,001–1,500	1,501–2,000
<i>Anoura caudifer</i>	107	92	54	14
<i>Anoura geoffroyi</i>	11	26	8	28
<i>Artibeus fimbriatus</i>	319	345	34	7
<i>Artibeus lituratus</i>	755	557	24	10
<i>Artibeus obscurus</i>	231	159	1	0
<i>Artibeus planirostris</i>	185	90	1	0
<i>Carollia perspicillata</i>	1,108	527	126	18
<i>Chiroderma doriae</i>	5	6	1	0
<i>Chiroderma villosum</i>	4	2	0	0
<i>Chrotopterus auritus</i>	7	3	5	1
<i>Dermanura cinerea</i>	20	4	1	0
<i>Desmodus rotundus</i>	117	112	79	63
<i>Diaemus youngii</i>	0	3	0	0
<i>Diphyla ecaudata</i>	1	8	0	0
<i>Glossophaga soricina</i>	61	54	5	0
<i>Lonchophylla peracchii</i>	17	5	0	0
<i>Lonchorhina aurita</i>	18	1	0	0
<i>Micronycteris hirsuta</i>	2	0	0	0
<i>Micronycteris megalotis</i>	6	10	1	3
<i>Micronycteris microtis</i>	3	1	1	0
<i>Micronycteris minuta</i>	9	6	0	0
<i>Mimon bennettii</i>	5	3	2	0
<i>Phylloderma stenops</i>	2	0	0	0
<i>Phyllostomus discolor</i>	0	10	0	0
<i>Phyllostomus hastatus</i>	14	16	1	0
<i>Platyrrhinus lineatus</i>	44	53	17	1
<i>Platyrrhinus recifinus</i>	27	99	11	4
<i>Pygoderma bilabiatum</i>	21	41	2	1
<i>Sturnira lilium</i>	275	874	248	184
<i>Sturnira tildae</i>	8	6	2	1
<i>Tonatia bidens</i>	23	11	1	0
<i>Tonatia saurophila</i>	0	1	0	0
<i>Trachops cirrhosus</i>	10	1	0	0
<i>Vampyressa pusilla</i>	26	26	1	4
<i>Vampyrodes caraccioli</i>	5	0	0	0
Total	3,446	3,152	626	339
Bat abundance (% of total of captures)	45.56	41.67	8.27	4.48

**TABLE 2** Total number of captures of phyllostomid bat species along an elevational gradient in the Atlantic Forest, south-eastern Brazil

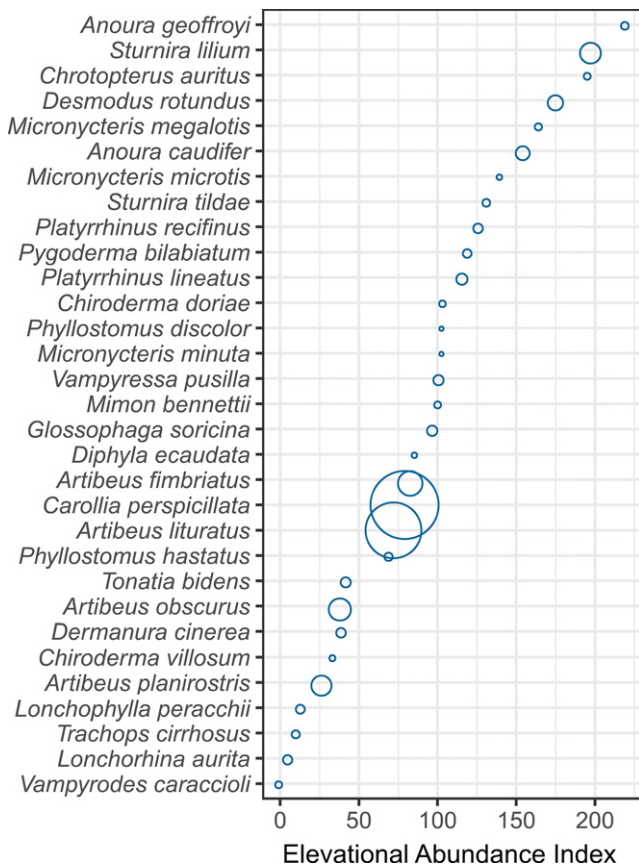
observations at higher elevations. This index is to be interpreted as a simple representation of how abundance changes with elevation, not as a habitat preference variable. To prepare the data for the DCA we used relatively narrow (300 m) bands to optimize the use of information about how the abundance of individual species varies with elevation. We included data for the 31 phyllostomid species that were represented by a total of at least five individuals (Table 2). This analysis was done in PAST version 3.17 (Hammer,

Harper, & Ryan, 2008), using segmentation as the detrending method.

## 2.4 | Species traits

We selected the following seven species traits as potential determinants of the capacity of phyllostomid bats to persist in elevated areas in tropical mountain ranges.





**FIGURE 2** Phyllostomid bat species included in the study, ranked according to their Elevational Abundance Index. The size of the circles is proportional to the overall abundance of each species in the surveys included in the study. All sites where data were collected are in an area of Atlantic Forest in south-eastern Brazil [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 2.4.1 | Trophic guild

We assigned species to one of the following guilds: frugivores, nectarivores, omnivores, gleaning animalivores and sanguivores (Schnitzler & Kalko, 1998). Productivity tends to decline with elevation (McCain & Grytnes, 2010), and this may affect the availability of resources for some of these guilds.

### 2.4.2 | Wing loading

Species with higher WL are faster and energetically efficient flyers, whereas those with low loadings have a slower but highly manoeuvrable flight. The former tend to forage in open spaces and the latter in cluttered habitats (Marinello & Bernard, 2014). We obtained this parameter from Tavares (2013) and Marinello and Bernard (2014). When not available we estimated it using data from a closely related species and the formula indicated in Jovanovic and Levy (1997). We expected species with low WL to be less adapted to elevated forest because vegetation in this habitat is shorter and less vertically stratified, and thus presumably has less subcanopy foraging volume for cluttered space foraging species (Marques et al., 2016).

### 2.4.3 | Independence on continuous forest

The level of independence of continuous and undisturbed forest habitat varies among phyllostomid bat species (Farneda et al., 2015). To quantify this trait for each species we adapted an index used by Davies, Margules, and Lawrence (2000), which relates the abundance of the species in fragments to that in continuous forest:  $y = \log_e$  (Mean abundance in fragments/Mean abundance in continuous forest). As such, a higher value indicates a species that is less dependent on continuous forest. Species that are highly dependent on continuous forest have the lowest index scores. This parameter was calculated using the sites included in the study, considering sites with more than 10,000 ha of relatively undisturbed forest to be 'continuous forest' (Table 1). Only well-forested sites were included, although in many of them the forest is secondary or substantially degraded.

### 2.4.4 | Underground roosting

Bat species use underground roosts to a variable extent. Such roosts provide shelter from cold and extreme weather, so we predicted that their use would facilitate survival in montane areas. We gathered published information on roost selection in the study region (e.g. Arnone, 2008; Guimarães & Ferreira, 2014; Rocha, 2013; Trajano, 1996) to assign each species to one of the following classes: never uses underground roosts (a), seldom uses (b), occasionally uses (c), frequently uses (d), always uses (e).

### 2.4.5 | Southernmost latitude

Species present at higher latitudes may cope better with colder conditions (Stevens, 1989), so we predicted that the southern limit of the range of species would be positively associated with their presence in montane areas. Southernmost latitudes (SLs) were extracted from Emmons and Feer (1997), Eisenberg and Redford (1999) and Gardner (2008).

### 2.4.6 | Body mass

Heat conservation increases with body mass due to a lower surface-area-to-volume ratio (Blackburn, Gaston, & Loder, 1999), so larger bats may be better adapted to cool high elevations. Alternatively, smaller bodies may facilitate torpor at low temperatures, and this may lead to a decrease in body mass with elevation (Espinoza, 2006). Moreover, smaller species need less resources per individual and may thus be able to maintain higher densities in high-elevation forest, where food resources are scarcer. We used body mass values in Reis, Fregonezi, Peracchi, and Shibatta (2013). Body mass was normalized with a natural logarithm transformation.

We examined the potential role of species traits as determinants of their use of the elevational gradient using phylogenetic generalized least squares (PGLS) models, to avoid problems associated to the statistical nonindependence of related species (Martins &

Hansen, 1997). The taxonomic relationships used in the PGLS were based on the most recent phylogeny for Chiroptera, proposed by Baker, Solari, Cirranello, and Simmons (2016). Nineteen species were not present in the phylogeny and were substituted by their closest congener as in, for example Cisneros, Fagan, and Willig (2015) or considering only the genus when it was included in Baker et al. (2016).

Univariate GLMs were used to test the relationship between individual traits and the Elevational Abundance Index. Traits with  $p > 0.3$  were excluded from further analyses, as there was no clear biological evidence to justify their inclusion (Mickey & Greenland, 1989). We then used the remaining variables to generate PGLS models linking the Elevational Abundance Index with all possible combinations of predictors. Spearman correlation between these predictors was very low (0.24–0.34) indicating that there were no collinearity problems among predictors. The response variable, Elevational Abundance Index, followed a normal distribution function (Shapiro–Wilks test,  $p = 0.34$ ). The generated models were ranked considering the Akaike's information criterion corrected for small sample size ( $AIC_c$ , Burnham & Anderson, 2002), where the best candidate model was that with the smallest  $AIC_c$  value to predict the Elevational Abundance Index. The models that presented delta values ( $\Delta_i$ )  $< 2$  and high values of Akaike weights ( $w_i$ ) (i.e. closest to 1) were considered to be those with strongest support. In addition, we computed weighted estimates of regression coefficients and unconditional SEs for the models in the 95% confidence set (Burnham & Anderson, 2002) using the package MuMIn (Bartón, 2018). Also, using the package MuMIn (Bartón, 2018), we measure the relative importance of predictor variables (see Burnham & Anderson, 2002, 2004). PGLS model generation and selection were carried out in R using the PGLS function in the package CAPER (Orme et al., 2013). **We followed the recommendation of Revell (2010) estimating the phylogenetic signal simultaneously (using Pagel's  $\lambda$ ; Pagel, 1999) with the regression model.**

Finally, we also tested for an influence of elevation on the mean community traits. We first obtained, for each of the seven studied traits, the average trait of all the individuals captured at each of the 32 sites (Table 1), that is the average trait of all the species present weighted by their abundances. We tested for these relationships with GLMs (Gaussian link function) using elevation as the predictor and the mean community trait of the sites as the dependent variable. The GLM was carried out in R using the package AICCMODAVG version 2.0-1 (Mazerolle, 2013).

### 3 | RESULTS

#### 3.1 | Changes in bat abundance and assemblage structure across the elevational gradient

The overall abundance of phyllostomid bats declined greatly above 1,000 m (Figure 3a); in the highest band (1,500–2,000 m), corresponding to the cloud forest zone, total abundance was only c. 35% of that observed at the base of the mountains. This reduction in

overall abundance is mostly due to a decline of species in the frugivore guild. There is some evidence that sanguivores (vampires) increase in abundance with elevation, but this increase is slight and insufficient to counter the trend in frugivores, which dominate the assemblages in all bands (Figure 4). There were no significant changes in abundance with elevation for the remaining guilds—nectarivores, omnivores and gleaning animalivores.

Hill numbers show that taxonomic diversity of species assemblages also varied greatly with elevation, although the differences between the two lowest bands were minor (Figure 3). Species richness ( $q = 0$ ) declined substantially, particularly in the 1,500–2,000 m elevational band. Shannon diversity ( $q = 1$ ) declined markedly with increasing elevation due to the disappearance, or increasing rarity, of several species (Figure 3b). However, the strongest decline was in Simpson diversity ( $q = 2$ ), which shows that as elevation rises the assemblages become increasingly dominated by a smaller number of species. The analysis of the confidence intervals associated with all these estimates confirms the tendencies (Figure 3). Rarefaction/extrapolation curves for  $q = 0$  also show that there is a progressive decline of species richness with increasing elevation, although the curves for the three lowest bands tend to converge as sample size increases (see Supporting Information Appendix S2).

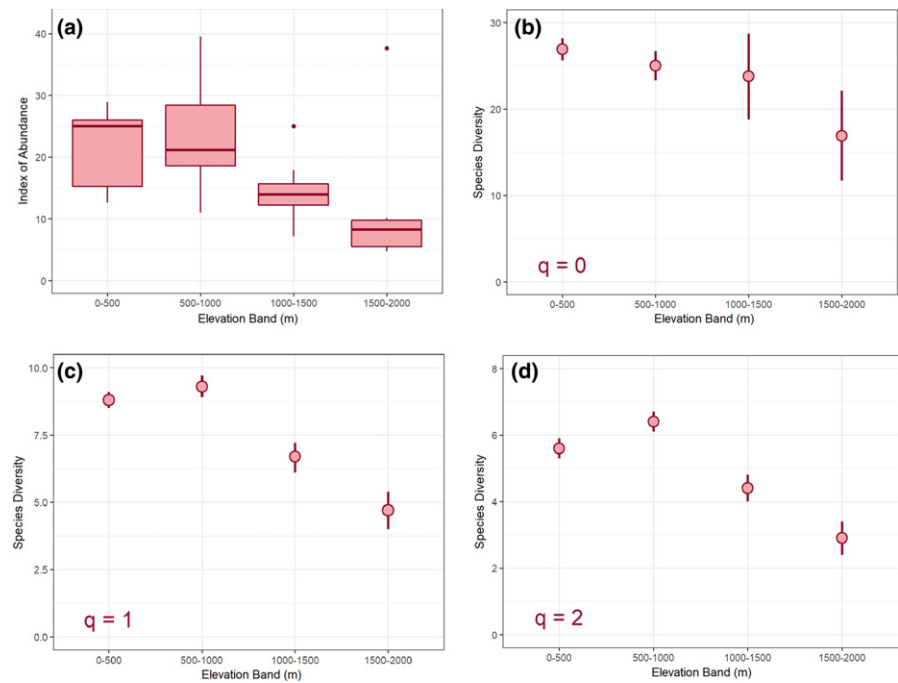
#### 3.2 | Species traits facilitating presence in elevated forest

Several univariate GLMs testing the relationship between individual traits and the Elevational Abundance Index resulted in large  $p$  values and were thus excluded from further analysis. That was the case with WL ( $p = 0.86$ ), body mass ( $p = 0.57$ ) and of all the guilds ( $p > 0.66$ ). All possible models combining the remaining traits—Underground roosting (UR;  $p = 0.002$ ), SL ( $p = 0.0009$ ) and ICF ( $p = 0.0011$ ) (Figure 5)—were then submitted to the PGLS modelling procedure.

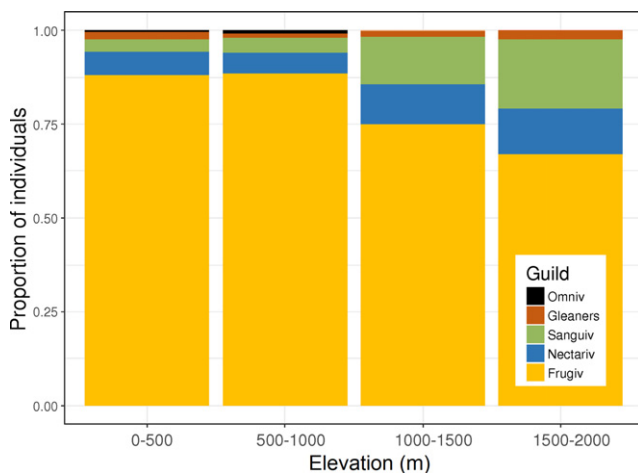
The best candidate model to predict the species Elevational Abundance Index, that is with the lowest  $AIC_c$ , included two traits: SL + ICF (Table 3). Two other models were also supported as they had a  $\Delta AIC_c < 2$  to the best model (SL and SL + UR + ICF). SL was the only trait present in the three best models, but ICF was in two of them.

Model-averaged parameter estimates indicated negative associations between SL and the Elevational Abundance Index and positive associations between ICF and the Elevational Abundance Index (Table 4). UR showed no association with the Elevational Abundance Index (Table 4). The relative importance of each predictor variable was of c. 94% for SL, 58% for ICF and 32% for UR.

In summary, these results indicate that three of the studied traits are potentially relevant facilitators of the colonization of elevated forest; bats are more likely to be present there if their geographical range includes high southern latitudes, if they have a high ICF, and if they often use underground roosts.



**FIGURE 3** Elevational changes in total phyllostomid bat abundance (a), and in species diversity based on Hill numbers of order  $q = 0$  (species richness—in [b]),  $q = 1$  (Shannon diversity—in [c]) and  $q = 2$  (Simpson diversity—in [d]) in an area of Atlantic Forest in south-eastern Brazil. The vertical lines in (a) represent the range, and in the remaining graphs bootstrapped 95% confidence intervals [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 4** Changes in guild composition of the phyllostomid bats sampled across the four elevational bands in an area of Atlantic Forest in south-eastern Brazil [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3.3 | Mean community traits across the elevational gradient

The species-level analysis showed that some of the studied traits facilitate the colonization of elevated forest by individual species. This relationship between elevation and traits is further corroborated by the community-level analyses, which show that the traits prevailing numerically at different elevations also change markedly (Figure 6). At higher elevations, phyllostomid assemblages were progressively more dominated by species with geographical ranges extending further south, that is latitudes with colder climates ( $b = -0.00266$ ,  $R^2 = 0.75$ ,  $p < 0.001$ ). The second trait most closely associated with elevation

was the use of underground roosts ( $b = 0.000842$ ,  $R^2 = 0.72$ ,  $p < 0.001$ ). Species that were less dependent on continuous forest became increasingly prevalent at higher elevations ( $b = 0.000142$ ,  $R^2 = 0.47$ ,  $p < 0.001$ ). Finally, the two morphological traits evaluated, although not significant in the species-level analysis, also changed in their mean value across elevations; mean body mass decreased with elevation ( $b = -0.00986$ ,  $R^2 = 0.39$ ,  $p < 0.001$ ), whereas WL increased ( $b = 0.0026$ ,  $R^2 = 0.59$ ,  $p < 0.001$ ).

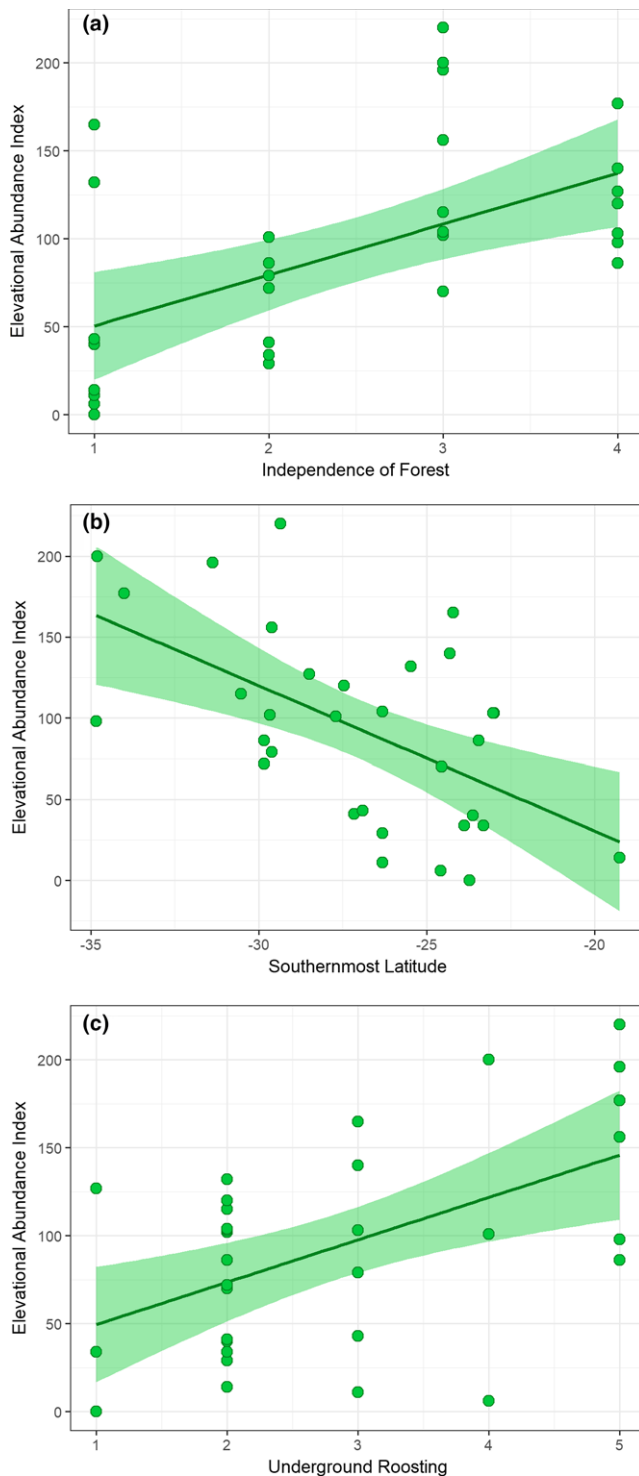
## 4 | DISCUSSION

### 4.1 | Abundance, richness and diversity decline with elevation

The marked elevational decline in overall phyllostomid bat abundance that we observed in the Atlantic Forest, particularly in the case of the frugivore guild, parallels that reported from the Amazon in the Eastern Andes (Graham, 1983). It is also similar to the pattern reported for birds in Atlantic Forest elevational gradients (Mallet-Rodrigues, Parrini, & Rennó, 2015).

It is important to note that all of the most frequently captured frugivorous species declined in abundance with elevation. Even species that are relatively common in high-elevation forest and known to be comparatively well adapted to elevation in the Atlantic Forest, such as *Sturnira lillium* (Luz, Costa, Jordão-Nogueira, Esbérard, & Bergallo, 2013; Martins et al., 2015; Mello, Kalko, & Silva, 2008; Nobre, dos Santos Rodrigues, de Almeida Costa, da Silva Moreira, & Moreira, 2009), are less abundant there than at lower elevations at this latitude; *S. lillium* peaked in abundance in the 500–1,000 m elevational band and declined above that. A similar decrease in *S. lillium* with elevation has also been reported in Argentina by Sánchez and





**FIGURE 5** Univariate relationship between individual species traits and the capacity of phyllostomid bat species to persist in elevated forest located in an area of Atlantic Forest in south-eastern Brazil. Each dot represents one of the 31 species and the line and statistics are the result of univariate GLMs. Only the three traits for which this relationship was significant are included in the figure. (a) Independence of continuous forest, (b) Southernmost latitude and (c) Underground roosting. For Independence of Forest, a higher value indicates a species that is less dependent on continuous forest. The shaded areas represent the 95% confidence intervals [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 3** Best-supported models from phylogenetic generalized least squares models relating species traits with the distribution of phyllostomid bat species along the Atlantic Forest elevational gradient, south-eastern Brazil. Models are ranked according to their  $AIC_c$ . The three traits that entered the models are independence of continuous forest (ICF), underground roosting (UR) and southernmost latitude (SL). Sample-size adjusted AIC ( $AIC_c$ ), Akaike differences ( $\Delta_i$ ) and Akaike weights ( $w_i$ ) are given. For the top model, lambda ( $\lambda$ ) was 1, indicating the evolution of the residual error is Brownian. For the two following models  $\lambda$  was 0 indicating little effect of the residual phylogeny on the relationship between Elevational Abundance Index and the predictor variables

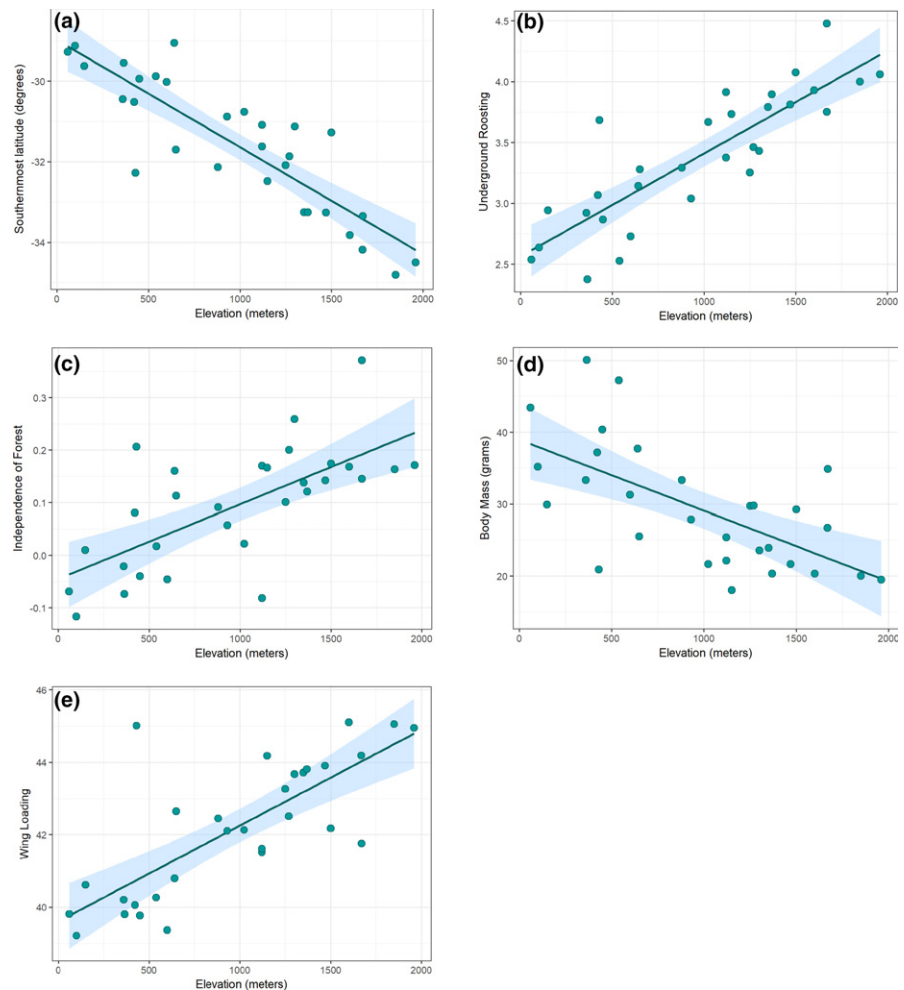
	logLik	$\lambda$	$AIC_c$	$\Delta_i$	$w_i$
Mod 1—SL + ICF	-163.330	1	333.5	0.00	0.387
Mod 2—SL	-164.869	0	334.2	0.62	0.284
Mod 3—SL + UR + ICF	-162.912	0	335.4	1.81	0.156
Mod 4—SL + UR	-164.532	1	336.0	2.40	0.116
Mod 5—UR + ICF	-165.852	1	338.6	5.04	0.031
Mod 6—UR	-167.694	0	339.8	6.27	0.017
Mod 7—ICF	-168.547	1	341.5	7.97	0.007

**TABLE 4** Model-averaged parameter estimates for each variable in the 95% confidence set of phylogenetic generalized least squares models relating species traits with the distribution of phyllostomid bat species along the Atlantic Forest elevational gradient, south-eastern Brazil. The three traits that entered the models are Independence of Continuous Forest (ICF), underground roosting (UR) and Southernmost latitude (SL)

	$\theta$	SE	z value	$p(> z )$
(Intercept)	122.314	44.673	2.738	0.00618
SL	-28.234	9.739	2.899	0.00374
ICF	14.560	8.489	1.715	0.08631
UR	15.834	16.803	0.942	0.34601

Giannini (2014). This indicates that the lower overall abundance of bats is not just due to a reduction in the number of available niches or to an absence of species that cannot persist in high elevation environments. An overall reduction in the availability of fruit resources that affects all species is also likely to be involved. In fact, there is evidence that fruit can be a limiting resource for phyllostomid bats (Palmeirim, Gorchoy, & Stoleson, 1989) and the lower temperatures and foggy conditions prevailing at higher elevations are known to reduce plant productivity and fruit production (Loiselle & Blake, 1991; McCain, 2009; Terborgh, 1977). Various authors have suggested that constraints in the availability of various types of food resources limit not only abundance but also richness of montane bat and bird assemblages (Graham, 1990; Patterson, Stotz, Solari, Fitzpatrick, & Pacheco, 1998; Presley, Cisneros, Patterson, & Willig, 2012; Willig & Presley, 2016).

As in the case of abundance, the decline in species richness with elevation also mirrors the trends reported for the Andes (Patterson et al., 1996; Presley et al., 2012; Willig & Presley, 2016). The



**FIGURE 6** Relationship between elevation and several community-weighted phyllostomid bat species traits in an area of Atlantic Forest in south-eastern Brazil. (a) Southernmost latitude, (b) underground roosting, (c) Independence of continuous forest, (d) body mass and (e) wing loading. For Independence of Continuous Forest, a higher value indicates a species that is less dependent on continuous forces [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

rarefaction/extrapolation for  $q = 0$  clearly shows a progressive decline in richness along the elevational gradient (see Supporting Information Appendix S2), despite the convergence to a similar level of richness in the three lowest bands as the sample size increases. This is probably due to an infrequent presence in elevated areas of species that are mostly present at low elevation; the small distances that separate low and high elevation in these mountain ranges can be easily covered by bats for long-distance dispersal (Esbérard, Godoy, Renovato, & Carvalho, 2017) or on foraging trips (Mello et al., 2008).

The strong influence of rare or occasional species on richness ( $q = 0$ ) estimates explains why the differences in structure of the assemblages across elevations is less evident in estimates of richness than of higher order diversity ( $q = 1, 2$ ). The latter take into consideration not just the total number of species present but also the evenness of their abundances; elevated forest assemblages have more uneven abundances and are clearly numerically dominated by a small number of species (Figure 3), particularly *S. lillium*, *Desmodus rotundus* and *Carollia perspicillata*.

Meta-analyses of the patterns of species richness across elevational ranges show that they vary substantially among taxonomic groups and with the prevailing climate (Guo et al., 2013; McCain & Grytnes, 2010). The three most common patterns of change in

richness with elevation are a steady decline with elevation, a plateau at low and mid elevations followed by a decline, and a peak at mid-elevations (see McCain & Grytnes, 2010). The pattern observed with phyllostomids in the Atlantic Forest gradient in this study was an initially slow decline, followed by a clear drop. It is worth noting that we truncated our gradient at 2,000 m to exclude the nonforested habitats prevailing above that elevation. However, the few available bat surveys above the tree line in the region (see Martins et al., 2015; Nascimento, 2007) show that bat abundance and richness there is even lower than in the high-elevation forests.

McCain (2007) formulated an elevational climatic model, based on temperature and water availability, to explain patterns of richness across elevational gradients. According to that model the peak of richness should be at the elevation with the warmest-wettest conditions. The observed patterns in this study fit well with the predictions of this model, as the highest temperatures are near the base of the mountains, and rainfall in the part of the Atlantic Forest included in this study is high across the elevational range (Delgado, Oliveira-Júnior, Gois, Ávila Rodrigues, & Teodoro, 2017; Lyra, Correia, Oliveira-Júnior, & Zeri, 2018). Indeed, the high temperatures and rainfall at low and mid elevations in the Atlantic Forest biome are presumably responsible for a more structured forest (Oliveira-Filho & Fontes, 2000), with a higher number of niches and a greater abundance

of resources, resulting in higher species richness and abundance. However, the greater richness at lower elevations may not be due just to these ecological factors but also to climatic filtering (Nogu , Rull, & Vegas-Vilarr bia, 2013; Weier, Linden, Gaigher, White, & Taylor, 2017; Wu et al., 2013), as discussed below.

#### 4.2 | Which traits allow bats to thrive in elevated forest?

It follows from the previous section of this discussion that lower ambient temperatures and the related lower abundance of resources are likely to be involved in the decline of the richness and abundance of phyllostomid bats with elevation. However, there are still many bat species in the assemblages harboured by these high elevation forests, and to understand the determinants of their structure it is necessary to identify which traits, if any, influence the capacity of species to succeed in high elevation forests (Graham et al., 2014).

We used two types of analyses to investigate the potential relationship between species traits and elevation: a species level analysis, directly testing for an association between traits and elevation, and a mean community trait analysis, testing for an association between elevation and the mean abundance of each trait across the elevational range. The results of the two analyses were in general interpretable and congruent. The species that have the highest relative abundances in high elevation forests are those that have a high tolerance to colder climates, here represented by the 'southernmost latitude' reached by each species. This was evident in both species and community mean analyses. In fact, the species present in high-elevation areas were those with a geographical range including higher southern latitudes, and this trait was also increasingly dominant in the assemblages moving up the elevation gradient. This result is in line with the predictions of niche conservatism theory (Wiens et al., 2010), which postulates that species have a limited capacity to adapt to climatic conditions that differ from those in which their ancestors evolved; the Phyllostomidae is a family with a tropical origin, and thus its species have not evolved efficient strategies to cope with low temperatures, unlike bats of other families (Ramos Pereira & Palmeirim, 2013; Stevens, 2006, 2011). Thus, we found evidence that climatic filtering is a very important determinant of the changes in the phyllostomid assemblages along the tropical elevational gradient. This is likely to happen in many other taxa that, like phyllostomids, have a tropical origin, because they may lack adaptations to colder climates or even the capacity to evolve those adaptations (Wiens et al., 2010). Furthermore, the results are also in line with the fundamental physiological niche hypothesis, which predicts that species' elevational limits are set by their thermal physiology (Jankowski, Londo o, Robinson, & Chappell, 2013). Phyllostomids vary in their capacity to thermoregulate at lower temperatures (Audet & Thomas, 1997; Dwyer, 1971; McNab, 1973; Soriano, Ruiz, & Arends, 2002), but it is worth noting that even the species that is most abundant at high elevations, *S. lillium*, resorts to seasonal elevational migrations to lower elevations to cope with low temperatures, even at times of the year when its food is abundant

(Mello et al., 2008). This pattern seems to be stronger in groups with few species that migrate altitudinally, like phyllostomids (McGuire & Boyle, 2013). However, this climatic filtering may be absent, or weaker, in taxa that have an evolutionary origin in colder climates and that have more species that migrate altitudinally, as in the case of the bat family *Vespertilionidae*.

The species that are most successful in colonizing high elevation forests are those that have a high score in the trait reflecting 'independence of continuous forest'. This includes, for example *S. lillium*, *Anoura* spp. and *D. rotundus*, which are comparatively abundant at high elevation. They tend to be generalist species that are known to occur in greater abundance in disturbed environments (Estrada & Coates-Estrada, 2002; Meyer, Fr nd, Lizano, & Kalko, 2008; Pardini et al., 2009). The lack of well-stratified forest at higher elevations (Ururahy et al., 1983; Veloso, Rangel Filho, & Lima, 1991) seems to filter out the more specialized species, whereas generalists can cope with the distinct types of forest that prevail at these elevations. In the absence of these species, and of any true elevation specialists, the assemblages of species tend to be numerically dominated by generalists, as shown by our mean community trait analysis.

The extent to which species use underground cavities to roost seems to be a relevant predictor of the success of species in high elevation forest, although not as important as the tolerance to lower temperatures or the ICF. Caves and other relatively large natural cavities may shelter bats from inclement weather, such as low temperatures, rain and strong winds (Dwyer, 1971; Furey & Racey, 2016). Furthermore, the concentration of large numbers of bats in roosts tends to generate warmer microclimates that result in metabolic energy savings (Dwyer, 1971; Lundberg & McFarlane, 2015) and may thus compensate lower environmental temperatures. The comparative abundance of cave dwelling phyllostomids in high elevation assemblages may be partly explained by a potentially greater availability of natural rocky cavities in the rugged terrain that often dominates the upper slopes of mountains (Zhou et al., 2017).

Our prediction that body mass would influence the probability of a species being present in high-elevation forest was not confirmed by the results of the species-level analysis. However, the mean community trait analysis demonstrated that smaller species were much more abundant at higher elevations than large species. In fact, the most common large phyllostomid species in the study region tend to be fig eaters, and figs tend to be less present at higher elevations (Graham, 1990; Pelissari & Neto, 2013; Shanee & Peck, 2008). This suggests that, although size does not filter out the species present at higher elevations, resources are less abundant for them in mountain forest. However, we cannot exclude the possibility that smaller species are more abundant because they enter torpor more easily, as suggested by Cisneros et al. (2014) for the Andes.

As in the case of body mass, wing shape did not have a statistically significant effect in the species level analyses, suggesting that this trait is not filtered by elevation. However, high elevation forest assemblages were clearly dominated by species with high WL. Together, these results indicate that while species with high and low WL are equally likely to be present in high elevation forest



assemblages, these forests have less resources for the latter. Presumably, the less vertically structured high elevation forest (Ururahy et al., 1983; Veloso et al., 1991) has fewer foraging opportunities for low WL species, whose slower but more manoeuvrable flight allows them to exploit cluttered subcanopy spaces (Marinello & Bernard, 2014; Marques et al., 2016). In any case, the interspecific variability in WL in phyllostomids is lower than in other bat families, which may indicate a comparatively high flexibility in the use of space and resources (Marinello & Bernard, 2014). Such a flexibility may minimize differences of community WL across ecological gradients.

The trophic guild of a species did not influence its probability of being present at higher elevations. However, the dominance of the most abundant guild, frugivores, was less marked at higher elevations because even though their abundance declined, that of other guilds remained roughly constant or, in the case of sanguivores, even increased. This suggests that, while elevation does not filter out any bat trophic guilds, the reduction in productivity with elevation (McCain & Grytnes, 2010) has a more substantial impact on fruit resources (e.g. figs) than on the other types of resources used by phyllostomid bats (e.g. blood).

In summary, the results of this study indicate that three of the studied traits are facilitators of the colonization of elevated forest. Specifically, bats are more likely to be present at high elevations if they: (a) tolerate colder climates (i.e. range including high southern latitudes); (b) are habitat generalists (i.e. high ICF); and (c) often use underground roosts. However, the structure of mountain forest phyllostomid assemblages is not only determined by this elevational trait filtering, but also by resource constraints that, while not hindering the presence of some species, do limit their abundance. Lowland forest has a more abundant and species-rich phyllostomid assemblage because it has fewer climatic constraints, a more structured forest with a greater abundance of resources and, presumably, a higher number of niches.

These conclusions on the structure of phyllostomid assemblages along forested elevational gradients are likely to apply to other major Neotropical mountain ranges, including the Andes and Central America, because their bats faunas, and changes in species composition with elevation (Patterson et al., 1996, 1998; Sánchez-Cordero, 2001; Willig & Presley, 2016), are quite similar to those of the Atlantic Forest.

### 4.3 | Consequences for conservation

Our multi-site Atlantic Forest analysis shows that the phyllostomid assemblages of high-elevation forest are very different from those of lowland forest, apparently due to both climatic and ecological filters, such as forest structure, acting on several species traits, and by changes in the availability of resources. Total abundance declined with elevation and so did species richness; mountain forest assemblages are dominated by a small number of species. There are no high elevation specialists, and assemblages are composed of predominantly lowland species that can overcome the filters associated with elevation. Nevertheless, the distinct character of species assemblages

of high-elevation forests supports their conservation importance. This importance is further enhanced by the ecological roles that phyllostomids play, especially as pollinators and seed dispersers; differences in the composition of phyllostomid assemblages are likely to have major cascading effects on vegetation, thus contributing to the differentiation of ecosystems across the elevational gradient.

The conclusion that mountain Atlantic Forest assemblages are an impoverished subset of those in lowlands and dominated by generalists, raises an important conservation issue; most Atlantic Forest remnants and protected areas are located in mountains (Costa et al., 2009), and much of their area is clearly unsuitable to preserve many of the species that can only thrive in lowland forest. The retreat of the Atlantic Forest to mountains creates an additional problem. Protected Areas (with large Atlantic forests remnants) are often isolated resulting in the fragmentation of the populations. Destruction of the lowland forest that once interconnected mountains is quite recent (Joly et al., 2014), so assemblages may still be going through the process of species impoverishment due to fragmentation, and extinction debt in the Atlantic Forest is reportedly high (De la Sancha, Higgins, Presley, & Strauss, 2014). Neotropical bats are sensitive to forest fragmentation (Farneda et al., 2015; Gorresen & Willig, 2004; Rocha et al., 2017) and the long-term consequences of fragmentation on bats are likely to be far more serious than those observed in short term studies (Jones, Bunnefeld, Jump, Peres, & Dent, 2016; Rainho & Palmeirim, 2017).

These conservation problems are likely to be relevant in other tropical mountain areas with humid forest, and for other taxa that decline in richness along elevational gradients of tropical forest, such as birds (Graham, 1990; Mallet-Rodrigues et al., 2015; Patterson et al., 1998; Terborgh, 1977). Higher elevation is likely to filter out species with certain traits, and limited resources may constrain abundance. As a consequence, while montane tropical forest has a great conservation value on its own, it is not an adequate replacement for the conservation of low elevation tropical forest habitat, which tends to have greater productivity, more resources, more complex vertical structure, a greater number of niches and less climatic constraints for taxa with a tropical origin.

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## DATA ACCESSIBILITY

All simulated datasets are available via DRYAD Repository entry <https://doi.org/10.5061/dryad.26ss3p0>.

Title: Data from: Traits that allow bats of tropical lowland origin to conquer mountains: bat assemblages along elevational gradients in South American Atlantic Forests

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## REFERENCES

- Albuquerque, H. G., Martins, P. F., Pessoa, F. S., Modesto, T. C., Luz, J. L., Raíces, D. S., ... Jordão-Nogueira, T. (2013). Mammals of a forest fragment in Cambuci municipality, state of Rio de Janeiro, Brazil. *Check List*, 9, 1505–1509. <https://doi.org/10.15560/9.6.1505>
- Arnone, I. S. (2008). Estudo da comunidade de morcegos na área cárstica do Alto Ribeira-São Paulo. Uma comparação com 1980. PhD Thesis, Universidade de São Paulo, São Paulo, Brazil.
- Audet, D., & Thomas, D. (1997). Facultative hypothermia as a thermoregulatory strategy in the phyllostomid bats, *Carollia perspicillata* and *Sturmira lilium*. *Journal of Comparative Physiology B*, 167, 146–152. <https://doi.org/10.1007/s003600050058>
- Baker, R. J., Solari, S., Cirranello, A., & Simmons, N. B. (2016). Higher level classification of phyllostomid bats with a summary of DNA synapomorphies. *Acta Chiropterologica*, 18, 1–38. <https://doi.org/10.3161/15081109ACC2016.18.1.001>
- Bartón, K. (2018). Package 'MuMIn' – Multi-model inference. R package version 1.42.1, Vienna, Austria. Retrieved from <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>
- Bertola, P. B., Aires, C. C., Favorito, S. E., Graciolli, G., Amaku, M., & Pinto-da-Rocha, R. (2005). Bat flies (Diptera: Streblidae, Nycteribiidae) parasitic on bats (Mammalia: Chiroptera) at Parque Estadual da Cantareira, São Paulo, Brazil: Parasitism rates and host-parasite associations. *Memórias do Instituto Oswaldo Cruz*, 100, 25–32. <https://doi.org/10.1590/S0074-02762005000100005>
- Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions*, 5, 165–174. <https://doi.org/10.1046/j.1472-4642.1999.00046.x>
- Burnham, K., & Anderson, D. (2002). *Model selection and inference: A practical information-theoretic approach*. New York, NY: Springer-Verlag.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33, 261–304. <https://doi.org/10.1177/0049124104268644>
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67. <https://doi.org/10.1890/13-0133.1>
- Cisneros, L. M., Burgio, K. R., Dreiss, L. M., Klingbeil, B. T., Patterson, B. D., Presley, S. J., & Willig, M. R. (2014). Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. *Journal of Animal Ecology*, 83, 1124–1136. <https://doi.org/10.1111/1365-2656.12201>
- Cisneros, L. M., Fagan, M. E., & Willig, M. R. (2015). Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, 21, 523–533. <https://doi.org/10.1111/ddi.12277>
- Costa, T. C. C., Fidalgo, E. C. C., Santos, R. F., Rocha, J. V., Metzger, J. P., Vicens, R. S., ... Bohrer, C. B. A. (2009). Diversidade de paisagens no Estado do Rio de Janeiro. In H. G. Bergallo, E. C. C. Fidalgo, C. F. D. Rocha, M. C. Uzêda, M. B. Costa, M. S. Alves, M. V. Sluys, M. A. Santos, T. C. C. Costa, & A. C. R. Cozzolino (Eds.), *Estratégias e ações para a conservação da biodiversidade no Estado do Rio de Janeiro* (pp. 101–110). Rio de Janeiro, Brazil: Instituto Biomas.
- Davies, K. F., Margules, C. R., & Lawrence, J. F. (2000). Which traits of species predict population declines in experimental forest fragments? *Ecology*, 81, 1450–1461. [https://doi.org/10.1890/0012-9658\(2000\)081\[1450:WTOSPP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1450:WTOSPP]2.0.CO;2)
- De la Sancha, N. U., Higgins, C., Presley, S. J., & Strauss, R. E. (2014). Metacommunity structure in a highly fragmented forest: Has deforestation in the Atlantic Forest altered historic biogeographic patterns? *Diversity and Distributions*, 20, 1058–1070. <https://doi.org/10.1111/ddi.12210>
- Delciellos, A. C., Novaes, R. L. M., de Castro Loguercio, M. F., Geise, L., Santori, R. T., de França Souza, R., ... Felix, S. (2012). Mammals of Serra da Bocaina National Park, state of Rio de Janeiro, southeastern Brazil. *Check List*, 8, 675–692. <https://doi.org/10.15560/8.4.675>
- Delgado, R. C., Oliveira-Júnior, J. F., Gois, G., Ávila Rodrigues, R., & Teodoro, P. E. (2017). Synoptic events associated with the land surface temperature in Rio de Janeiro. *Bioscience Journal*, 33, 1038–1047. <https://doi.org/10.14393/BJ-v32n1a2016>
- Dias, D., Esbérard, C. E. L., & Peracchi, A. (2008). Riqueza, diversidade de espécies e variação altitudinal de morcegos na Reserva Biológica do Tinguá, Estado do Rio de Janeiro, Brasil (Mammalia, Chiroptera). In N. R. Reis, & A. L. Peracchi (Eds.), *Morcegos no Brasil* (pp. 125–142). Rio de Janeiro, Brazil: Technical Books.
- Dwyer, P. (1971). Temperature regulation and cave-dwelling in bats: An evolutionary perspective. *Mammalia*, 35, 424–455.
- Eisenberg, J., & Redford, K. (1999). *Mammals of the Neotropics: The central Neotropics – Ecuador, Peru, Bolivia, Brazil*. Chicago, IL: University of Chicago Press.
- Emmons, L. H., & Feer, F. (1997). *Neotropical rainforest mammals*. Chicago, IL: University of Chicago Press.
- Esbérard, C. E. L. (2004). *Morcegos no Estado do Rio de Janeiro*. PhD Thesis. Universidade do Estado do Rio de Janeiro, Rio de Janeiro.
- Esbérard, C. E. L., Godoy, M. S. M., Renovato, L., & Carvalho, W. D. (2017). Novel long-distance movements by Neotropical bats (Mammalia: Chiroptera: Phyllostomidae) evidenced by recaptures in south-eastern Brazil. *Studies on Neotropical Fauna and Environment*, 52, 75–80. <https://doi.org/10.1080/01650521.2016.1273751>





- Espinoza, A. R. (2006). Termoregulación, recursos y límites altitudinales en murciélagos frugívoros y nectarívoros andinos. PhD Thesis, Universidad de Los Andes, Mérida, Venezuela.
- Estrada, A., & Coates-Estrada, R. (2002). Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biological Conservation*, 103, 237–245. [https://doi.org/10.1016/S0006-3207\(01\)00135-5](https://doi.org/10.1016/S0006-3207(01)00135-5)
- Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., ... Meyer, C. F. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, 52, 1381–1391. <https://doi.org/10.1111/1365-2664.12490>
- Fenton, M., & Simmons, N. (2015). *A world of science and mystery bats*. Chicago, IL: The University of Chicago Press. <https://doi.org/10.7208/chicago/9780226065267.001.0001>
- Furey, N. M., & Racey, P. A. (2016). Conservation ecology of cave bats. In C. Voigt, & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 463–500). Cham, Switzerland: Springer. <https://doi.org/10.1007/978-3-319-25220-9>
- Gardner, A. L. (2008). *Mammals of South America, volume 1: Marsupials, xenarthrans, shrews, and bats*. Chicago, IL: University of Chicago Press. <https://doi.org/10.7208/chicago/9780226282428.001.0001>
- Gorresen, P. M., & Willig, M. R. (2004). Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *Journal of Mammalogy*, 85, 688–697. <https://doi.org/10.1644/BWG-125>
- Graham, G. L. (1983). Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of Mammalogy*, 64, 559–571. <https://doi.org/10.2307/1380511>
- Graham, G. L. (1990). Bats versus birds: Comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *Journal of Biogeography*, 17, 657–668. <https://doi.org/10.2307/2845147>
- Graham, C. H., Carnaval, A. C., Cadena, C. D., Zamudio, K. R., Roberts, T. E., Parra, J. L., ... Baines, S. B. (2014). The origin and maintenance of montane diversity: Integrating evolutionary and ecological processes. *Ecography*, 37, 711–719. <https://doi.org/10.1111/ecog.00578>
- Guimarães, M. M., & Ferreira, R. L. (2014). Morcegos cavernícolas do Brasil: Novos registros e desafios para conservação. *Revista Brasileira de Espeleologia*, 2, 1–33.
- Guo, Q., Kelt, D. A., Sun, Z., Liu, H., Hu, L., Ren, H., & Wen, J. (2013). Global variation in elevational diversity patterns. *Scientific Reports*, 3, 3007. <https://doi.org/10.1038/srep03007>
- Hammer, Ø., Harper, D., & Ryan, P. (2008). PAST-paleontological statistics, ver. 1.89. *Paleontological Museum*, 4, 1–9.
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: Na R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Jankowski, J. E., Londoño, G. A., Robinson, S. K., & Chappell, M. A. (2013). Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. *Ecography*, 36, 1–12. <https://doi.org/10.1111/j.1600-0587.2012.07785.x>
- Joly, C. A., Metzger, J. P., & Tabarelli, M. (2014). Experiences from the Brazilian Atlantic Forest: Ecological findings and conservation initiatives. *New Phytologist*, 204, 459–473. <https://doi.org/10.1111/nph.12989>
- Jones, I. L., Bunnefeld, N., Jump, A. S., Peres, C. A., & Dent, D. H. (2016). Extinction debt on reservoir land-bridge islands. *Biological Conservation*, 199, 75–83. <https://doi.org/10.1016/j.biocon.2016.04.036>
- Jovanovic, B. D., & Levy, P. S. (1997). A look at the rule of three. *The American Statistician*, 51, 137–139.
- Körner, C., & Ohsawa, M. (2005). Mountain systems. In R. Hassan, R. Scholes, & N. Ash (Eds.), *Ecosystems and human well-being: Current state and trends* (pp. 681–716). Washington, DC: Island Press.
- Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T. M., ... Badman, T. (2013). Protected areas and effective biodiversity conservation. *Science*, 342, 803–805. <https://doi.org/10.1126/science.1239268>
- Loiselle, B. A., & Blake, J. G. (1991). Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology*, 72, 180–193. <https://doi.org/10.2307/1938913>
- Lundberg, J., & McFarlane, D. A. (2015). Microclimate and niche constructionism in tropical bat caves: A case study from Mount Elgon, Kenya. *Geological Society of America Special Papers*, 516, SPE516-17.
- Luz, J. L., Costa, L. M., Jordão-Nogueira, T., Esbérard, C. E. L., & Bergallo, H. G. (2013). Bats from a Montane Forest, Visconde de Mauá, Resende, Rio de Janeiro. *Biota Neotropica*, 13, 190–195. <https://doi.org/10.1590/S1676-06032013000200018>
- Luz, J. L., Costa, L. M., Lourenço, E. C., & Esbérard, C. E. L. (2011). Bats (Mammalia, Chiroptera) from Reserva Rio das Pedras, Rio de Janeiro, Southeastern Brazil. *Biota Neotropica*, 11, 95–101. <https://doi.org/10.1590/S1676-06032011000100009>
- Lyra, G. B., Correia, T. P., Oliveira-Júnior, J. F., & Zeri, M. (2018). Evaluation of methods of spatial interpolation for monthly rainfall data over the state of Rio de Janeiro, Brazil. *Theoretical and Applied Climatology*, 134, 955–965.
- Mallet-Rodrigues, F., Parrini, R., & Rennó, B. (2015). Bird species richness and composition along three elevational gradients in southeastern Brazil. *Atualidades Ornitológicas*, 188, 39–58.
- Marinello, M., & Bernard, E. (2014). Wing morphology of Neotropical bats: A quantitative and qualitative analysis with implications for habitat use. *Canadian Journal of Zoology*, 92, 141–147. <https://doi.org/10.1139/cjz-2013-0127>
- Marques, J. T., Ramos Pereira, M. J., & Palmeirim, J. M. (2016). Patterns in the use of rainforest vertical space by Neotropical aerial insectivorous bats: All the action is up in the canopy. *Ecography*, 39, 476–486. <https://doi.org/10.1111/ecog.01453>
- Martins, M. A., Carvalho, W. D., Dias, D., França, D. S., Oliveira, M. B., & Peracchi, A. L. (2015). Bat species richness (Mammalia, Chiroptera) along an elevational gradient in the Atlantic Forest of Southeastern Brazil. *Acta Chiropterologica*, 17, 401–409. <https://doi.org/10.3161/15081109ACC2015.17.2.016>
- 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. *American Naturalist*, 149, 646–667. <https://doi.org/10.1086/286013>
- Mazerolle, M. (2013). Package 'AICcmodavg': Model selection and multi-model inference based on (Q) AICc. Retrieved from <https://cran.r-project.org/web/packages/AICcmodavg/index.html>
- 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. <https://doi.org/10.1111/j.1466-8238.2006.00263.x>
- McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346–360. <https://doi.org/10.1111/j.1466-8238.2008.00443.x>
- McCain, C. M., & Grytnes, J. A. (2010). *Elevational gradients in species richness*. Chichester, UK: eLS. John Wiley & Sons Ltd, pp. 1–10. <https://doi.org/10.1002/9780470015902.a0022548>
- McGuire, L. P., & Boyle, W. A. (2013). Altitudinal migration in bats: Evidence, patterns, and drivers. *Biological Reviews*, 88, 767–786. <https://doi.org/10.1111/brv.12024>
- McNab, B. K. (1973). Energetics and the distribution of vampires. *Journal of Mammalogy*, 54, 131–144. <https://doi.org/10.2307/1378876>
- Mello, M. A. R., Kalko, E. K. V., & Silva, W. R. (2008). Diet and abundance of the bat *Sturmira lilium* (Chiroptera) in a Brazilian montane Atlantic Forest. *Journal of Mammalogy*, 89, 485–492. <https://doi.org/10.1644/06-MAMM-A-411R.1>
- Meyer, C. F., Fründ, J., Lizano, W. P., & Kalko, E. K. (2008). Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, 45, 381–391.

- Mickey, R. M., & Greenland, S. (1989). The impact of confounder selection criteria on effect estimation. *American Journal of Epidemiology*, 129, 125–137. <https://doi.org/10.1093/oxfordjournals.aje.a115101>
- Modesto, T., Pessoa, F., Enrici, M., Attias, N., Jordão-Nogueira, T., Costa, L., ... Bergallo, H. (2008). Mamíferos do Parque Estadual do Desengano, Rio de Janeiro, Brasil. *Biota Neotropica*, 8, 153–159. <https://doi.org/10.1590/S1676-06032008000400015>
- Modesto, T. C., Pessoa, F. S., Jordão-Nogueira, T., Enrici, M. C., Costa, L. M., Attias, N., ... Pereira, B. C. (2008). Mammals, Serra da Concórdia, state of Rio de Janeiro, Brazil. *Check List*, 4, 341–348. <https://doi.org/10.15560/4.3.341>
- Moras, L. M., Bernard, E., & Gregorin, R. (2013). Bat assemblages at a high-altitude area in the Atlantic Forest of southeastern Brazil. *Mastozoología Neotropical*, 20, 269–278.
- Nascimento, J. L. (2007). Variação altitudinal na composição e riqueza de espécies de Morcegos (Chiroptera: Mammalia) no Parque Nacional da Serra dos Órgãos, RJ. PhD Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
- Nobre, P. H., dos Santos Rodrigues, A., de Almeida Costa, I., da Silva Moreira, A. E., & Moreira, H. H. (2009). Similaridade da fauna de Chiroptera (Mammalia), da Serra Negra, municípios de Rio Preto e Santa Bárbara do Monte Verde, Minas Gerais, com outras localidades da Mata Atlântica. *Biota Neotropica*, 9, 151–156. <https://doi.org/10.1590/S1676-06032009000300015>
- Nogué, S., Rull, V., & Vegas-Villarrúbia, T. (2013). Elevational gradients in the neotropical table mountains: Patterns of endemism and implications for conservation. *Diversity and Distributions*, 19, 676–687. <https://doi.org/10.1111/ddi.12017>
- Oliveira-Filho, A. T., & Fontes, M. A. L. (2000). Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica*, 32, 793–810. <https://doi.org/10.1111/j.1744-7429.2000.tb00619.x>
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2013). Caper: Comparative analyses of phylogenetics and evolution in R. R package version 1.0.1. Retrieved from <https://cran.r-project.org/web/packages/caper/index.html>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Palmeirim, J., Gorchoy, D., & Stoleson, S. (1989). Trophic structure of a neotropical frugivore community: Is there competition between birds and bats? *Oecologia*, 79, 403–411. <https://doi.org/10.1007/BF00384321>
- Pardini, R., Faria, D., Accacio, G. M., Laps, R. R., Mariano-Neto, E., Paciencia, M. L., ... Baumgarten, J. (2009). The challenge of maintaining Atlantic forest biodiversity: A multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation*, 142, 1178–1190. <https://doi.org/10.1016/j.biocon.2009.02.010>
- Patterson, B., Pacheco, V., & Solari, S. (1996). Distribution of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology*, 240, 637–658. <https://doi.org/10.1111/j.1469-7998.1996.tb05313.x>
- Patterson, B. D., Stotz, D. F., Solari, S., Fitzpatrick, J. W., & Pacheco, V. (1998). Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, 25, 593–607. <https://doi.org/10.1046/j.1365-2699.1998.2530593.x>
- Pelissari, G., & Neto, S. R. (2013). *Ficus* (Moraceae) da Serra da Mantiqueira, Brasil. *Rodriguésia*, 64, 91–111. <https://doi.org/10.1590/S2175-78602013000100009>
- Pereira, S. N., Dias, D., Lima, I. P. d., Maas, A. C. S., Martins, M. A., Bolzan, D. P., ... Ferreira, M. F. S. (2013). Mamíferos de um fragmento florestal em volta redonda, estado do Rio de Janeiro. *Bioscience Journal*, 29, 1017–1027.
- Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. *Annual Review of Environment and Resources*, 37, 25–50. <https://doi.org/10.1146/annurev-environ-042911-093511>
- Presley, S. J., Cisneros, L. M., Patterson, B. D., & Willig, M. R. (2012). Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: A comparison of bats, rodents and birds. *Global Ecology and Biogeography*, 21, 968–976. <https://doi.org/10.1111/j.1466-8238.2011.00738.x>
- Rainho, A., & Palmeirim, J. M. (2017). Understanding the long term consequences of fragmentation: Lessons from the bats of Bijagós (Guinea-Bissau, West Africa). *Hystrix, The Italian Journal of Mammalogy*, 28, 173–179.
- Ramos Pereira, M. J., & Palmeirim, J. M. (2013). Latitudinal diversity gradients in new world bats: Are they a consequence of niche conservatism? *PLoS ONE*, 8, e69245. <https://doi.org/10.1371/journal.pone.0069245>
- Reis, N. R., Fregonezi, M. N., Peracchi, A. L., & Shibatta, O. A. (2013). *Morcegos do Brasil: Guia de campo*. Rio de Janeiro, Brazil: Technical Books.
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1, 319–329. <https://doi.org/10.1111/j.2041-210X.2010.00044.x>
- 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. <https://doi.org/10.1016/j.biocon.2009.02.021>
- Rocha, P. A. (2013). Quiroptero fauna cavernícola: fatores influenciam a composição, estrutura de comunidades, distribuição geográfica e aspectos ecológicos das populações. PhD Thesis, Universidade Federal da Paraíba, João Pessoa, Brazil.
- Rocha, R., López-Baucells, A., Farneda, F. Z., Groenenberg, M., Bobrowiec, P. E., Cabeza, M., ... Meyer, C. F. (2017). Consequences of a large-scale fragmentation experiment for Neotropical bats: Disentangling the relative importance of local and landscape-scale effects. *Landscape Ecology*, 32, 31–45. <https://doi.org/10.1007/s10980-016-0425-3>
- Sánchez, M. S., & Giannini, N. P. (2014). Altitudinal patterns in two syntopic species of *Sturnira* (Mammalia: Chiroptera: Phyllostomidae) in the montane rain forests of Argentina. *Biotropica*, 46, 1–5. <https://doi.org/10.1111/btp.12082>
- Sánchez-Cordero, V. (2001). Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecology and Biogeography*, 10, 63–76. <https://doi.org/10.1046/j.1466-822x.2001.00235.x>
- Santos, C. S. (2013). Quiroptero fauna da Reserva Ecológica de Guapiaçu, Cachoeiras de Macacu, RJ: considerações sobre a composição e a diversidade e comparações com comunidades de morcegos de outras áreas de Mata Atlântica no Sudeste do Brasil. PhD Thesis, Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.
- Schnitzler, H., & Kalko, E. (1998). How echolocating bats search and find food. In T. H. Kunz, & P. A. Racey (Eds.), *Bat biology and conservation* (pp. 183–196). Washington, DC and London, UK: Smithsonian Institution Press.
- Shanee, S., & Peck, M. (2008). Elevational changes in a neotropical fig (*Ficus* spp.) community in North Western Ecuador. *iForest-Biogeosciences and Forestry*, 1, 104–106. <https://doi.org/10.3832/for0462-0010104>
- Silva, W., Metzger, J., Simões, S., & Simonetti, C. (2007). Relief influence on the spatial distribution of the Atlantic Forest cover on the Ibiúna Plateau, SP. *Brazilian Journal of Biology*, 67, 403–411. <https://doi.org/10.1590/S1519-69842007000300004>
- Soriano, P. J. (2000). Functional structure of bat communities in tropical rainforests and Andean cloud forests. *Ecotropicus*, 13, 1–20.
- Soriano, P. J., Ruiz, A., & Arends, A. (2002). Physiological responses to ambient temperature manipulation by three species of bats from



- Andean cloud forests. *Journal of Mammalogy*, 83, 445–457. [https://doi.org/10.1644/1545-1542\(2002\)083<0445:PRTATM>2.0.CO;2](https://doi.org/10.1644/1545-1542(2002)083<0445:PRTATM>2.0.CO;2)
- Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, 133, 240–256. <https://doi.org/10.1086/284913>
- Stevens, R. D. (2006). Historical processes enhance patterns of diversity along latitudinal gradients. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2283–2289. <https://doi.org/10.1098/rspb.2006.3596>
- Stevens, R. D. (2011). Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2528–2536. <https://doi.org/10.1098/rspb.2010.2341>
- Stevens, R. D. (2013). Gradients of bat diversity in Atlantic Forest of South America: Environmental seasonality, sampling effort and spatial autocorrelation. *Biotropica*, 45, 764–770. <https://doi.org/10.1111/btp.12056>
- Tavares, V. C. (2013). Phyllostomid bat wings from Atlantic Forest bat ensembles: An ecomorphological study. *Chiroptera Neotropical*, 19, 57–70.
- Teeling, E. C., Springer, M. S., Madsen, O., Bates, P., O'Brien, S. J., & Murphy, W. J. (2005). A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science*, 307, 580–584. <https://doi.org/10.1126/science.1105113>
- Terborgh, J. (1977). Bird species diversity on an Andean elevational gradient. *Ecology*, 58, 1007–1019. <https://doi.org/10.2307/1936921>
- Trajano, E. (1996). Movements of cave bats in southeastern Brazil, with emphasis on the population ecology of the common vampire bat, *Desmodus rotundus* (Chiroptera). *Biotropica*, 28, 121–129. <https://doi.org/10.2307/2388777>
- Ururahy, J. C. C., Collares, J. E. R., Santos, M. M., & Barreto, R. A. A. (1983). *Folhas SF.23/24 Rio de Janeiro/Vitória; geologia, geomorfologia, pedologia, vegetação e uso potencial da terra*. Rio de Janeiro, Brazil: Ministério das Minas e Energia.
- Veloso, H. P., Rangel Filho, A. L. R., & Lima, J. C. A. (1991). *Classificação da vegetação brasileira, adaptada a um sistema universal*. Rio de Janeiro, Brazil: Ministério da Economia, Fazenda e Planejamento, Fundação Instituto Brasileiro de Geografia e Estatística, Diretoria de Geociências, Departamento de Recursos Naturais e Estudos Ambientais.
- Weier, S. M., Linden, V. M., Gaigher, I., White, P. J., & Taylor, P. J. (2017). Changes of bat species composition over altitudinal gradients on northern and southern aspects of the Soutpansberg mountain range, South Africa. *Mammalia*, 81, 49–60.
- Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., ... Harrison, S. P. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, 13, 1310–1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>
- Willig, M. R., & Presley, S. J. (2016). Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. *Journal of Tropical Ecology*, 32, 421–436. <https://doi.org/10.1017/S0266467415000589>
- Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, 40, 2310–2323. <https://doi.org/10.1111/jbi.12177>
- Zhou, Z., Zhang, S., Xiong, K., Li, B., Tian, Z., Chen, Q., ... Xiao, S. (2017). The spatial distribution and factors affecting karst cave development in Guizhou Province. *Journal of Geographical Sciences*, 27, 1011–1024. <https://doi.org/10.1007/s11442-017-1418-0>

## BIOSKETCH

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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