The prevalence of temperature and dispersal limitation as drivers of diversity in Neotropical small mammals

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Abstract   The spatial distribution of biodiversity is driven by species dispersal and their response to the environment. Therefore, diversity patterns should differ across taxonomic groups depending on differences in traits associated with dispersal, metabolism, and foraging. We compared the distribution of rodents and marsupials in the Atlantic forest and investigated how species traits direct their responses to climate, habitat loss, and habitat fragmentation. To understand the effect of historic processes associated with dispersal and environmental filters, we also tested for the association of the taxonomic, functional, and phylogenetic dissimilarities with spatial distance and differences in climate and habitat loss. We hypothesise that marsupials would be more limited by the temperature gradient than rodents, which are more cold-tolerant and dispersal-limited. We compiled a database of 73 sites with data on small-mammal species occurrences and conducted multiple regression analyses to determine the influence of the environment on species richness and trait measures. Multiple regressions on distance matrices (MRM) were used to assess the relationship of species taxonomic, functional, or phylogenetic dissimilarities with geographical and environmental distances. Species with higher tail/body ratio and arboreality were found in warmer temperatures, but species richness increased mostly in areas with low precipitation and large forest fragments. Taxonomic dissimilarity was mostly associated with geographic distance and the distance-decay relationship was steeper for taxonomic than for phylogenetic or functional dissimilarities. As predicted, temperature had a stronger effect on the trait distribution of marsupials than of rodents. However, for both groups, spatial distance was the most important predictor of species dissimilarity. These results might suggest that, at broad scales, dispersal shaped the distribution of Neotropical small-mammal regardless of species adaptations to climatic conditions.

Key words: environmental filtering, functional diversity, marsupials, neutral processes, rodents.

INTRODUCTION

The natural distribution of a species in a region is determined by its dispersal limitation and its adaptation to environmental conditions (Qian 2008; Cáceres *et al.* 2014). The distribution ranges of dispersal limited taxa show strong associations to geographical barriers (like mountain chains, large rivers or dry areas), whereas taxa with specific habitat requirements show strong associations with environmental gradients (Gilbert & Lechowicz 2004; Steinitz *et al.* 2006). In spite of the overall relevance of barriers and the environment, determining their relative importance as constraints of species distributions is usually difficult.

When species ranges are limited by dispersal, evolutionary processes can produce divergent communities over time in areas farther apart from each other (Hubbell 2001). However, distant areas also have distinct environments (Tuomisto *et al.* 2003; Chang *et al.* 2013), and this correlation makes it difficult to attribute the spatial segregation of species solely to dispersal limitation or selection by the environment. Although spatial barriers and environmental gradients can cause similar patterns in species distribution, the split of phylogenetic lineages by geographical barriers can provide clues about the effect of dispersal limitation (Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009). Similarly, the association of species traits and environmental conditions can indicate that environmental filtering is important (Cáceres *et al.* 2014). Therefore, comparing taxa with distinct traits and evolutionary histories can help to assess the relative importance of the effects of dispersal limitation and selection by the environment.

Marsupials and rodents are widely distributed in the Neotropical Region, but different processes are likely to affect the distribution of species in these groups (Maestri & Patterson 2016; Cerezer *et al.* 2022). Marsupials tend to be larger than rodents (average biomass of 349g vs. 62 g; Schloss *et al.* 2012), more mobile (dispersal velocity of 1.645 km/yr vs. 1.475 km/yr; Schloss *et al.* 2012) and have

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broader distributions than rodents (Davis 1945; Moraes & Chiarello 2005; Püttker *et al.* 2006). In other words, rodents have slower dispersal than marsupials, being more prone to be limited by geographical barriers. Despite the taxonomic variability in morphology, mobility and range size differences that could affect the distribution of Neotropical marsupials and rodents are poorly known, as well as how species with distinct traits or from different lineages are distributed along geographical barriers and environmental gradients.

The Atlantic Forest is the second largest tropical forest in the continent, and it extends from the northeast to the southeast coast of Brazil, reaching eastern Paraguay and north-eastern Argentina. This ecosystem harbours several endemic and patchily distributed species, such as rodents, distributed in a north-south biogeographic gradient (Costa *et al.* 2000; Maestri *et al.* 2019). Due to the high level of biotic endemism, the Atlantic Forest has been recognised as a hotspot of biodiversity (Myers *et al.* 2000). Besides, the Atlantic Forest is not homogenous, exhibiting different biogeographic regions in the north-south gradient (Costa *et al.* 2000) that historically are supposed to be faunal refuges (Carnaval & Moritz 2008). This regional segmentation of the Atlantic Forest is driven by different geographic features like rivers (e.g. Doce River), mountains (Espírito Santo Mountain), and plains, which act as barriers for species with low dispersal abilities (Pellegrino *et al.* 2005; Carnaval & Moritz 2008; Leite *et al.* 2016), particularly small-mammal clades (Leite *et al.* 2016; Maestri & Patterson 2016; Maestri *et al.* 2019). This ecosystem encompasses a large latitudinal gradient, covering annual mean temperatures from 12 to 25 degrees and annual precipitation from 1100 to 2500 mm (Carnaval *et al.* 2014; de la Sancha *et al.* 2014; Dambros *et al.* 2015). However, this ecosystem is also highly fragmented and disturbed (Ribeiro *et al.* 2009) by human populations that are distributed in around 3,000 cities (Morellato & Haddad 2000).

Focusing on small mammals, different biogeographic patterns have been observed in rodents and marsupials. At a continental level, rodent diversity appears to be more affected by rainfall regimes than marsupial diversity (Maestri & Patterson 2016; Cerezer *et al.* 2022). Additionally, an important effect can be expected regarding habitat loss (Fahrig 2013) and local patch area, which vary greatly across the Atlantic Forest (de la Sancha *et al.* 2020). A recent study comparing habitat loss (forest cover) and patch size (habitat fragmentation) revealed that the latter is more important for small-mammal species diversity in the Atlantic Forest (but note that habitat loss was measured at a relatively small scale – 500 m radius buffer; Bovendorp *et al.* 2018).

Regarding local diversity, we investigated how climatic, habitat loss, and fragmentation gradients are associated with marsupial and rodent species richness and functional traits. We hypothesised that, overall, marsupials' distributions would be more positively associated with the temperature gradient than rodents, with the rodents being more cold-tolerant (McNab 2008; Sánchez-Villagra 2013) and having a lower dispersal rate (Schloss *et al.* 2012). If this hypothesis is true, we can derive the following predictions: at the local scale, (1) marsupial species richness and body mass have stronger associations with the temperature gradient than rodents; (2) rodent species richness has a stronger association with the precipitation gradient, and (3) marsupial functional diversity is more correlated to the environmental variation (because their better dispersal ability; Cáceres *et al.* 2014) such as increasing mean body size in landscapes with less forest cover or having proportionally longer tails in warmer places (Alroy 2019; Melo 2022).

Regarding beta-diversity, we tested for the association of the taxonomic, functional, and phylogenetic similarity in the assemblage composition of marsupial and rodent species with geographic distance, climatic difference, and degree of habitat loss. De la Sancha *et al.* (2020) found that climatic variables (temperature and precipitation) are important drivers of the small-mammal beta diversity gradient in the Atlantic Forest but they did not test the concomitant effect of the spatial distance. Taking into account that rodents are more cold-tolerant and are more limited in dispersal than marsupials (McNab 2008; Schloss *et al.* 2012; Sánchez-Villagra 2013), we can derive the following predictions: (1) rodent assemblage similarity is more strongly associated with spatial distance, whereas marsupial assemblage similarity is more strongly associated with differences in temperature or habitat loss; (2) marsupial functional similarity is expected to be more correlated with the climatic gradients than that of rodents, and (3) the decay of phylogenetic and functional similarity is steeper in rodents than in marsupials, being more correlated with the geographical distance than environmental differences.

METHODS

Study site

The data compiled for this study were collected across the entire area recognised as the Atlantic Forest (Appendix S1). This ecoregion encompasses an extent of 98,800 km^2 of remnants, of which only 7.6% has remained intact, distributed mostly in small and medium-sized forest patches (Morellato & Haddad 2000). Habitat types in intact areas include rainforests, mixed *Araucaria* moist forests, deciduous forests,

and upland grasslands. Rainforests tend to occur near the coast, whereas deciduous forests occur far from the coast and *Araucaria* forests are common in the south. The climate is moist tropical and subtropical, without a defined dry season, and with annual mean temperatures above 15°C (Leite 2002).

Data collection

We compiled a database of 46 studies from the primary literature, plus four unpublished studies from our research team, in which small mammals were sampled in the Atlantic Forest (Appendix S2). We used the Google Scholar search tool with the keywords 'small mammal', OR 'marsupial', OR 'rodent', combined with (AND) 'community', 'composition', 'richness', 'diversity' and 'Atlantic Forest'. In our database, we included only those studies that established a minimum sampling effort of at least 1000 trap-nights, 6 months of fieldwork and use of wire and/or Sherman live-traps installed on the ground or understory level of the forest. The studied areas (patch size) ranged from 5 to 185,000 ha (mean = 16,295), with sampling effort from 600 to 64,000 h of trapping (mean = 9,178). The distance between sites ranged from 31 to 3,249 km (mean = 1026). The sampling sites ranged from 32°33'S to 8°15'S and from 54°58'12"W to 35°4'48"W. The number of species recorded in each study ranged from 1 to 27 (mean = 8.16). From each selected survey, we obtained the presence and absence data from all studied species. We recorded 73 sites where didelphid marsupial and cricetid rodent assemblages were sampled (Appendix S1). Our database differs from another available Atlantic-Forest small mammal database (Bovendorp *et al*. 2017) because it has fewer small mammal species but, after corrections for imprecise coordinate locations and low sample size in most locations (reduction from 300 locations to 132; see Melo 2022), the differences are reduced both in the number of locations (73 vs. 132) and species (e.g. 21 marsupial species are present in our database vs. 27 in the corrected database of Bovendorp *et al*. 2018). Furthermore, our database was validated in a recent high-standard publication (Dambros *et al*. 2015). The difference in species richness is given by marginal species from the other adjacent biomes.

To reduce variation in the data caused by differences in sampling among studies and to improve detection of rare species in each sampling unit, we grouped small mammal data into 38 1×1 degree grid cells. In addition, to account for possible sampling effects, we included the average number of trapping hours in each grid cell as a covariate in our models (description below).

In each cell, we obtained species presence-absence data as response variables and measures of vegetation cover, mean annual temperature, and mean annual precipitation as predictor variables (Table 1). Climatic variables (temperature and precipitation) were obtained from Bioclim (http://www.worldclim.org/bioclim) in 2.5 arc minutes rasters. Vegetation cover was obtained from the Ministério do Meio Ambiente, Brazil (http://mapas.mma.gov.br), and was measured as the percentage of forest cover (i.e. habitat loss) in a 20 km radius from the centre of each sampled locality and after transformed to a mean value for each cell. Forest patch area was computed according to the information given in each publication where we gathered the animal data.

We obtained trait data for individual species from Jones *et al*. (2009) and Paglia *et al*. (2012). For each individual species, we calculated relative tail length (tail length divided by head-body length) and body mass. These traits are usually associated with the vertical use of habitat, dispersal limitation, and basal metabolism (Miles *et al*. 1987; McNab 2008; Whitmee & Orme 2013). To differentiate how species use the habitat based on locomotion, we classified species into five categories and attribute a numeric value for locomotion using the following behavioural habits: arboreal (5), scansorial (4), terrestrial (3), semiaquatic (2), and semifossorial (1) (Appendix S3). That is, the higher the locomotion value, the higher is the dispersal capacity. Although this rule is not always true when comparing pairs of species due to the large variation in arboreal and terrestrial species, it is valid for most comparisons regionally (e.g. scansorial species, such as *Sooretamys angouya* and *Philander quica* (=*frenata*), having more dispersal capacity than terrestrial and semifossorial species; Schloss *et al*. 2012). We also used the diet breadth to evaluate the dimensionality of dietary niche, by counting the number of dietary categories appearing in species samples according to the PanTheria database (Jones *et al*. 2009).

Phylogenies for each taxonomic group were obtained from Faurby and Svenning (2015). The authors provided the 100 ultrametric trees with the highest posterior probability estimated by Bayesian inference (Faurby & Svenning 2015). All analyses were repeated using each individual tree (see below).

Analyses

To characterise the local diversity in each grid cell, we measured species richness and performed the Forth-Corner analysis of each trait as an alternative method to the CWM (Community Weighted Means; Peres-Neto *et al*. 2016). In addition, we reported the CWM of each trait in the supplementary material (Appendix S4). To measure changes in species composition (i.e. identity) between pairs of grid cells (beta-diversity, an important component of the regional diversity), we calculated the Sorensen pairwise similarity index. The Sorensen index of species composition was calculated using species presence-absence data only (taxonomic similarity), and presence-absence data weighted by species traits (functional similarity; Villéger *et al*. 2013) and species position in a phylogeny (phylogenetic similarity; Leprieur *et al*. 2012).

The Sorensen similarity index is based on the number of shared species between pairs of cells (Baselga 2010). However, the Sorensen index is also affected by differences in the number of species between cells and may be correlated with species richness as well as the turnover in species composition. To investigate the changes in species composition between two cells independently from differences in species richness, we partitioned the Sorensen similarity index into the turnover and nestedness components (Baselga, 2010), and used these components as response variables in further analyses of species composition.

Table 1.   List of variables and related terms used in this study, based on our hypotheses

Scale	Response variable	Type	Predictors (hypotheses)	Related terms
Local (alpha)	Species richness and Trait diversity	Taxonomic and functional	Environment (niche)	Environmental filtering, adaptation
Local to regional (beta)	Pairwise dissimilarity in species composition	Taxonomic, phylogenetic, and functional	Differences in environment (niche) and geographical distance (neutral)	Environmental filtering (niche); dispersal limitation (neutral), similarity and dissimilarity, distance-decay (both).

Phylogenetic similarity was calculated independently for each of the 100 phylogenetic trees with the highest posterior probability provided by Faurby and Svenning (2015). We used the average similarity in species composition obtained in the 100 phylogenies for all models.

For local diversity analyses, we conducted multiple regression analyses to determine the association of species richness or Forth-Corner trait measures (response variables) with temperature, precipitation, forest cover, and patch area (predictor variables) (Table 1). Sampling effort (total time of sampling) in each grid cell was included as a covariate in all multiple regression models.

For beta-diversity analyses, we compared the effects of geographical distance and environmental distances on the overall similarity in species composition and on the turnover and nestedness components of similarity. We calculated the spatial distance and environmental distance between all pairs of grid cells. We then performed multiple regressions on distance matrices (MRM) using species taxonomic, functional, or phylogenetic similarity as response variables and geographical and environmental distances as predictor variables (Table 1). Permutation tests were used for significance testing (999 permutations; Millar *et al*. 2011).

All analyses were conducted in the R program (R Core Team, 2019) using the raster (Hijmans *et al*. 2015), vegan (Oksanen *et al*. 2016), betapart (Baselga *et al*. 2017) and ecodist (Goslee & Urban 2007) packages.

RESULTS

Overall taxa distribution

We recorded 52 small-mammal species, 21 of didelphid marsupials and 31 of cricetid rodents. Variation in mean body size was greater for marsupials (11 to 1250 g) than for rodents (20 to 249 g). Marsupials included species from arboreal lifestyle to terrestrial and semiaquatic, whereas rodents varied from arboreal to terrestrial, semiaquatic and semifossorial.

Local diversity

Small-mammal species richness was high in areas with low precipitation mainly in the central areas of the Atlantic Forest and in areas with large forest patches, whereas there is no effect of habitat loss (Table 2). The association of patch size was significant when small mammals were analysed together, but separately, species richness was positively correlated only for rodents. In contrast, rodent species richness was strongly reduced in areas of high temperature, whereas only a positive and non-significant association between species richness and temperature was found for marsupials (Table 2).

Temperature was the most important predictor variable for Forth-Corner traits when considering all species (Table 3, Fig. 1). On average, species with higher tail/body ratio and arboreality (as opposed to fossoriality) were found in warmer temperatures (Table 3, Fig. 1a–b). The increase in temperature towards the northern part of the Atlantic Forest (Appendix S1) was associated with a decrease in diet breadth for marsupials (Fig. 1d, Fig. 2c). In contrast, rodent body mass was not significantly associated with temperature (Table 3) and, besides the geographical trend to the south (Fig. 2b), there is no statistical significance for this relationship in marsupials (Table 3). Patch area was positively associated with body mass only for marsupials (Table 3, Fig. 1c).

Table 2.   Species richness of marsupials and rodents in the Atlantic Forest and predictors for their variation

	Temp	Prec	FCover	Area	Sampling	df	R^2	$R^2_{exc.samp}$
All species	−0.12	−0.41**	0.10	0.32**	0.52***	31	0.66***	0.27***
Marsupials	0.22	−0.51*	0.29	0.04	0.26	26	0.26*	0.24*
Rodents	−0.32*	−0.45**	0.08	0.48***	0.25*	30	0.57***	0.31***

Temp: mean temperature; Prec: annual precipitation; FCover: forest cover measured in a 20 km-buffer radio; Area: patch area size where animals were sampled; Sampling: effort in trap-night. R2 represents the explanatory power of the complete model, whereas R^2exc.samp represents the explanatory power of all variables excluding sampling effort (sampling effects).
   *<0.05, **<0.01, ***<0.001.

Table 3. Alpha diversity of marsupials and rodents in the Atlantic Forest, measured by the Forth-Corner analysis on each trait

	Temp	Prec	FCover	Area	Sampling
All species					
Body mass	−0.02	0.06	−0.08	0.04	−0.05
Habitat	−0.10	−0.02	−0.07	0.01	−0.02
Locomotion	0.24*+	−0.13+	−0.13*	−0.15*+	−0.05
Tail/body ratio	0.21*+	−0.03	−0.04	−0.09*	−0.04
Diet breadth	−0.01	−0.02	−0.12*	−0.02	−0.05
Trophic level	0.04	0.03	0.04	−0.07	0.01
Marsupials					
Body mass	−0.21*	0.12	−0.10	0.18*+	−0.06
Habitat	0.01	−0.14+	−0.07	−0.11	−0.11
Locomotion	0.12	−0.06	−0.04	0	0
Tail:body ratio	0.30*+	0	0.07	−0.08	−0.04
Diet breadth	−0.31*+	0.06	−0.15	0.11	−0.13
Trophic level	−0.01	0.01	0.12*	−0.01	0.09
Rodents					
Body mass	0.12	−0.01	−0.06	−0.02	0.01
Habitat	−0.10	−0.02	−0.09	−0.01	0
Locomotion	0.20*	−0.13+	−0.15*	−0.13*	−0.06
Tail:body ratio	0.16*	−0.04	−0.08	−0.09	−0.05
Diet breadth	0.21*	−0.10	−0.13	−0.11	0.02
Trophic level	−0.04	0.10	0.01	−0.04	−0.06

Temp: mean temperature; Prec: annual precipitation; FCover: forest cover measured in a buffer of 20 km radio; Area: size (ha) of the forest patch; Sampling: local effort in trap-night. *P*-values were calculated by permuting rows and columns of the trait and environment matrices based on Peres-Neto *et al.* (2016). Trait-environment associations were considered significant when both *P*-values were below the 0.05 threshold.
*P-value <0.05 for trait-species occurrence association.
+P-value <0.05 for environment-species occurrence association.

The results from the Forth-Corner analysis were similar to CWM correlations using marsupials and rodents combined. However, when the groups were analysed separately, there was evidence for an association of species occurrences and the environment, but not of species occurrences and species traits, except for the roles of temperature on tail/body ratio and on diet breadth (all species and marsupials), of patch area on locomotion (all species), and the role of patch area on body size (marsupials) (Table 3; Appendix S4).

Beta-diversity

The similarity in species composition strongly decayed with the increase of spatial distance for both groups (Fig. 3a,b), more than with the increase of climatic difference. The decay was mostly associated with the replacement of species than with nestedness, and the decay of taxonomic similarity was steeper than the decay of phylogenetic or functional similarities (Fig. 3). The decay of phylogenetic and functional similarity with spatial distance was steeper for rodents than for marsupials (*P* < 0.02; Fig. 3). For rodents, the phylogenetic similarity was also associated with differences in temperature, precipitation,

and forest cover. There was a stronger correlation between functional and phylogenetic similarities for rodents (*r* = 0.46, *P* < 0.01) than for marsupials (*r* = 0.31, *P* < 0.01). Functional similarity was only weakly associated with environmental or spatial distances when marsupials and rodents were analysed separately, but functional similarity of rodents was associated with geographic distance and precipitation whereas that of marsupials was not (Table 4).

DISCUSSION

Species richness and community weighted means

Contrary to the results reported from studies on a wide variety of taxa (Hawkins *et al.* 2003), small-mammal species richness was lower in areas with the highest precipitation in the Atlantic Forest. Moreover, temperature was not associated with marsupial species richness and was negatively associated with rodent species richness. These results suggest that, at the grain size and geographical extent we are analysing, the gradients of productivity associated with precipitation and temperature are not the main drivers
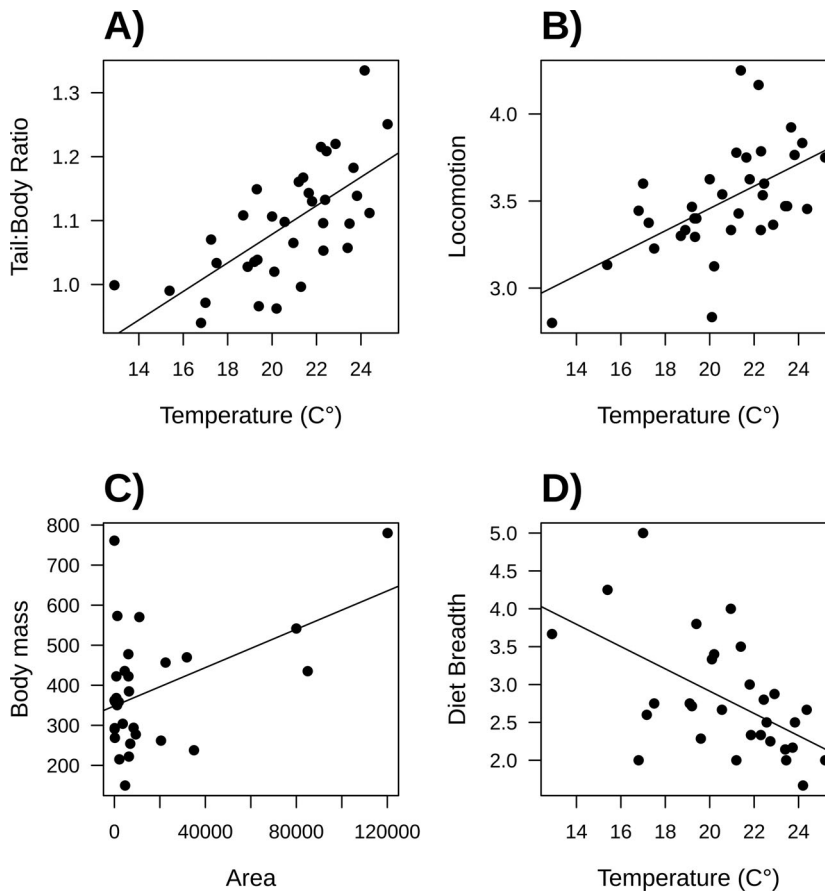
Fig. 1. Relationships between temperature and tail/body ratio (a) and locomotion (b), between patch area (in ha) and body mass (c), between and temperature and diet breadth (d). a, b represent relationships found for all small mammal species. The relationship depicted in c, d was found only for marsupials. Temperature was the environmental variable associated with most changes in average trait values (CWM).

of the distribution of South American small mammals or the latitudinal gradient of species diversity.

In spite of the strong association of rodent species richness with temperature, the direction of this relationship was the opposite of the relationship observed for most taxa (Hawkins *et al.* 2003). The low species richness in the warmer regions of the Atlantic Forest might indicate that sigmodontine rodents are limited by their maximum thermal limits in the region. As the northern Atlantic Forest has the highest mean temperature (Appendix S1), rodent communities there should be around their upper thermal limit (see Bozinovic *et al.* 2014), which is accentuated due to the proximity of Caatinga semi-desert. The finding that South-American rodent diversity peaks in the Andes, and not in the warmer Amazonia, also supports this interpretation (Maestri & Patterson 2016).

The Atlantic Forest has a specific climatic structure compared to the South American continent as a whole: the northern region of the Atlantic Forest is hotter than the southern region because of the proximity of the Caatinga semi-desert (Fiaschi & Pirani 2009; Appendix S1). In addition to its relationship with temperature, rodent species richness was low in areas with high precipitation. These results might suggest that the increase of precipitation in tropical

areas do not necessarily generate higher diversity of species, as expected by the increase of productivity. Previous studies have found similar results for rodents in the whole South American continent (Maestri & Patterson, 2016), and suggested that the distribution of biomes and the presence of the Andes are more important in explaining species richness in the region than precipitation (Maestri & Patterson, 2016).

With respect to overall species traits, small mammals with longer tails and arboreal habits were found in the warmer areas of the Atlantic Forest (Fig. 1a). The central and northern parts of the Atlantic Forest have denser forests with high structural complexity (Pardini *et al.* 2005), which could favour arboreal species with longer tails. As expected, the direct association of tail length and temperature was also stronger for marsupials than for rodents. This suggests that the variation in tail length is more associated with the arboreal, complex habitats in marsupials and that rodents with longer tails are not necessarily arboreal in these habitats. The effect of temperature is expected to be stronger on marsupials than on rodents (Sánchez-Villagra, 2013) and thus the more cold-tolerant species of marsupials will remain in the southern and colder parts of the Atlantic Forest
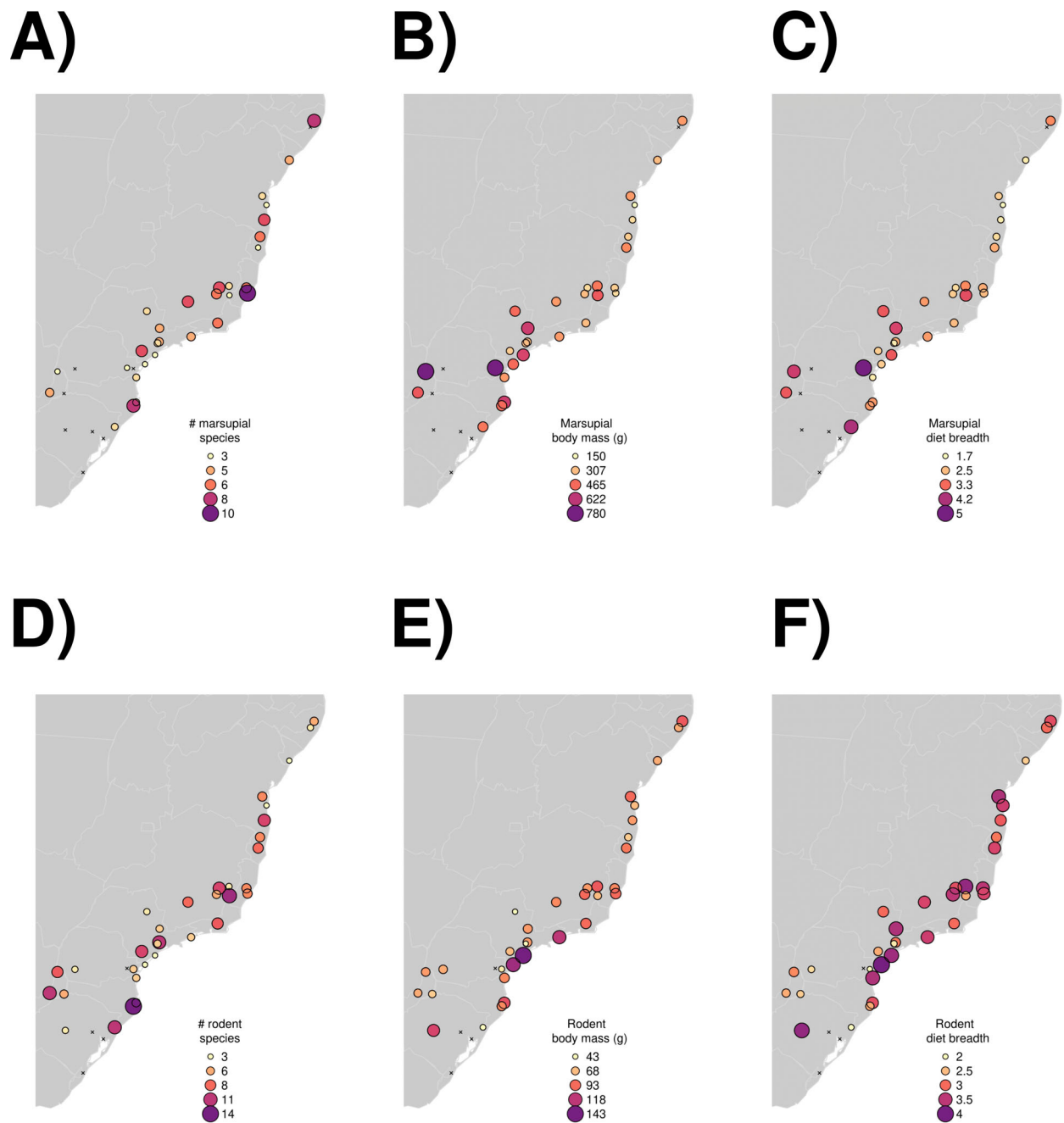
Fig. 2. Marsupial (a–c) and rodent (d–f) species richness, mean body mass, and diet breadth variations across the Atlantic Forest.

(Appendix S1), being less arboreal, larger in size, and more generalist in feeding habit (Table 3, Fig. 1d).

Marsupials and placentals (here represented by rodents) are recognised as having different diversification rates, which are based on their past ecological opportunities (Sánchez-Villagra 2013) and their different physiological adaptations, with placentals being more cold-tolerant than marsupials (McNab 2008).

In contrast to the extensive literature on latitudinal gradients on body mass (Gaston & Blackburn 2000), only a few marsupial species with large bodies increase in frequency in colder regions of the Atlantic forest (Appendix S1). The increase in body mass in colder regions is thought to be a strategy to reduce energy loss (Allen *et al*. 2007) and have been extensively reported in large mammals (Safi *et al*. 2011), especially at the intraspecific level (Meiri & Dayan

Marsupials

Rodents

A)

B)

C)

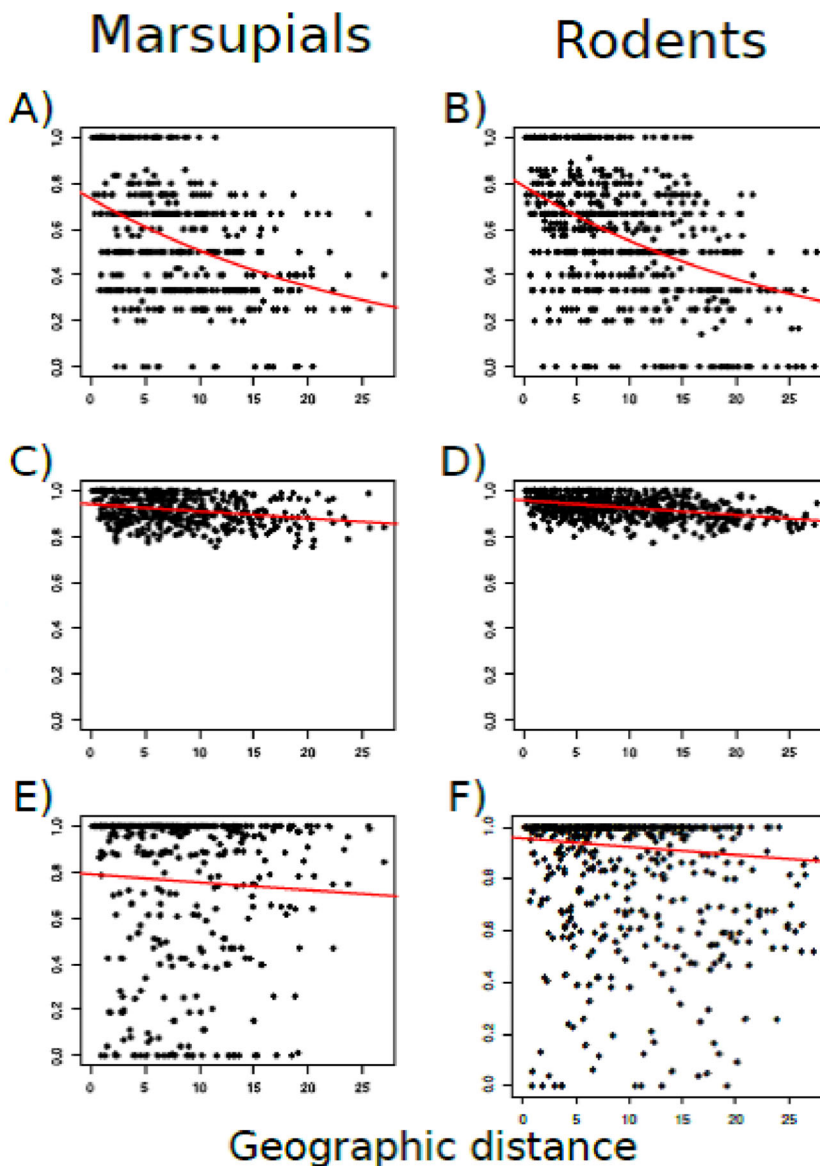D)

E)

F)

Geographic distance

Fig. 3. Taxonomic (a, b), phylogenetic (c, d) and functional (e, f) Simpson similarities (i.e. the complement of the turnover component of beta diversity) in response to spatial distance for paired small mammal communities in the Atlantic Forest.

2003; Meiri *et al*. 2007). Although the increase of body mass towards the colder regions might allow some marsupial species to occupy these habitats (e.g. *Didelphis* spp.), we have not found a consistent pattern across species (i.e. larger species are not necessarily more frequent in colder regions). These results contrast with those observed for rodent species richness, which strongly increased at low temperatures, evidencing the adaptation of most species to cold climates (see Sánchez-Villagra 2013 for a comparative view between marsupials and placentals).

In accordance with the energy efficiency hypothesis (Somveille *et al*. 2018), we found that marsupial species in colder regions had a broader diet. Diet breadth could increase because animals are either more mobile (home range encompasses larger areas), have a broader range of distribution, or have higher energetic requirements. Although marsupial

communities in cold regions were dominated by larger species such as *Didelphis*, exhibiting higher movement rates and wider diet breadth (Pires *et al*. 2002; Jones *et al*. 2009), temperature was more strongly associated with marsupial diet breadth than to body mass, suggesting that in colder regions marsupials have a broader diet than would be expected by the increase of body mass alone. Therefore, temperature might have an association to diet breadth that is not simply the result of an increase in species body mass.

We found a significant association of body mass of marsupials and patch area, but not with forest cover. According to Melo (2022), habitat loss is expected to drive a relationship of body mass with forest cover, but not with patch area. Here, we did not find any association of body mass with forest cover maybe because our buffer (20 km radius) was too much

Table 4. Beta diversity of marsupials and rodents in the Atlantic Forest

	Spatial distance	Temperature	Precipitation	ForestCover	R-squared
All species					
Taxo. dissimilarity	0.50***	0.09	0.03	0.20	0.31
Taxo. nestedness	−0.14*	−0.06	0.08	0.01	0.03
Taxo. turnover	0.45***	0.10	−0.22	0.15*	0.25
Phylo. similarity	0.21[+]	0.05	−0.03	0.09	0.05
Phylo. nestedness	0.12	−0.11	−0.02	0.04	0.02
Phylo. Turnover	0.18*	0.34***	−0.04	0.01	0.18
Funct. similarity	0.26*	−0.42	0.14	0.02	0.08
Funct. nestedness	0.21*	−0.09	0.20*	−0.55	0.08
Funct. turnover	0.11	0.07	−0.08	0.12	0.03
Marsupials					
Taxo. dissimilarity	0.37***	0.15	0.11	−0.05	0.19
Taxo. nestedness	−0.17*	−0.03	0.22*	−0.09	0.09
Taxo. Turnover	0.36***	0.13	0.12	−0.13	0.20
Phylo. similarity	0.24*	0.19*	0.05	−0.04	0.12
Phylo. nestedness	−0.02	0.05	0.15[+]	−0.02	0.02
Phylo. Turnover	0.23*	0.14	−0.15[+]	0.06	0.11
Funct. similarity	0.07	0.06	0.16[+]	−0.1	0.04
Funct. nestedness	0.07	−0.13[+]	−0.19*	−0.01	0.06
Funct. turnover	−0.01	0.19[+]	−0.03	−0.01	0.04
Rodents					
Taxo. dissimilarity	0.41***	0.18*	0.15*	0.18*	0.29
Taxo. nestedness	−0.26*	0.05	0.13[+]	−0.08	0.08
Taxo. Turnover	0.44***	0.11	0.18*	0.05	0.26
Phylo. similarity	0.30***	0.41***	0.03	0.26***	0.37
Phylo. nestedness	−0.09	0.21*	0.02	0.04	0.04
Phylo. Turnover	0.34***	0.20*	0.01	0.21***	0.25
Funct. similarity	0.16	−0.02	0.25*	0.05	0.09
Funct. nestedness	−0.02	−0.06	0.23*	−0.04	0.05
Funct. turnover	0.20*	0.04	0.04	0.11	0.06

Taxo. = Taxonomic; Phylo. = Phylogenetic; Funct. = Functional. Taxonomic, Phylogenetic and Functional dissimilarities were measured using the Pairwise Sorensen dissimilarity index. Phylogenetic and Functional dissimilarities were measured using the shared phylogenetic branches between communities or the shared functional space in convex hulls delimited by species traits. Sorensen dissimilarities were partitioned into the nestedness and turnover components (Baselga, 2010).
[+]<0.10, *<0.05, **<0.01, ***<0.001.

larger to capture the landscape effects on small mammals; Melo (2022) used a 4 km radius buffer and found important effects. In turn, we found that patch area is positively correlated to marsupial body size. This positive relationship seems to be related to the loss of median to larger sized marsupials (such as species of *Caluromys*, *Marmosa*, *Metachirus*, and *Philander*) in small areas, probably as a consequence of the fragmentation process that the Atlantic forest has been suffering (Morellato & Haddad 2000). This interpretation is also supported by previous results by Bovendorp *et al.* (2018), who found that small-mammal species richness and functional diversity in the Atlantic forest increase with patch area. Interestingly, our finding that body size is positively related to patch size is the opposite of Melo (2022), in which smaller sized species are associated with higher values of forest cover (Püttker *et al.* 2013). This shows that habitat loss (forest cover) and fragmentation (patch size when controlling for forest cover) provide

information on different facets of conservation status (see Pardini *et al.* 2010; Melo *et al.* 2017).

Locomotion was negatively related to forest cover and patch area (Table 3). Although these results are opposite to the expectation, it is important to note that our study only includes forests, and arboreal species were usually present in all communities. Our results might indicate that large and preserved patches have semifossorial species that are sensitive to habitat loss (see Püttker *et al.* 2013 and Melo, 2022, for a terrestrial vs. arboreal perspective). For example, *Oxymycterus judex* and *Thaptomys nigrita* are semifossorial species found predominantly in large patches with high percentages of forest cover (results not shown; see Pardini *et al.* 2005). The presence of these species in such landscapes reduces the average locomotion type observed at the community level. These results could be different if grasslands and other contrasting environments were included in the sampling because locomotion would reflect changes

in species as a direct result of forest loss; not the loss of species caused by indirect changes in the forest environment (e.g. in soil moisture).

Beta-diversity

For marsupials, species with distinct traits (e.g. species with large and small bodies) were frequently found in all regions of the Atlantic Forest (Appendix S1). Consequently, the composition of functional traits, including body size, was not strongly associated with the temperature gradient or spatial distance. However, species were not randomly distributed in the region, so spatial distance was strongly associated with the decay in species taxonomic similarity both for marsupials and rodents.

Changes in the taxonomic similarity between sites decoupled from a functional decay have been observed in plants (Helsen *et al.* 2012; Ricklefs & Renner 2012), birds (Si *et al.* 2016), and bacteria (Louca *et al.* 2017). However, the processes that lead distant areas to have species with similar traits likely differ among these organisms. For taxa that are not dispersal limited, such as bacteria (Louca *et al.* 2017), colonisation of species from a regional pool followed by competitive exclusion or niche filling can lead all areas to have distinct sets of species (all niche space is occupied by distinct species). However, the taxonomic composition of both marsupials and rodents was strongly associated with the spatial distance (Fig. 3), which suggest that dispersal limitation is important for small mammals (Dambros *et al.* 2015).

Geographically distant communities evolving under similar environments might converge to have species with similar traits (Losos 2008; Cavender-Bares *et al.* 2009; Ricklefs & Renner 2012). For example, different *Anolis* lizard species in most of the Caribbean islands occupy similar sets of habitats on each island (Losos 2008). The low variation in functional similarity between sites has been used as evidence of niche filling or convergent evolution following dispersal (Ricklefs & Renner 2012; Penone *et al.* 2016; Louca *et al.* 2017). Although we observed the functional decay in species similarity with spatial distance to be weaker than the taxonomic decay, we have not found the local variability in species traits to be higher than would be expected by chance (previous section; Table 3). Moreover, functional beta diversity was not associated with any climatic or habitat variable measured but was associated only with spatial distance. As we expected for beta-diversity (prediction 2), rodent taxonomic and phylogenetic similarities were more associated with geographic distance than the taxonomic and phylogenetic similarity of the more mobile marsupials (Schloss *et al.* 2012).

Nevertheless, both groups show stronger associations of species similarity with spatial distance than to any other measured environmental variable, although they are important to explain diversity variation in the entire group (de la Sancha *et al.* 2020). These results might suggest that species dispersal is more important for Neotropical small mammal distribution than adaptations to climatic conditions, especially for rodents (but see the findings of Maestri & Patterson 2016).

CONCLUSION

Mammals are thought to have more variable traits in tropical regions because these regions have a diverse range of available niches (Safi *et al.* 2011). We have found species mean traits to differ between tropical and subtropical regions of the Atlantic Forest along the temperature gradient, and that marsupial and rodent species respond differently to temperature gradients (alpha diversity and mean traits). In spite of these differences, there is no evidence that species within marsupial and rodent taxa are occupying different niches throughout the temperature, precipitation, or forest cover gradients. While mixed support exists for the effect of the environment on species distribution, our current and previous results (Dambros *et al.* 2015) consistently reveal an effect of spatial distance on beta-diversity, which might suggest that dispersal limitation (either contemporary or historic) is the main driver of species beta diversity in the Neotropics.

AUTHOR CONTRIBUTION

Cristian Dambros: Conceptualization (equal); Formal analysis (equal); Validation (equal); Writing – original draft (equal). **Nilton Carlos Caceres:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Writing – original draft (equal). **Andres Baselga:** Conceptualization (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal).

CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

Supplementary material will be available for readers after publication.

REFERENCES

Allen A. P., Gillooly J. F. & Brown J. H. (2007) Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. In: *Scaling Biodiversity* (eds G. Storch, P. Marquet & J. H. Brown) pp. 283–99. Cambridge University Press, Cambridge.

Alroy J. (2019) Small mammals have big tails in the tropics. *Glob. Ecol. Biogeogr.* **28,** 1042–50.

Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. *Glob. Ecol. Biogeogr.* **19,** 134–43.

Baselga A., Orme D., Villeger S., De Bortoli J. & Leprieur F. (2017) *Partitioning beta diversity into turnover and nestedness components.* Package betapart Version: 1–4.

Bovendorp R. S., Brum F. T., McCleery R. A. *et al.* (2018) Defaunation and habitat loss erode small mammal diversity dimensions in tropical forests. *Ecography* **69,** 473–514.

Bovendorp R. S., Villar N., Abreu-Junior E. F. *et al.* (2017) Atlantic small-mammal: a dataset of communities of rodents and marsupials of the Atlantic forests of South America. *Ecology* **98,** 2226.

Bozinovic F., Ferri-Yáñez F., Naya H., Araújo M. B. & Naya D. E. (2014) Thermal tolerances in rodents: Species that evolved in cold climates exhibit a wider thermoneutral zone. *Evol. Ecol. Res* **16,** 143–52.

Cáceres N. C., Dambros C. S., Melo G. L., Sponchiado J., Della-Flora F. & Moura M. O. (2014) Local randomness, vegetation type and dispersal drive bird and mammal's diversity in a tropical South American region. *Ecosphere* **5,** art114.

Carnaval A. C. & Moritz C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *J. Biogeogr.* **35,** 1187–201.

Carnaval A. C., Waltari E., Rodrigues M. T. *et al.* (2014) Prediction of phylogeographic endemism in an environmentally complex biome. *Proc. Royal Soc. B: Biol. Sci.* **281,** 20141461.

Cavender-Bares J., Kozak K. H., Fine P. V. & Kembel S. W. (2009) The merging of community ecology and phylogenetic biology. *Ecol. Lett.* **12,** 693–715.

Cerezer F. O., Cáceres N. C., Battistella T. F. & Baselga A. (2022) Species richness and beta diversity of American marsupials. In: *American and Australasian Marsupials: an evolutionary, biogeographical, and ecological approach* (eds N. C. Cáceres & C. R. Dickman) Springer, Cham. (in press).

Chang L. W., Zelenỳ D., Li C. F., Chiu S. T. & Hsieh C. F. (2013) Better environmental data may reverse conclusions about niche-and dispersal-based processes in community assembly. *Ecology* **94,** 2145–51.

Costa L. P., Leite Y. L., Fonseca G. A. & Fonseca M. T. (2000) Biogeography of South American forest mammals: Endemism and diversity in the Atlantic Forest. *Biotropica* **32,** 872–81.

Dambros C. S., Cáceres N. C., Magnus L. & Gotelli N. J. (2015) Effects of neutrality, geometric constraints, climate, and habitat quality on species richness and composition of Atlantic Forest small-mammals. *Glob. Ecol. Biogeogr* **24,** 1084–93.

Davis D. E. (1945) The home range of some Brazilian mammals. *J. Mammal.* **26,** 119–27.

De la Sancha N. U., Higgins C. L., Presley S. J. & Strauss R. E. (2014) Metacommunity structure in a highly fragmented forest: has deforestation in the Atlantic Forest altered historic biogeographic patterns? *Divers. Distrib.* **20,** 1058–70.

De la Sancha N. U., Maestri R., Bovendorp R. S. & Higgins C. L. (2020) Disentangling drivers of small mammal diversity in a highly fragmented forest system. *Biotropica* **52,** 182–95.

Fahrig L. (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. *J. Biogeogr.* **40,** 1649–63.

Faurby S. & Svenning J. C. (2015) A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Mol. Phylogenet. Evol.* **84,** 14–26.

Fiaschi P. & Pirani J. R. (2009) Review of plant biogeographic studies in Brazil. *J. Syst. Evol.* **47,** 477–96.

Gaston K. J. & Blackburn T. M. (2000) *Pattern and Process in Macroecology.* Blackwell Science, Oxford.

Gilbert B. & Lechowicz M. J. (2004) Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Natl. Acad. Sci. USA* **101,** 7651–6.

Goslee S. & Urban D. (2007) *Ecodist: Dissimilarity-based functions for ecological analysis.* R package version, 1.

Hawkins B. A., Field R., Cornell H. V. *et al.* (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84,** 3105–17.

Helsen K., Hermy M. & Honnay O. (2012) Trait but not species convergence during plant community assembly in restored semi-natural grasslands. *Oikos* **121,** 2121–30.

Hijmans R. J., van Etten J., Cheng J. *et al.* (2015) *Package raster. R package.*

Hubbell S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton University Press, Princeton.

Jones K. E., Bielby J., Cardillo M. *et al.* (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090–184. *Ecology* **90,** 2648.

Leite P. F. (2002) Contribuição ao conhecimento fitoecológico do sul do Brasil. *Cien. Amb.* **24,** 51–73.

Leite Y. L. R., Costa L. P., Loss A. C. *et al.* (2016) Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proc. Nat. Acad. Sci. USA* **113,** 1008–13.

Leprieur F., Albouy C., De Bortoli J., Cowman P. F., Bellwood D. R. & Mouillot D. (2012) Quantifying

phylogenetic Beta diversity: Distinguishing between 'True' turnover of lineages and phylogenetic diversity gradients. *PLoS One* **7**, e42760.

Losos J. B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**, 995–1003.

Louca S., Jacques S. M., Pires A. P. *et al.* (2017) High taxonomic variability despite stable functional structure across microbial communities. *Nat. Ecol. Evol.* **1**, 15.

Maestri R. & Patterson B. D. (2016) Patterns of species richness and turnover for the South American rodent fauna. *PLoS One* **11**, e0151895.

Maestri R., Upham N. S. & Patterson B. D. (2019) Tracing the diversification history of a Neogene rodent invasion into South America. *Ecography* **42**, 683–95.

McNab B. K. (2008) An analysis of the factors that influence the level and scaling of mammalian BMR. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **15**, 5–28.

Meiri S. & Dayan T. (2003) On the validity of Bergmann's rule. *J. Biogeogr* **30**, 331–51.

Meiri S., Yom-Tov Y. & Geffen E. (2007) What determines conformity to Bergmann's rule? *Glob. Ecol. Biogeogr* **16**, 788–94.

Melo G. L. (2022) Didelphid marsupials from the Atlantic Forest: Effects of habitat loss and fragmentation per se. In: *American and Australasian Marsupials: an evolutionary, biogeographical, and ecological approach* (eds N. C. Cáceres & C. R. Dickman) Springer, Cham. (in press).

Melo G. L., Sponchiado J., Cáceres N. C. & Fahrig L. (2017) Testing the habitat amount hypothesis for South American small mammals. *Biol. Conserv.* **209**, 304–14.

Miles D., Ricklefs R. E. & Travis J. (1987) Concordance of ecomorphological relationships in three assemblages of passerine birds. *Am. Naturalist* **129**, 347–64.

Millar R. B., Anderson M. J. & Tolimieri N. (2011) Much ado about nothings: using zero similarity points in distance-decay curves. *Ecology* **92**, 1717–22.

Moraes-Junior E. A. & Chiarello A. G. (2005) A radio tracking study of home range and movements of the marsupial *Micoureus demerarae* (Thomas) (Mammalia, Didelphidae) in the Atlantic forest of south-eastern Brazil. *Rev. Bras. Zool.* **22**, 85–91.

Morellato L. P. C. & Haddad C. F. B. (2000) Introduction: The Brazilian atlantic forest. *Biotropica* **32**, 786–92.

Myers N., Mittermeier R. A., Mittermeier C. G., da Fonseca G. A. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–8.

Oksanen J., Blanchet F. G., Friendly M. *et al.* (2016) *Vegan: community ecology package.*

Paglia A. P., da Fonseca G. A., Rylands A. B. *et al.* (2012) Lista Anotada dos Mamíferos do Brasil 2a Edição/ Annotated Checklist of Brazilian Mammals. *Occasional Pap. Conserv. Biol* **6**, 1–82.

Pardini R., Bueno A. A., Gardner T. A., Prado P. I. & Metzger J. P. (2010) Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. *PLoS One* **5**, e13666.

Pardini R., de Souza S. M., Braga-Neto R. & Metzger J. P. (2005) The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biol. Conserv.* **124**, 253–66.

Pellegrino K. C. M., Rodrigues M. T., Waite A. N., Morando M., Yassuda Y. Y. & Sites J. W. Jr (2005) Phylogeography

and species limits in the *Gymnodactylus darwinii* complex (Gekkonidae, Squamata): Genetic structure coincides with river systems in the Brazilian Atlantic Forest. *Biol. J. Linn. Soc. Lond.* **85**, 13–26.

Penone C., Weinstein B. G., Graham C. H. *et al.* (2016) Global mammal beta diversity shows parallel assemblage structure in similar but isolated environments. *Proc. Roy. Soc. B.* **283**, 20161028.

Peres-Neto P. R., Dray S. & ter Braak C. J. (2016) Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography* **40**, 806–16.

Pires A. S., Lira P. K., Fernandez F. A., Schittini G. M. & Oliveira L. C. (2002) Frequency of movements of small mammals among Atlantic Coastal Forest fragments in Brazil. *Biol. Conserv.* **108**, 229–37.

Püttker T., Martins T. K., Bueno A. A., Rossi N. F. & Pardini R. (2013) Respostas de marsupiais da Mata Atlântica à perda e fragmentação do habitat – um índice de vulnerabilidade baseado em padrões de ocupação. In: *Os Marsupiais do Brasil: Biologia, Ecologia, e Conservação* (ed. N. C. Cáceres) pp. 455–70. UFMS, Campo Grande.

Püttker T., Meyer-Lucht Y. & Sommer S. (2006) Movement distances of five rodent and two marsupial species in forest fragments of the coastal Atlantic rainforest, Brazil. *Ecotropica* **12**, 131–9.

Qian H. (2008) Effects of historical and contemporary factors on global patterns in avian species richness. *J. Biogeogr.* **35**, 1362–73.

R Core Team (2019) *R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria. Available from URL: http://www.R-project.org/.

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. *Biol. Conserv.* **142**, 1141–53.

Ricklefs R. E. & Renner S. S. (2012) Global correlations in tropical tree species richness and abundance reject neutrality. *Science* **335**, 464–7.

Safi K., Cianciaruso M. V., Loyola R. D., Brito D., Armour-Marshall K. & Diniz-Filho J. A. (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos. Trans. R. Soc. Lond., B. Biol. Sci.* **366**, 2536–44.

Sánchez-Villagra M. R. (2013) Why are there fewer marsupials than placentals? On the relevance of geography and physiology to evolutionary patterns of mammalian diversity and disparity. *J. Mammal. Evol.* **20**, 279–90.

Schloss C. A., Nuñez T. A. & Lawler J. J. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. USA* **109**, 8606–11.

Si X., Baselga A., Leprieur F., Song X. & Ding P. (2016) Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *J. Anim. Ecol.* **85**, 409–18.

Somveille M., Rodrigues A. S. & Manica A. (2018) Energy efficiency drives the global seasonal distribution of birds. *Nat. Ecol. Evol.* **2**, 962.

Steinitz O., Heller J., Tsoar A., Rotem D. & Kadmon R. (2006) Environment, dispersal and patterns of species similarity. *J. Biogeogr.* **33**, 1044–54.

Tuomisto H., Ruokolainen K. & Yli-Halla M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **299**, 241–4.

Vamosi S. M., Heard S. B., Vamosi J. C. & Webb C. O. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.* **18,** 572–92.

Villéger S., Grenouillet G. & Brosse S. (2013) Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Glob. Ecol. Biogeogr.* **22,** 671–81.

Whitmee S. & Orme C. D. (2013) Predicting dispersal distance in mammals: a trait-based approach. *J. Anim. Ecol.* **82,** 211–21.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Map showing the localization the Atlantic Forest in the eastern South America (at left) and the gradients of altitude, forest cover, precipitation, and temperature (at right).

Appendix S2. List of studies included in the analyses.

Appendix S3. List of species included in the study and their traits.

Appendix S4. Results of CWM (Community Weighted Means).

Appendix S5. Species occurrence versus the temperature gradient in the Atlantic Forest for marsupials (A) and rodents (B). Each line represents a given species, and the color gradient represent the increase in body mass, from the lighter (red) to the heavier (yellow) species.