

Research

Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests

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Forest fragmentation and defaunation are considered the main drivers of biodiversity loss, yet the synergistic effects of landscape changes and biotic interactions on assemblage structure have been poorly investigated. Here, we use an extensive dataset of 283 assemblages and 105 species of small mammals to understand how defaunation of medium and large mammals and forest fragmentation change the community composition and diversity of rodents and marsupials in tropical forests of South America. We used structured equation models to investigate the relationship between small mammal species, functional and phylogenetic diversity with forest size, forest cover and the occurrence of medium and large mammals. The best-fit model showed that defaunation reduced functional diversity, and that species diversity of small mammals increased with forest patch size. Forest cover did not affect functional and phylogenetic diversity. Our results indicate that occurrence of medium and large sized mammals (probably acting as predators, or competitors of small mammals) and forest patch size help to retain species and functional diversity in small mammal communities. Further, the number of species in a small mammal community was critical to the maintenance of phylogenetic diversity, and may have a pronounced influence on the ecological functions played by small mammals. Identifying how phylogenetic and functional diversity change in function of human pressures allows us to better understand the contribution of extant lineages to ecosystem functioning in tropical forests.

Keywords: cascade effect, functional and phylogenetic diversity, Atlantic-small mammals

Introduction

Anthropogenic disturbances such as habitat loss and the decline of large vertebrates populations are primary drivers of biodiversity loss (Foley et al. 2005, Cardillo et al. 2008, Wilkie et al. 2011). Tropical forests hold most of world's biodiversity and are facing dramatic reduction in forest cover and declines in species richness and size of



vertebrate populations. The functional loss of large bodied vertebrates at local, regional or global scales, a phenomena known as ‘defaunation’, has been particularly pronounced in tropical ecosystems (Galetti et al. 2013, 2017, Dirzo et al. 2014), leading to increasing density of smaller fecund species (Young et al. 2015, Galetti et al. 2017). Several studies have shown that large herbivores such as ungulates, can suppress the population of small mammals in savannas and forest ecosystems indirectly, through changes in vegetation structure (e.g. trampling), or directly through food competition (e.g. seed predation) (Belsky 1992, Galetti et al. 2015a, Young et al. 2015). In temperate communities mammalian mesopredators appear to be directly influenced by the abundance and diversity of rodents (Crooks and Soule 1999, Ritchie and Johnson 2009), however, we still do not know if these relationships are present in to species-rich tropical communities (Adler and Levins 1994, Hooper et al. 2005, Galetti et al. 2015b).

Although considerable effort has been devoted to understanding the factors that determine community assembly in human-modified landscapes, most studies have focused on species richness (S) and species diversity (SD), that accounts for species abundance (Umetsu et al. 2008, Pardini et al. 2010, Pavoine and Bonsall 2011, Rocha et al. 2011, Estavillo et al. 2013). These two dimensions of biodiversity consider species to be equally different and are unaffected by the ecological and evolutionary attributes of the species in question. The effects of anthropogenic disturbances, including forest fragmentation, habitat loss and defaunation can shape the community species composition (Umetsu et al. 2008, Galetti et al. 2015b, Beca et al. 2017), but investigating these taxonomic dimensions alone may provide an incomplete or misleading impression on the consequences of human pressure on local, regional or global biodiversity (Cisneros et al. 2015, Oliveira et al. 2016).

Combine the taxonomic dimension of diversity with information on the evolutionary relationship among species (e.g. phylogenetic diversity, PD) and the role of those species in the ecosystem (e.g. functional diversity, FD) can better inform the researcher about the mechanism underlying the community assembly (Faith 1992, Webb et al. 2002, Petchey and Gaston 2006, Poos et al. 2009, Swenson 2014) and the ecosystem services provided by it (Diaz and Cabido 2001, Petchey et al. 2007, Flynn et al. 2009, Trindade-Filho and Loyola 2011). While PD emphasizes the accumulated evolutionary history of a community (Safi et al. 2011, Dreiss et al. 2015), FD provides information about the diversity of ecological, morphological and physiological traits found within it (Petchey and Gaston 2002, Poos et al. 2009). Studies have shown that PD and FD can increase with species richness by chance, since the occurrence of more species should mean that more taxonomic lineages and functional groups are present (Petchey and Gaston 2006, Safi et al. 2011), but these relationships are not necessarily linear (Rosenfeld 2002). Two communities with equal number of species but different in composition might differ significantly in PD and FD (Petchey and Gaston 2006, Safi et al. 2011) due to different

levels of functional redundancy (FR) (Petchey et al. 2007), different evolutionary histories, and/or different environmental disturbances. The loss of functionally unique species may result in a disproportional loss of function from a given ecosystem (Walker 1992, Elmqvist et al. 2003), while functional redundancy maintains system stability during disturbance (Naeem 1998, Gonzalez and Loreau 2009, Kang et al. 2015). Nevertheless, a link between FD and PD would be expected if the functional traits that allow species to persist in the environment are evolutionarily conserved, that is to say, they display phylogenetic signals (Safi et al. 2011, Cadotte et al. 2012, Miller et al. 2017). So far, however, little is known about how PD and FD of wildlife communities change in response to anthropogenic disturbance and environmental conditions, especially in the Neotropical rainforests.

The Atlantic rainforest of Brazil contains 22 species of marsupials and 98 species of rodents (Paglia et al. 2012). Given their small size and rapid reproductive rates, rodents and marsupials are less vulnerable to extirpation from human disturbances compared to larger mammals (Dirzo and Miranda 1991, Keesing 2000, Smith 2001, Gardner et al. 2007, Galetti et al. 2009, Pardini et al. 2010). Yet, many small mammal species are still vulnerable to different drivers of disturbance such as fragmentation, reduced landscape connectivity (Pardini et al. 2010, Banks-Leite et al. 2014), defaunation (Cardillo et al. 2008, Fritz et al. 2009, Lira et al. 2012, Galetti et al. 2015b), and climate change (Loyola et al. 2012) making them ideal models for addressing questions about the direct and indirect causes of environmental change within vertebrate communities (Pickett et al. 2001, Pardini et al. 2010, Lira et al. 2012, Costa et al. 2014, Caudill et al. 2015).

Given the complexity of factors that determine species diversity along environmental changes the use of structural equation model (SEM) is a powerful tool to test direct and indirect causal effects with a series of dependent and independent variables that may be correlated (Grace et al. 2010, Lamb et al. 2014, Hao et al. 2018). For example, a study using SEM revealed that species diversity of mammals depends directly on environmental factors while functional diversity depends on the species evolutionary history (Oliveira et al. 2016). Similarly, cascade effects on forest mammal assemblages using SEM showed that both direct predation by foxes and depletion of understored vegetation by herbivores (indirect effect) were related to a decline in the abundance of non-volant small mammals (Colman et al. 2014).

Here, we test the influence of defaunation, forest patch size and forest cover on the diversity of non-volant small mammal communities in the Atlantic forest of Brazil. We hypothesized that: species (SD), functional (FD) and phylogenetic diversity (PD) will be directly affected by forest size, forest cover and the occurrence of medium and large mammals. We used SEM to the test of direct and/or indirect relationships driving small mammal communities in the Atlantic forest. In the first conceptual model, called ‘direct model’, patch size, percentage of forest cover and defaunation had a direct effect on PD, FD and richness, and PD had a direct effect on FD (Fig. 1a). The second model was the ‘indirect model’, where patch size,

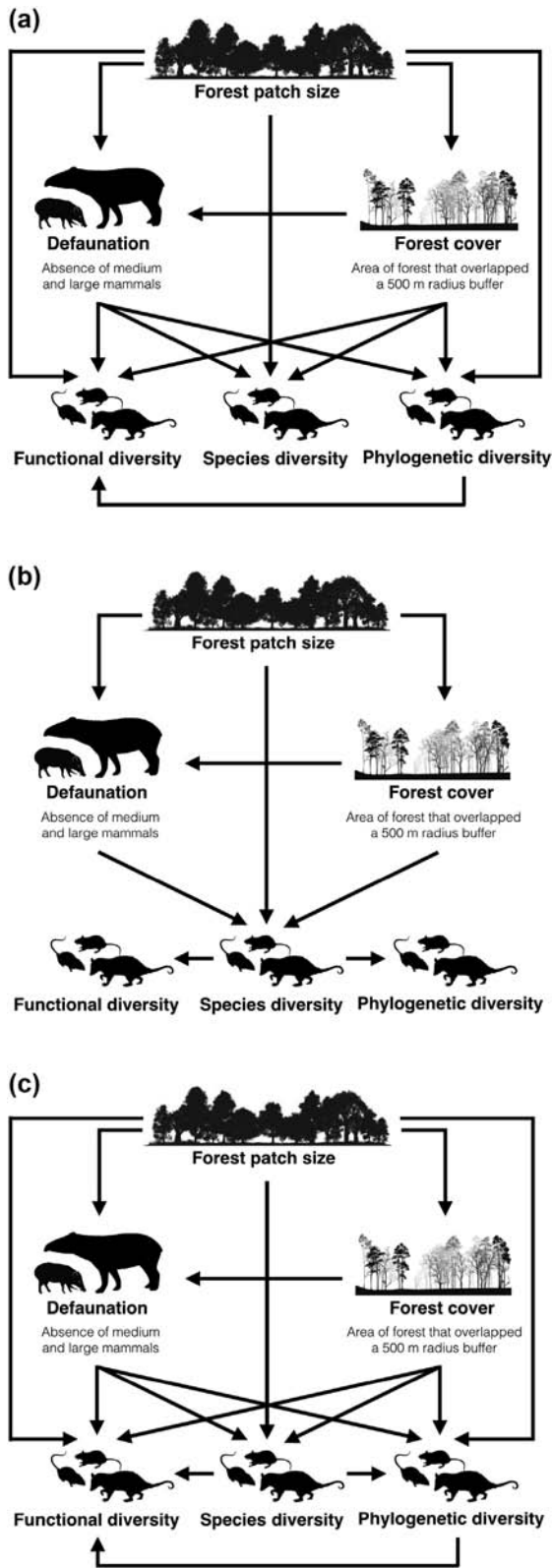


Figure 1. Schematic representation of structural equation models (SEM). Figures with wording represent measured variables. Arrows represent unidirectional relationships among variables. Panel (a) represents the direct model (phylogenetic diversity → functional

percentage of forest cover and defaunaation influence richness first, then richness influences PD and FD (Fig. 1b). The third and last model was the ‘direct + indirect model’, where patch size, percentage of forest cover and defaunaation influenced richness, PD and FD, but richness also influenced PD and FD, a direct effect of PD on FD (Fig. 1c).

Material and methods

Extent of study

The Atlantic forest is considered one of the world’s most species-rich, yet endangered ecosystems (Myers et al. 2000), characterized by a complex topography and a wide latitudinal distribution along the Brazilian coast (from 6° to 31°) and interior of Argentina and Paraguay. These forests provide essential ecosystem services (e.g. carbon sequestration, purification of water and maintenance of soil fertility) for one of the most populated areas of Brazil (Ditt et al. 2010). The forest used to cover more than 150 million ha but currently only ~12% of the original area remains, distributed across ~245 173 forest fragments (Ribeiro et al. 2009). Today, these forest remnants are under threat from illegal hunting (Galetti et al. 2009, 2017), logging (Chiarello 1999), and human-made infrastructure (e.g. pipelines, roads), all of which increase the occurrence of large mammal mortalities (Miotto et al. 2012, Galetti et al. 2017).

We compiled information from 283 study sites (see Small mammal assemblage database topic and Bovendorp et al. (2017b) for more information about the study sites) located in eight vegetation types in the Atlantic forest region: ombrophilous dense (evergreen forest), mixed ombrophilous (characterized by the *Araucaria* forest), seasonal semi-deciduous (tropical moist broadleaf forest), seasonal deciduous (transitional zone between the humid and dry forests) and open ombrophilous (tolerant of wet conditions), and associated ecosystems such as restingas, mangroves and native highland grasslands, which generally are accompanied by mixed or deciduous forests (Veloso et al. 1991, Oliveira-Filho and Fontes 2000). These forests receive between 700–4000 mm of precipitation annually with a distinct dry season with temperature ranges from 10° to 40° C (Morellato and Haddad 2000, Galindo-Leal and Câmara 2003). Sites were located in different biogeographic regions of the Atlantic forest. Most studies were conducted in ombrophilous (66%) and

Figure 1. (Continued)

diversity): the establishment of all possible and plausible causal connections between variables and a connection of phylogenetic diversity to functional diversity; (b) represents the indirect model: all connections between variables connect first to species diversity which then connects to phylogenetic diversity and functional diversity and (c) represents the direct + indirect model (phylogenetic diversity → functional diversity): all links as in the direct model (a), plus the connections from species diversity to phylogenetic diversity and functional diversity in the indirect model (b).

semideciduous (21%) forests (Bovendorp et al. 2017b), which are the dominant vegetation type of this biome (Ribeiro et al. 2009).

Patch size

For each study area, we recorded the size of forest patches in hectares (ha) from the study document or using a shape file for Atlantic forest patches, last updated in December 2008 (Ribeiro et al. 2009), in WGS 84 – EPSG:4326 projection and the polygon function on QGIS® (QGIS 2017). We transformed patch size values into logarithm (Log_{10}) to reduce skewness. Atlantic forest patches have changed little in recent years because the remaining forest patches are located in mountainous or protected areas with little potential for agriculture, livestock or urbanization.

Forest cover

To quantify the percentage of forest cover surrounding sampling sites, we calculated the area of forest that overlapped a 500-m radius buffer around each sampling site using QGIS®. We created buffers using the reported capture station point inside the fragment. The 500-m radius buffer was selected a priori based on studies that used this distance to assess connectivity and quality of habitat (Umetsu et al. 2008, Pardini et al. 2010, Cassano et al. 2014) and the potential dispersal distance of non-volant small mammals from the Atlantic forest Biome (Püttker et al. 2012, 2013).

Medium and large mammal assemblages

We did a literature search in English and Portuguese for studies of medium and large mammals in the same or nearby localities in which we had found the assemblage of small mammals to assess their presence or absence. We also searched for papers not indexed by ‘Web of Science’ and from gray literature, such as dissertations, reports and monographs. We included studies with lists of medium and large mammals, irrespective of survey methods used (Lima et al. 2017). A complete list of studies can be found in Supplementary material Appendix 1. When we could not find information on medium and large mammals at the same site as the small mammals, we used information from the nearest sampled site. This information was used to calculate the defaunation intensity of medium and large mammals for each site in our dataset.

Defaunation intensity

To calculate an index of defaunation intensity for each area, we overlap the range maps of 33 medium and large mammals belonging to three Orders (Carnivora, with 23 species; Artiodactyla, with nine species; and Perissodactyla, with one species) on the 283 studied sites. We downloaded the range maps from IUCN Red List website (<www.redlist.org> – downloaded in May 2017). We did not include animals from the superorder Xenarthra in our index due to absence

of information on them at our sites. The large mammal species used in this study were chosen because of their potential direct competition with and predation on small mammals. Ungulates can modify small mammal habitats by trampling and competing for food with small mammals while carnivores are known to prey on small mammals (Fragoso 1999, Keuroghlian and Eaton 2009, Perez et al. 2012, Galetti et al. 2015a, b). We used these range maps to generate a baseline of the potential community composition (Supplementary material Appendix 2 Fig. A1 Table A1) and used the presence/absence data from the medium and large mammal assemblage database to estimate the actual composition. Then, we calculated the defaunation index (DI) described in Giacomini and Galetti (2013) for medium and large mammals for each community (i.e. sampling site) as follows

$$DI = 1 - \frac{\sum_j^N BWES_j}{\sum_i^N BWES_i}$$

where: N is the total number of species in the community; j is the total number of species in the actual community composition; i is the total number of species in the potential community composition; $BWES$ is the average body mass for each species of medium and large mammal.

To make the scale more intuitive the result of the division of sums was subtracted from 1. Thereby, DI ranged from 0 (non-defaunated sites) to 1 (which indicates a completely defaunated site; Supplementary material Appendix 2 Fig. A2).

Small mammal assemblages

We used the Atlantic small mammal database published by Bovendorp et al. (2017b). For our analysis, we only included studies that live-trapped (Pitfall, Sherman and Tomahawk) mammals on or near the ground (below 1.5-m) and that provided appropriate geographical reference for the forest remnants sampled. From these studies, we compiled a dataset on the sampling effort including, site location (coordinates), patch size (ha), trapping effort (total trap-nights), trapping type (pitfall and live traps). For each sampling site (here considered a community) we recorded the presence, absence, number of species and abundance of small mammal species. A complete list of studies and sites can be found in (Bovendorp et al. 2017a, b).

Trait selection

We used continuous, categorical (binary) and nominal trait data (Table 1) available in the literature (Bonvicino et al. 2008, Paglia et al. 2012). Body mass and tail length are good indicators of species foraging strategies. For example, high structural investment (e.g. high body mass) can provide greater thermoregulation but has greater metabolic costs (Lovegrove 2005), and tail length influences locomotion and balance and indicates which species are arboreal or ground-dwelling (Vieira and Cunha 2008, Prevedello et al. 2010). Adaptation of terrestrial, fossorial, aquatic and arboreal habitat indicate

Table 1. Trait data used to calculate functional diversity of small mammals at Atlantic forest, Brazil.

Type of data	Functional component	Attribute	Trait values
Measure	Size	Body mass	Mean (g)
		Tail length	Mean (mm)
Categorical	Habitat	Terrestrial	0, 1
		Fossorial	0, 1
		Aquatic	0, 1
	Activity	Arboreal	0, 1
		Diurnal	0, 1
		Nocturnal	0, 1
	Food type	Crepuscular	0, 1
		Small vertebrates	0, 1
		Invertebrates	0, 1
		Fruit (pulp)	0, 1
		Seeds	0, 1
		Grass	0, 1
		Leaves branches and bark stem	0, 1
Roots and tubers	0, 1		

where a species spends its time foraging. These adaptations can provide niche partitioning, thus avoiding competition between species along the forest (Prevedello et al. 2010, 2013, Püttker et al. 2013, Galetti et al. 2016). Period of activity (diurnal, crepuscular and nocturnal) has been associated with the sharing of resources and is considered one of the most important components of the niche (Schoener 1974, Graipel et al. 2003). Food resource type is closely related with growth and reproduction and directly associated to the average fitness of organisms (Kozłowski 1992, Lindstrom 1999). The partitioning of food resources between co-occurring species can favor coexistence via lessening the niche overlap and the intensity of interspecific competition (Brown and Lieberman 1973, Palmer et al. 2003, Gibbs and Barrett 2011, Galetti et al. 2016). Most of these traits have been shown to be robust indicators for where a species falls along a few key dimensions of mammalian functional variation (Flynn et al. 2009, Carvalho et al. 2010, Safi et al. 2011) and we provide the linear correlation values between traits (Supplementary material Appendix 2 Fig. A3).

Diversity metrics

For each community, we calculated species functional and phylogenetic diversity using Rao's quadratic entropy (Rao 1982, Botta-Dukát 2005). We choose the Rao's metric since it's less correlated with species richness and was designed as a general dissimilarity metric using a distance matrix among taxa and has been applied to both phylogenetic and trait-based investigations (Swenson 2014).

Because our functional trait matrix included different types of traits (both continuous and categorical), we used an adaptation of Gower's distance to produce the distance matrix (Pavoine et al. 2009). In addition, we split the Atlantic forest in three main regions (northeast, southeast and south) to calculate the SD, PD and FD for each region. This is because it is unlikely that the same individual species occurs in all the

three regions (non-homogeneous pool) (Swenson 2014) due to geographic barriers and distinct biogeographical processes.

For the phylogenetic analysis, we generated a molecular phylogeny. To generate the phylogeny for Atlantic forest small mammals we searched and compiled the cytochrome B sequences for 95 of 105 species present on National Center for Biotechnology Information (NCBI; Bethesda, MD, USA). We exclude 10 species from the analyses that did not have Cytochrome B sequences. To perform the sequence alignment for species we used Geneious[®] (Biomatters) (Kearse et al. 2012). To generate the Atlantic forest small mammal tree, we imported species alignments to MEGA[®] software and generated pairwise distances for each species. We built the phylogenetic tree based on Nei–Gojobori method, widely used to reconstruct mammalian phylogenies (Tobe et al. 2010). Thus, our Atlantic forest small mammal phylogenetic tree had a strong degree of agreement with other phylogenies (Voss and Jansa 2009, Fabre et al. 2012, Jansa et al. 2014) and we used expert validation to insure our phylogenetic tree had the most parsimonious taxonomic inference (Percequillo et al. 2011). We also assessed functional redundancy (FR), which is the difference between functional diversity (FD) and species diversity (SD) (Rosenfeld 2002, Bello et al. 2007). The method is based on the idea that functional redundancy is the part of the species diversity in the community that has not been explained by functional diversity (Pillar et al. 2013). To calculate FR we used the formula

$$FR = SD - FD$$

where SD was calculated by using Simpson's diversity, representing community complexity. The index FR ranges from 0 to 1, which means no redundant species in a community and completely redundant species in community, respectively. All functional and phylogenetic analyses were carried out using 'Vegan' (Oksanen et al. 2016) and 'Picante' packages (Kembel et al. 2010) in the R platform (R Development Core Team).

Analyses

To evaluate how patch size, forest cover and defaunation influence patterns of species, functional and phylogenetic diversity we used path analysis, in which the cause–effect relationships between variables are hierarchically represented and tested by path diagrams (for standardized models design see Supplementary material Appendix 2 Fig. A4) (Shiple 2000, 2013, Lefcheck 2016). We used d-separation procedure (Shiple 2000) to validate/reject the models by evaluating the independent relationships between the variables in each path model (for more detailed information see Supplementary material Appendix 2 Path model analysis).

We needed to remove a causal connection (arrow) to test the model (Supplementary material Appendix 2 Fig. A5) since the direct+indirect model had no independence relationships conceptually (saturated model, no basis set to test). We computed the C statistics for variations of direct + indirect

model, removing one causal relation (arrow) at a time. Then, we chose to remove the causal relationship between forest cover and phylogenetic diversity, because it generated a model with the smallest C statistics (Fisher's test) and the highest p -value ($C=0.2$ and $p=0.903$, Supplementary material Appendix 2 Table A2).

Path models were implemented with generalized linear mixed-effects models framework (GLMM), using trap type (Pitfall, Sherman and Tomahawk traps) and region (north-east, southeast and south) as random effects (Lefcheck 2016). We did not use sampling effort (trap-nights) as a random effect in our analysis because it was strongly correlated with trap type (Bovendorp et al. 2017a). We obtained path coefficients by using the standardized β coefficient. The marginal and conditional coefficients of determination (R^2) describe the proportion of the variance explained by fixed factors alone and together with random factors, respectively (Supplementary material Appendix 2 Table A3).

In addition to the direct causal effects (path coefficients), we also computed the indirect effects and the total net effect of the predictors on species, phylogenetic and functional diversity of small mammals. The Indirect effect was obtained by the product of the path coefficients on the sequence of arrows that lead from a variable to another (Shipley 2000) (Supplementary material Appendix 2 Fig. A6). Since we might have more than one path connecting two variables, we computed the overall indirect effect along all paths, by the sum of all the indirect effects along all paths between two variables. The net effect was then the sum of the direct and the overall indirect effect (Shipley 2000) (Supplementary material Appendix 2 Fig. A6).

As our data were spatially distributed, we evaluated the spatial autocorrelation present in the raw data and in the residuals of the linear models by looking at the Moran's correlogram (Supplementary material Appendix 2 Fig. A7). In all models, spatial autocorrelation was lower in the residuals than in raw data, showing that the predictors captured the spatial structure effectively, avoiding the issue of lack of independence among residuals (Legendre 1993). We conducted our analysis using the R platform (R Development Core Team) and 'piecewiseSEM' (Lefcheck 2016), 'nmls' (Pinheiro et al. 2017) and the 'reghelper' (Hughes 2017) packages. We also use the software SAM (Rangel et al. 2010) for spatial analysis.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.p7h807v>> (Bovendorp et al. 2018).

Results

Our dataset included 105 species of small mammals (Supplementary material Appendix 2 Fig. A8), where south and southeast regions had greater species richness compared to the northeast of Atlantic forest (Fig. 2a). Three exotic

species (*Rattus rattus*, *Rattus norvegicus* and *Mus musculus*) were present in 24.4% of the sites (Fig. 2b).

High values of FD were widely distributed in the Atlantic forest with no significant difference between regions (Fig. 2c), however high PD values were concentrated in the southeast region with significant difference between southeast and south ($X^2=47.8$; $df=2$; $p < 0.01$) and southeast and north-east regions ($X^2=30.8$; $df=2$; $p < 0.01$) (Fig. 2d).

Five families of rodents and one family of marsupials compose our phylogenetic tree (Supplementary material Appendix 2 Fig. A9). Our results showed that the 12 communities with the highest FD and PD were composed of 11 species on average (from 6 to 23) and included forest specialist and generalist species (Supplementary material Appendix 2 Fig. A8, Table A4). The 12 communities with the lowest FD and PD are composed of two species on average (1–4), forest specialist species were absent in these patches and included only habitat and diet generalist species (Supplementary material Appendix 2 Fig. A10, Table A5). Communities with more than five species began to accumulate an intrinsic redundancy of functions and functional redundancy grew slowly after reaching more than 13 species in a community (Fig. 3).

In regards to our three conceptual path models, our best-fit model was the third model, direct+indirect path model (Fisher's $C=0.2$, $K=34$, $df=2$, $p=0.90$) (Table 2). We found that forest patch size and defaunation had direct and indirect effects on species, phylogenetic and functional diversity (Fig. 4, Supplementary material Appendix 2 Table A6). The model indicated that communities in larger forest patches had significantly more small mammal species ($\beta=0.18$, $p < 0.05$), more medium and large mammals ($\beta=0.42$, $p < 0.001$) and a larger percentage of forest cover ($\beta=0.17$, $p < 0.05$). Further, communities with more species had expressively higher phylogenetic diversity ($\beta=0.73$, $p < 0.001$) but lower functional diversity ($\beta=-0.20$, $p < 0.05$).

We also found that communities with more medium and large mammals had significantly lower functional diversity ($\beta=-0.23$, $p < 0.001$), but functional diversity increased with forest patch size ($\beta=0.12$, $p < 0.05$). Communities with high phylogenetic diversity had notably more functional diversity ($\beta=0.68$, $p < 0.001$). Defaunation had a direct negative influence on functional diversity and a direct positive influence on species diversity ($\beta=0.14$, $p < 0.01$) as did forest cover ($\beta=0.13$, $p < 0.05$). Forest cover did not directly influence medium and large mammals or functional diversity and forest patch size and medium and large mammals did not directly influence phylogenetic diversity. However, all three factors (forest patch size, defaunation and forest cover) indirectly influenced functional and phylogenetic diversity through species diversity (Fig. 4, Supplementary material Appendix 2 Table A6).

Discussion

We demonstrate that species, functional and phylogenetic diversity of small mammals are directly and indirectly

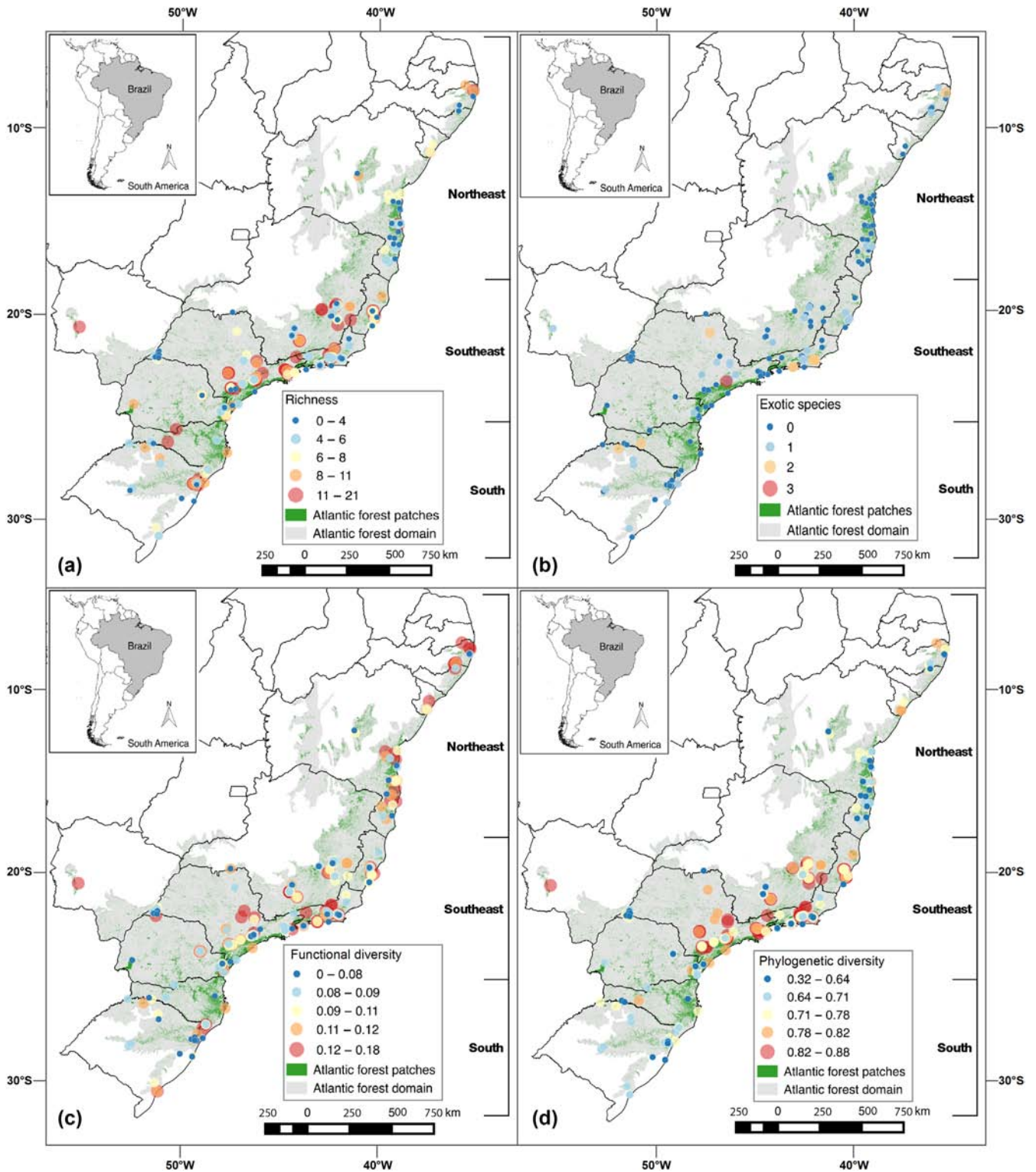


Figure 2. Distribution of (a) species richness; (b) exotic species; (c) functional diversity and (d) phylogenetic diversity of small mammals on Atlantic forest, Brazil.

influenced by landscape attributes (forest patch size, forest cover), but also by the occurrence of medium and large mammals. We found that forest patch size and defaunation level directly and indirectly influence species and functional

diversity and indirectly shape phylogenetic diversity of small mammals. Species diversity had the strongest direct influence on phylogenetic diversity, which in turn had a pronounced influence on functional diversity. Our results also show that

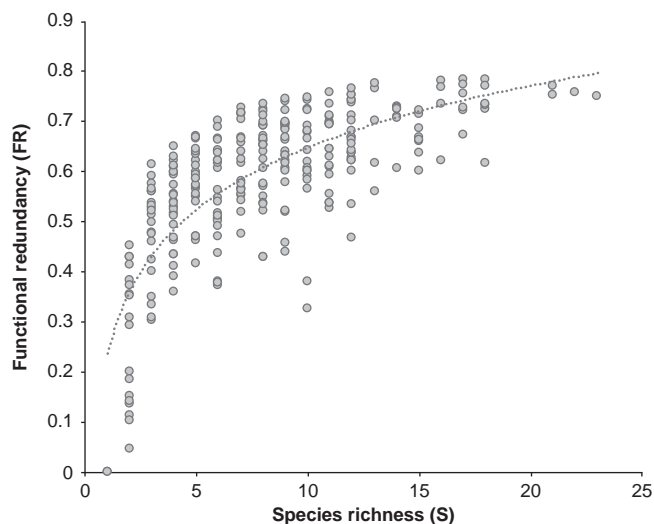


Figure 3. The relationship between functional redundancy and species richness in the communities of small mammals in the Atlantic forest, Brazil. The dashed line represents the logarithmic trend line.

an increased richness of medium and large mammals directly decreased the functional diversity of small mammals. Overall, we demonstrated how species, phylogenetic and functional diversity of small mammals can shift under anthropogenic pressures, allowing us to better understand the relationship between species in defaunated and fragmented Neotropical rainforests.

The significant relationships between both forest patch size and species diversity and forest cover and species diversity for small mammals in the Atlantic forest observed in our best-fit model were also observed in other studies (Pardini 2004, Pardini et al. 2005, Püttker et al. 2011, Estavillo et al. 2013). Larger forest patches and greater forest cover were associated with high species diversity (Pardini et al. 2010) based on a variety of habitat types and levels of habitat complexity (Umetsu et al. 2008). Thus, differences in habitat use among species are important in structuring tropical small mammal communities (Pardini et al. 2005). Our results shown that some species (e.g. *Oligoryzomys nigripes*; *Akodon montensis*) seem not to be affected by anthropogenic pressures, appearing both in low and high phenotypically and functionally diverse communities (Supplementary material Appendix 2 Table A4 and A5), greatly increasing many times in abundance in intermediately-forested landscapes (Estavillo et al. 2013). However, species more sensitive to anthropogenic

Table 2. Concurrent candidate path model through three steps: direct+indirect model selected as best model, indirect model and direct model. All models were generated and concurred with two random effects (region and trap type) fitted on Poisson distribution.

Models	Fisher's C	K	df	P
Direct+indirect (PD → FD)	249.85	34	2	0.903
Indirect	95.4	28	14	< 0.0001
Direct (PD → FD)	0.2	33	4	< 0.0001

pressures, like *Phyllomys brasiliensis* and *Caluromys philander*, were not detected in communities with low PD and FD (Supplementary material Appendix 2 Table A5), demonstrating their sensitivity to habitat modification (Fahrig 2003, Banks-Leite et al. 2014). Even when considering species less sensitive to habitat degradation, deforested landscapes support very few species (Pardini 2004, Estavillo et al. 2013) with potential consequences for ecological functioning in these landscapes (Banks-Leite et al. 2014).

A novel aspect of our study is that we found that the composition of medium and large mammals had a strong direct influence on small mammal species and their functional diversity. Currently, 96% of the Atlantic forest is likely experiencing changes in trophic cascades due to the lack of large mammals (Jorge et al. 2013). Our best-fit model showed a positive correlation between defaunation and richness of small mammals, however defaunation showed a strong negative effect on functional diversity. Medium and large mammals can suppress the abundance of small mammals via food competition (Mendoza and Dirzo 2007, Keesing and Young 2014, Young et al. 2015) or predation (Rocha-Mendes et al. 2010, Seibert et al. 2015, Giordano et al. 2018). Defaunated sites have small mammal communities with higher abundance of generalist species and lower diversity of small mammals (Pardini et al. 2009, Galetti et al. 2015b). Previous studies have shown that communities with high diversity exhibit species with phylogenetically conserved traits and present narrow niche breadths and high efficiency in resource exploitation (Estavillo et al. 2013, Banks-Leite et al. 2014), so the loss of medium and large mammals potentially affects trophic cascades, ecological functions and evolutionary history (Galetti and Dirzo 2013, Dorresteijn et al. 2015, Dreiss et al. 2015, Fergnani and Ruggiero 2015).

Regarding evolutionary history, our best-fit model showed that the phylogenetic diversity of small mammals was directly affected by species diversity, hence indirectly affected by defaunation, forest cover and patch size (Supplementary material Appendix 2 Table A6). Adding a species to a community normally adds phylogenetic diversity; however, addition or loss of phylogenetically unique species (e.g. *Phyllomys brasiliensis* and *Euryoryzomys russatus*) disproportionately changes phylogenetic diversity relative to species which have many close relatives (such as species of the same genus) (May 1990, Vane-Wright et al. 1991, Rodrigues and Gaston 2002, Nascimento et al. 2013). The strong link between species diversity and phylogenetic diversity reinforces the idea that closely related species often do not co-occur in the same microhabitat or site (Ewers et al. 2013, Luza et al. 2015).

Furthermore, the direct connection between phylogenetic and functional diversity we found in this study indicates that changes in phylogenetic composition broadly correspond to changes across functionally important traits (Cavender-Bares et al. 2009, Winter et al. 2013). The loss of evolutionarily distinct species is assumed to constitute an irreversible loss of evolutionary history and unique functions for an entire ecosystem (Bracken and Low 2012). Our results

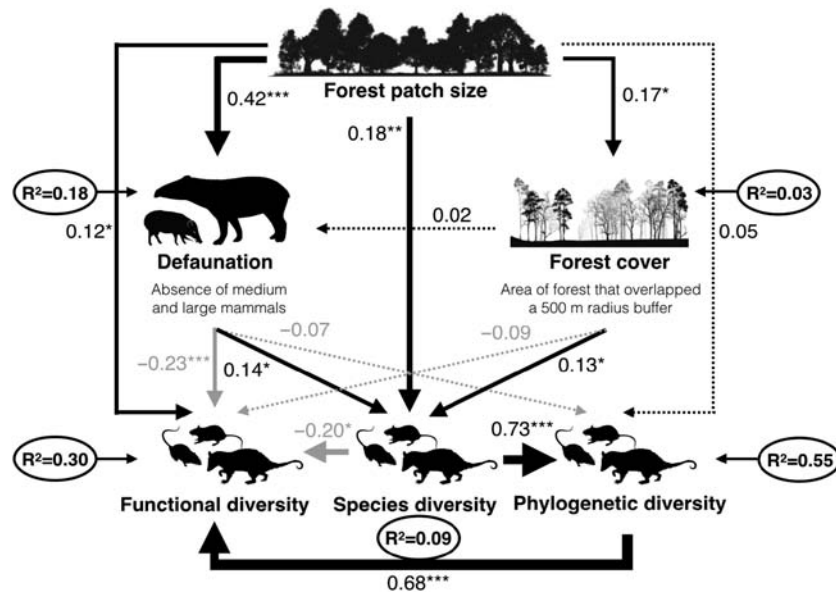


Figure 4. Best-fitting structural equation model (full direct + indirect model). Positive and negative pathways are indicated by black and gray lines, respectively. Arrow thickness is scaled to illustrate the relative strength of effects and significant coefficients are indicated with asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The marginal coefficient of determination (R^2) is shown in the black circles for all response variables.

reinforce that native small mammals that have a more basal lineage composition (Kemp 2005) were the first group affected by defaunaation and habitat loss. Indeed, large rodents from Caviidae and Echimyidae and marsupials from *Caluromys* genus were the first groups to disappear in the presence of anthropogenic pressure, such as fragmentation and defaunaation (Chiarello 1999, Costa et al. 2005). Knowing that biodiversity loss is not a random process (Dirzo et al. 2014), even for small mammals, there are biased impacts on these species that influence important functions such as seed dispersal and predation (Vieira et al. 2003, 2006, 2011, Sunyer et al. 2013), controlling the seeds reservoir of the forests, as well as in the dispersal of mycorrhizal fungi (Janos and Sahley 1995, Mangan and Adler 2002).

Phylogenetic and functional diversity are often loosely correlated (Pavoine et al. 2013) and has been reported in birds (Trindade et al. 2012, Sobral and Cianciaruso 2016), large mammals (Safi et al. 2011), fish (Cachera and Le Loc'h 2017) and plants (Flynn et al. 2011). However, the convergence of functional traits should promote the existence of species with similar trait values, leading to functional redundancy (de Bello et al. 2009, Oliveira et al. 2016) influencing the resilience of communities (Naeem 1998, Pillar et al. 2013). The trade-off between of high redundancy and low FD as a function of elevated numbers of species was also shown in bird communities (Sobral and Cianciaruso 2016). Nonetheless, the idea that some species perform similar functions in ecosystems and that species can be lost without losing functions in the ecosystem worries conservationist because redundant species in a community have been considered essential to guarantee ecosystem resilience to perturbation (Walker 1995, Bolnick et al. 2011, Diaz et al. 2013).

Controversial opinions still exist on whether the redundant communities are more stable (Mori et al. 2013). In a functional group containing a variety of species, such as small mammals, the species often manifest functional redundancy, and a functional group or community containing higher redundancy tends to achieve niche differentiation (Walker 1992, Elmquist et al. 2003) during periods of disturbance. According to McCann (2000), complexity may lead to stability, but the driving force for generating this relationship is the structure and function of the system instead of the complexity itself.

Here, we reinforce the need to preserve large non-defaunated forest remnants to achieve the highest diversity of small mammals. The occurrence of medium and large mammals can efficiently control abundant small mammals species, maintaining diverse communities (Pardini et al. 2010, Banks-Leite et al. 2014, Young et al. 2014, Galetti et al. 2015a, 2017). Maintaining mammal community diversity should be a goal in conservation planning, once functional and phylogenetic diversity allow us to better understand species resilience to changes in the environment (Srivastava and Vellend 2005, Rolland et al. 2012, Brum et al. 2014, Loyola et al. 2014, Sobral et al. 2014, Hidas-Neto et al. 2015). Our findings highlight the significance of defining priority sites for species conservation that are also essential for the preservation of evolutionary history and unique functions of evolutionarily distinct animals (Sechrest et al. 2002, Mace et al. 2003, Diniz-Filho 2004, Safi et al. 2011). Given the unprecedented rates of defaunaation globally (Dirzo et al. 2014), the insights from our findings may serve as a warning for cascading effects about the loss of large mammals on the biodiversity of hyper-diverse groups such as small mammals.

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Supplementary material (Appendix ECOG-03504 at <www.ecography.org/appendix/ecog-03504>). Appendix 1–2.