



## What would be the diversity patterns of medium- to large-bodied mammals if the fragmented Atlantic Forest was a large metacommunity?



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### ABSTRACT

Mammals play innumerable ecological functions in terrestrial ecosystems and are in decline in the Atlantic Forest. Using a biogeography approach with tools to analyze metacommunities, this study aimed to understand how mammal diversity would vary spatiotemporally across the Atlantic Forest. Secondary data about mammal communities was obtained using search engines. A nestedness analysis and spatial autocorrelations were used to evaluate the spatial patterns of richness. Metacommunity models were used based on species-neutral diversity to measure partitioning and estimate and compare diversity at different spatial and temporal scales, and regression models were made to evaluate the diversity variation obtained in relation to biogeographical predictors. The richness of mammals had intermediary nestedness and a spatial autocorrelation. We obtained high beta diversity for the entire Atlantic Forest, which was similar to simulated values and decreased at smaller spatial and temporal scales. The diversity of medium- to large-bodied mammals along the Atlantic Forest is composed of a nested summary of local to regional diversities, yet the tropical region was very important to the composition of the overall diversity. The different multiscale approaches and results may contribute to better understanding the diversity of medium- to large-bodied mammal communities and how they vary in the Atlantic Forest. Both the neutral paradigm and other metacommunity paradigms have complementary strengths in species diversity at several scales. We conclude that conservation strategies should consider all scales in the Atlantic Forest, because the diversity of mammals is dependent both the local and regional pool of mammals. Some of the most important standing issues are to find out whether dispersal across regional landscapes occurs for most species and, if it does, to ensure that this is maintained or increased, to maintain species diversity and ecological processes.

### 1. Introduction

Mammals play many important ecological functions, such as community structuring and forest regeneration (Roemer et al., 2009; Galetti and Dirzo, 2013). Their populations are under decline in many terrestrial biomes (Davidson et al., 2009; Ceballos et al., 2015), especially in the Brazilian Atlantic Forest (Galetti et al., 2015). In terms of biodiversity and endemism, the Atlantic Forest is in one of the five most important ecoregions in the world (Myers et al., 2000) and has 318 mammal species, of which 90 are endemic (Paglia et al., 2012; Graipel et al., 2016). Although mammals are the focus of several studies, there are shortfalls in biology, such as lack of abundance data, uncertain in the geographic distribution and taxonomy of species (Rosado et al., 2016). There are several geographic sampling gaps

and large differences in sampling methods and efforts – factors that can affect the estimative of local richness (Lyra-Jorge et al., 2008). Mammals of the Atlantic Forest are extremely threatened to result in high defaunation caused by several factors, including biological invasions, hunting, habitat loss, fragmentation and isolation (Galetti et al., 2009; Bogoni et al., 2016a).

The average isolation distance for Atlantic Forest fragments is ~1.5 km, varying from a few meters to dozens of kilometers, and the remaining 11.73% (16,377,472 ha) of the original vegetation cover comprises mostly disturbed and small remnant fragments (Ribeiro et al., 2009). These small (< 50 ha) fragments may serve as stepping-stones between larger fragments (Haddad et al., 2003), increasing landscape connectivity (Magioli et al., 2015). For the Atlantic Forest, the major functional connectivity occurs in the highland region (i.e.,

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Serra do Mar and Serra Geral) that spreads from the state Rio de Janeiro to the state of Rio Grande do Sul (Ribeiro et al., 2009). The patch size affects abundance and diversity of mammal species (Canale et al., 2012; Maglioli et al., 2016), and the landscape-scale features, such as the intensity of human occupation, change the composition of communities (Bogoni et al., 2016a). Environmental and landscape conditions, such as fragmentation, habitat type, land use and resource availability, vary across spatial scales (Declerck et al., 2011). These aforementioned characteristics and their variations lead to non-random shifts in plant and animal communities, changing the diversity patterns (e.g., species richness and functional diversity), ecological processes (e.g., the trophic web, seed dispersal, detritivore webs) and community structure (Galetti et al., 2009; Bogoni et al., 2016a, 2016b).

Community structure has recently been reevaluated and reinterpreted within a metacommunity framework (Leibold et al., 2004). Metacommunity was defined as a set of local communities connected by the dispersal of many species that are potentially interacting (Leibold et al., 2004). The paradigms of metacommunity theory (i.e., patch dynamics, species sorting, mass effects and neutral model) depend on spatial scale, extent, or spatial distances between areas (Declerck et al., 2011; Chase, 2014). The paradigms depend on the environment and taxonomic group, due to the idiosyncrasies of the ecosystem type and its filters, and due to dispersal, colonization and interactions among species (Holyoak et al., 2005; Logue et al., 2011). Neutral models are the simplest paradigm of a metacommunity and can be useful to understand species diversity from a perspective where all species are similar in their competitive ability, movement and fitness (Hubbell, 2001; Leibold et al., 2004).

Analytical advances allow the identification of species and areas that contribute the most to diversity along ecological gradients by partitioning the variance of community datasets to estimate diversity components (Jost, 2007; Legendre and De Cáceres, 2013) and can be compared to values obtained from null models based on several scenarios (Gotelli and Graves, 1996; Gotelli and Ulrich, 2012). Alpha, beta, and gamma diversity are classical diversity components defined as the number of species in a locality or habitat, the turnover of species between habitats or localities, and the estimated number of species present within a larger area, respectively (Whittaker, 1975). Other diversity metrics based on the entropy concept defined as a measure of uncertainty calculated from the frequency distribution of a community (Jost, 2006). These metrics show important properties, such as the number of equally frequent species that represents the same level of diversity of the data that can be converted into “true diversity” (Jost, 2006, 2007).

Beta entropy has no intuitive interpretation in general (Marcon and Hérault, 2015), defined as the information gain brought by the knowledge of each community composition (Marcon et al., 2014). Beta entropy gives a value of divergence between each local community's species probabilities and the metacommunity species probabilities, with properties interpretable, self-contained, and with a generalized information function (Marcon et al., 2014). Another phenomenon that influences beta diversity is nestedness, which occurs when the biota of an area with a lower number of species is a subset of a biota with a greater number of species (Baselga, 2010a, 2010b). In this case, the dissimilarity among sites is because of differences in species richness and occurs even in the absence of actual species turnover (Koleff et al., 2003a, 2003b; Baselga, 2012). The occurrence and persistence of mammal species in different patches within a landscape are related to ecological traits, especially body size and diet, influencing both the nestedness such as the dissimilarity among areas (Canale et al. 2016; Bogoni et al., 2016a).

In areas of the Atlantic Forest, few studies have dealt with mammal distributions at continental scales and investigated dissimilarities in species composition among areas (Melo et al., 2009). Still, it is expected that beta diversity is not seasonal, and that it increases because of endemic species, local extinctions and the presence of some species

with low dispersal capacity, and decreases because of large spatiotemporal scales and by other species with high dispersal capacity (Leibold et al., 2004; Declerck et al., 2011). In this study, mammal inventories along the Atlantic Forest were compiled and the mammal diversity was partitioned into different spatial and temporal scales. By generating an overview of the richness and composition of several communities of medium to large mammals that occur along the Atlantic Forest, based on the neutral paradigm of the metacommunity framework, two goals for this study were defined: (1) to evaluate the nestedness and spatial autocorrelation of richness and biomass among mammal communities distributed along the Atlantic Forest; and (2) to partition mammal diversity from local to biogeographical scales, in order to evaluate and indicate which spatiotemporal theoretical scenario of the metacommunities within the Atlantic Forest has greater alpha and beta diversity, understand the relationship between the beta entropy and biogeographical variables, and list the species that contribute the most to the metacommunity model with the greatest spatial extent.

Our two main hypotheses are: (1) mammal nestedness is high (> 70%), and higher than expected at random, due the large distribution of most species, and richness and biomass are spatially autocorrelated due to the homogenization of composition caused by a decrease in distance; and (2) in a neutral metacommunity paradigm, the alpha and beta diversity depend on the delimitation of the metacommunity model. The predictions of our second hypothesis are: (a) the diversity metrics increase in congruence with an increase in scale, remaining equal in comparison to null models that have equal probability of observed species occurrence and larger beta diversity than expected randomly when the species presence or absence probability is symmetric (i.e., 50%); (b) the beta entropy is negatively related to alpha diversity, species richness and fragment size, because the entropy of communities is buffered by the largest pool of species in large fragments; (c) the beta diversity is greater in the tropical portion of the Atlantic Forest compared to the subtropical portion, due to the endemism in some tropical areas; and (d) the species that contribute to decreasing the beta diversity have wide distributions, tolerate habitat changes, and have a higher probability of occurrence in the theoretical metacommunity model.

## 2. Material and methods

### 2.1. Data source and organization

Secondary data of mammal communities along the Atlantic Forest was obtained using search engines regardless of publication year. We used the terms (in English, Portuguese and Spanish) “medium- to (and) large-sized (bodied) mammals” and “Atlantic Forest” in Scopus (<http://www.scopus.com/>), Web of Science (<https://apps.webofknowledge.com/>) and Scielo (<http://www.scielo.br/>), in addition to searching the first 200 results of Google Web Search (<https://www.google.com>) and ResearchGate (<https://www.researchgate.net/>) (Allen et al., 2011; Maglioli et al. 2015). The data search was conducted between 15 June 2015 and 30 December 2015 and included published and *in press* peer-reviewed papers of studies throughout most of the original extent of the Atlantic Forest (Fig. 1). We considered all medium- to large-sized species (i.e., with an adult weight  $\geq 1$  kg; Chiarello, 2000); indeterminate species (listed at the genus level) were not included in the presence-absence data set. Taxonomy and body mass follow Paglia et al. (2012). Based on this reference, mammal species were classified into the trophic guilds: carnivores/piscivores, herbivores/frugivores and omnivores/insectivores, the habits in: arboreal or scansorial, terrestrial and semi-aquatic. Recent taxonomic issues concerning *Sapajus*, *Galictis* and *Coendou*, and consequently their species distributions, were resolved using IUCN (2015) distribution maps (Voss, 2011; Bornholdt et al., 2013). Additional taxonomic changes along the period of the study did not compromise the current classification.

For each study, we counted how many methodologies were used in

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