

Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest

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Keywords

biodiversity; ecological functions; conservation planning; Brazil; patch size; mammal assemblages; fragmented habitat; functional diversity.

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Abstract

Patch size affects abundance and diversity of mammal species, but there is little information on threshold regarding this relationship or relating it to functional diversity. Therefore, we aimed with this study to (1) evaluate if the functional diversity of medium- and large-sized mammal assemblages can be explained by patch size; (2) if this relationship is positive, evaluate whether it is linear (neutral hypothesis) or has critical thresholds (threshold hypothesis); (3) propose specific conservation strategies for each situation. We used primary and secondary mammal database for different forest remnants sizes in the Brazilian Atlantic Forest biome. We calculated functional diversity (FD), using an ecologically meaningful set of traits: body mass and locomotion form, behavioral and dietary traits, and environmental sensitivity of species. We compared linear models with threshold models using Akaike information criterion (AIC). FD values increased with patch size, possibly associated with the high complexity and heterogeneity of larger areas. The threshold model better explained the pattern between FD values and patch sizes than the linear one (Δ AIC = 35.8), confirming our threshold hypothesis. Two thresholds (at 60 and 2050 ha) were identified. Our results highlight the need of compliance with the Brazilian Forest Code for assemblages in fragments lower than 60 ha. For assemblages in fragments between the two thresholds whose FD values significantly increased with patch size, we recommend improvements in conservation planning. For assemblages in fragments bigger than 2050 ha, we suggest the establishment of new protected areas, or at least, the maintenance of the existent ones. Our approach can serve as the basis for analysis with other taxonomic groups and ecosystems, increasing chances of maintaining faunal ecological functions, and improving species conservation.

Introduction

Ecological thresholds between response and explanatory variables have been pursued in recent years (Groffman *et al.*, 2006), particularly to support conservation and biological restoration plans (Briske, Fuhlendorf & Smeins, 2006). By definition, thresholds are abrupt changes from one ecological condition to another, which are driven by small additional changes in parameters in an already compromised situation (Bennett & Radford, 2003). Thresholds may reflect species sensitivity to processes such as habitat loss or fragmentation (Lindenmayer & Luck, 2005). Thresholds aiming at species conservation have been identified for birds (Radford, Bennett & Cheers, 2005; Martensen *et al.*,

2012), plants, frogs, fungi (Drinnan, 2005) and small mammals (Pardini *et al.*, 2010; Estavillo, Pardini & Rocha, 2013). Although acting directly and indirectly on structuring and maintenance of natural environments through fundamental ecosystem services such as seed dispersal and predation (Jorge *et al.*, 2013), there are no records about the existence of thresholds for the response of medium- and large-sized mammals to landscape structure.

It is known that patch size affects abundance and diversity of mammal species (August, 1983; Pardini *et al.*, 2005; Michalski & Peres, 2007), but there is little information on thresholds regarding this relationship; for example, what is the limit of habitat loss or patch size reduction that a species can tolerate before becoming locally extinct (Lindenmayer

et al., 2008)? Previous studies of ecological thresholds have used traditional methods (e.g. species richness and diversity) to evaluate natural communities (Andrén, 1994; Fahrig, 2003; Pardini *et al.*, 2010; Martensen *et al.*, 2012; Estavillo *et al.*, 2013), but these methods do not explicitly consider species ecological functions, such as functional diversity (Poos, Walker & Jackson, 2009).

Functional diversity is the range and values of biodiversity traits that influence how an ecosystem operates (Tilman, 2001). Recently, functional diversity measures have been used to establish a link between biodiversity and ecosystem functions (Díaz & Cabido, 2001; Petchey *et al.*, 2007; Flynn *et al.*, 2009; Trindade-Filho *et al.*, 2011) such as resource use complementarity (Hooper *et al.*, 2002; Petchey & Gaston, 2002). These measures behave differently from traditional approaches because they consider the unique set of ecological traits of each species in a community (Petchey & Gaston, 2002; Poos *et al.*, 2009). Functional diversity is strongly related to species richness when species traits are equally complementary (Petchey & Gaston, 2002). As there is strong evidence of the positive relationship between species richness, patch size and critical thresholds (Radford *et al.*, 2005; Pardini *et al.*, 2010; Martensen *et al.*, 2012; Estavillo *et al.*, 2013; Banks-Leite *et al.*, 2014; Lima & Mariano-Neto, 2014), the association between ecological processes, and the presence of thresholds may provide important additional information for a wide range of environmental management strategies (Briske *et al.*, 2006).

In this study we aimed to identify thresholds between functional diversity of medium- and large-sized mammal assemblages and patch size using information available for forest remnants of the Brazilian Atlantic Forest biome. This biome is a biodiversity hotspot (Myers *et al.*, 2000), and one of the most threatened tropical ecosystems globally because of indiscriminate destruction of its original vegetation (Ribeiro *et al.*, 2009). Protected areas are still the main form of protecting biodiversity and ecosystem services (Gaston *et al.*, 2008). However, these areas are suffering from downgrading, downsizing and degazettement, especially in the Brazilian Amazonia and Atlantic Forest (Bernard, Penna & Araújo, 2014). Despite of the ecological importance of small forest remnants (Turner, 1996), most are located outside protected areas (Ribeiro *et al.*, 2011).

The most effective way to preserve these sites is compliance with the Brazilian Forest Code (Federal Law No 12,651/2012) by landowners, as most of the unprotected areas are within private farmlands (Sparovek *et al.*, 2010). Although the Brazilian Forest Code is a nationwide legislation, it aimed to provide a set of very good guidelines that can also be used worldwide, such as the protection of riparian forest ecosystems, which allow the maintenance of the connectivity between key habitats within the landscape (Martensen *et al.*, 2012; Banks-Leite *et al.*, 2014). As it defines the minimum amount of natural habitats to be maintained in the landscapes, it reinforces the importance of conserving large blocks of functionally connected habitat mosaics (Ribeiro *et al.*, 2011). Finally, by defining the contribution of riparian vegetation as ecological corridors, and

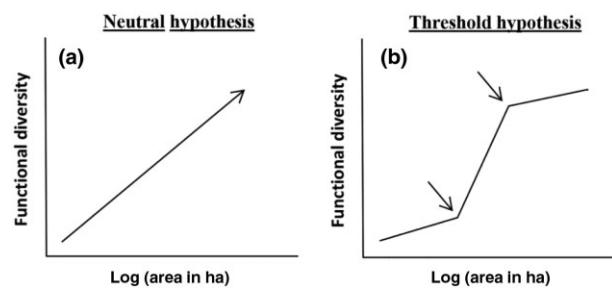


Figure 1 Relationship between functional diversity and patch size: (a) a linear relationship (neutral hypothesis); and (b) a threshold-like relationship with two breaking points indicated by the arrows (threshold hypothesis).

the minimum amount of habitats to be kept or archived, the Brazilian Forest Code is a very good strategy to prioritize areas for restoration at regional (Martensen *et al.*, 2012) and nationwide scales (Banks-Leite *et al.*, 2014; Tambosi *et al.*, 2014). However, recent changes in the Forest Code (Metzger *et al.*, 2010; Martinelli, 2011) and lower compliance with restoration of 'areas of permanent preservation' and 'legal reserves' in the Atlantic Forest (Sparovek *et al.*, 2010; Soares-Filho *et al.*, 2014) threaten biodiversity maintenance in most of these areas.

Particularly, we aimed in this study: (1) to evaluate if the functional diversity of medium- and large-sized mammal's assemblages can be predicted by patch size; (2) if positive, to evaluate if this relationship is linear or has critical thresholds; (3) to propose specific conservation strategies for each situation.

We hypothesized that the relationship between functional diversity and patch size is better explained by a threshold-like response (threshold hypothesis) than a linear one [neutral hypothesis (Fig. 1a)]. We choose to test the existence of two thresholds based on the results of previous studies that related critical thresholds and patch size, like those obtained by Radford *et al.* (2005) and Martensen *et al.* (2012) with birds, and Pardini *et al.* (2010) and Estavillo *et al.* (2013) with small mammals. These studies show three situations: (1) landscapes with fewer than 10% of forest cover have low species richness and abundance; (2) an intermediate situation of landscapes with forest cover between 10 and 30/50% with increasing species richness and abundance; (3) and finally, for landscapes with 30/50% or more of forest cover, species richness and abundance seem to be more stable. Thus, observing these situations, we assumed that our data could follow the same pattern, as all these studies, except Radford *et al.* (2005), were conducted in Atlantic Forest landscapes; also because functional diversity is closely related to species richness.

We expected a response similar to fragmentation and percolation thresholds (see Andrén, 1994; Swift & Hannon, 2010), that is presenting a critical reduction of ecological functions for smaller forest remnants and a more stable situation for larger remnants (Fig. 1b), but with an steep increase of functional diversity as patch size increases

characterizing two distinct thresholds. As conservation strategies, we intend to propose guidelines for conservation planning, such as setting up measures for different situations where landscapes are (1) highly degraded; (2) under intermediate conservation; (3) where the conservation is good enough to maintain the biodiversity and ecosystem functions.

Material and methods

Mammal assemblage database

We performed a literature search for studies of medium- and large-sized mammals in Atlantic Forest using the search tools ‘Google Scholar’ and ‘Web of Science’, with the following keywords: mammal(s), survey(s), inventory(ies) and Atlantic Forest. We used the operator ‘AND’ to make different combinations with these words. We searched for these words in both title and abstract. Additionally, a ‘Google’ search was performed with the same keywords in Portuguese to find papers published in journals not indexed by ‘Web of Science’ and those from

gray literature, such as theses, dissertations and monographs. As a selection criterion for the studies, we only included studies whose survey methods were based on active search, that consists in walking in a constant speed searching for direct and indirect evidence of mammalian presence on trails, dirt roads or transects (Voss & Emmons, 1996), as well as, sand plots and camera trapping. In some cases, interview data were considered, but only when combined with the aforementioned methods. Only studies that provided appropriate geographic coordinates and patch size for the forest remnants were included, which allowed us to verify the studied areas with satellite images using Google Earth. We consider forest remnants with more than 5000 ha as reference areas, because their assemblages have a more diverse species composition and support most of the mammalian species that occurs in the Atlantic Forest, indicating better conservation conditions. From these studies, we used the species list for each forest remnant, considering only presence/absence of species. We calculated functional diversity indices based on these information. The studies that compose the database cover the period from 1996 to 2012.

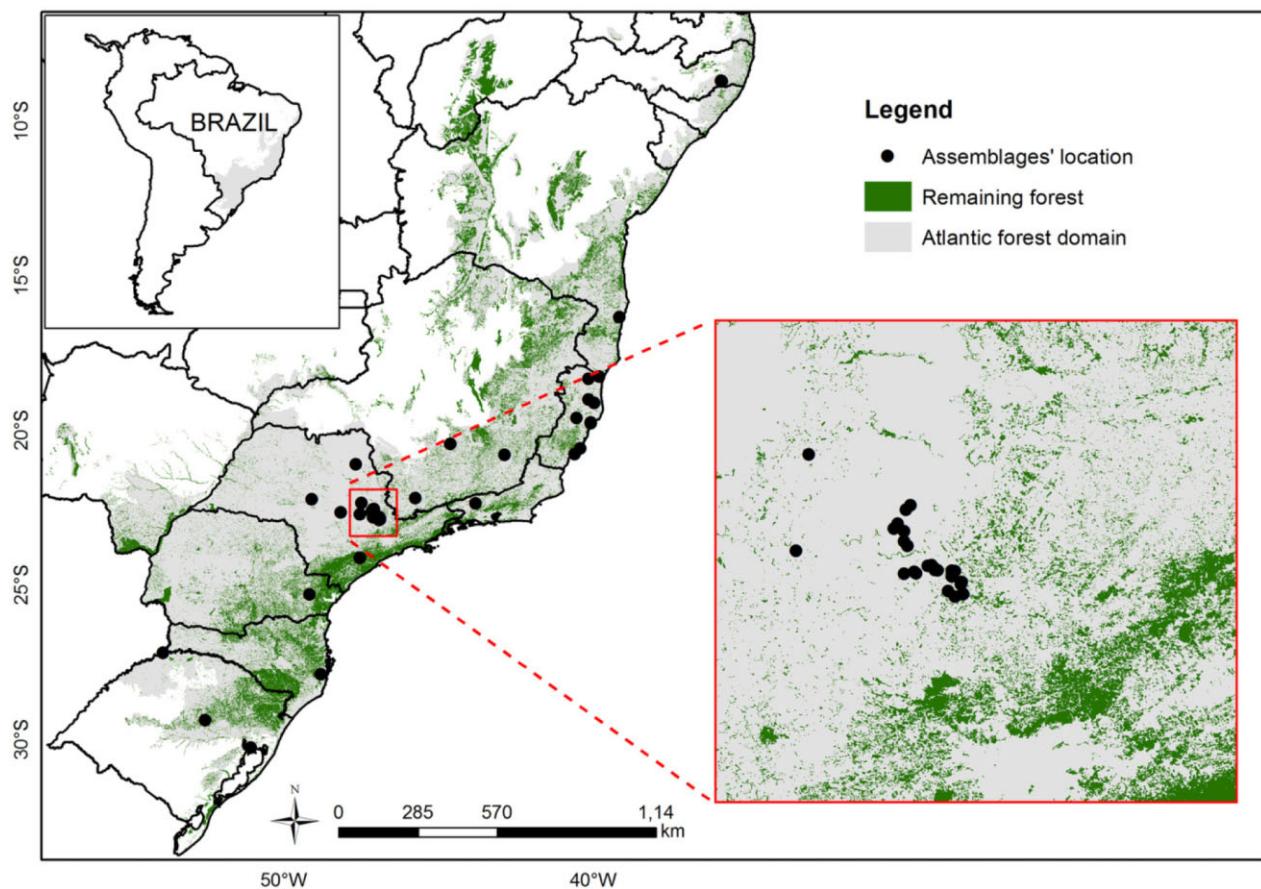


Figure 2 Mammal assemblages' distribution within Atlantic Forest domain, Brazil, used to estimate functional diversity to assess patch thresholds influences. The highlighted area indicated forest remnants that are close to each other, part of them collected by Magioli (2013).

Under these criteria, we selected 53 mammal assemblages (Fig. 2) – 45 were selected from secondary data (Table S1). We also included data from eight forest fragments collected by Magioli (2013) for this study.

The assemblages selected in this study were located in forest remnants of various sizes (min = 1 ha, med = 3900 ha, max = 85 000 ha) representing the major gradients [latitude (min = 8°42'26"S, max = 30°16'04"S), longitude (min = 35°50'27"W, max = 53°53'41"W), elevation (min = 5 m, max = 1400 m)] and biogeographic regions of the Atlantic Forest (Silva & Casteletti, 2003). We included in the analysis medium- and large-sized mammals species weighing over 1 kg (Chiarello, 2000a) and also species that are commonly registered based on sightings and/or vestiges in inventories (e.g. *Guerlinguetus* sp., *Leontopithecus* sp. and *Cavia* sp.).

Data analysis

Functional diversity calculation

Among the various existing measures of functional diversity (see Mouchet *et al.*, 2010), we choose the one proposed by Petchey & Gaston (2002, 2006), henceforth called FD. This measure allows us to produce a dendrogram based on the unique set of traits of each species in an assemblage and to calculate an FD value by summing the dendrogram branches length. For each assemblage (1) we built a trait matrix; (2) then converted it into a distance matrix; later (3) grouped species to produce a functional dendrogram; (4) and finally, we calculated an FD value for each assemblage by summing the total branch length of the dendrogram. For the distance matrix construction we used the modified Gower's distance (Pavoine *et al.*, 2009) because it best matches the combination of categorical and continuous data, and unweighted pair-group method with arithmetic mean clustering (UPGMA), which together yielded dendograms with good cophenetic correlation coefficients.

An assemblage including all medium- and large-sized mammal species of Atlantic Forest ($N = 88$; Table S2) was compiled according to Paglia *et al.* (2012) and species listed in studies that compose the database (Table S1; Magioli, 2013). From that assemblage, we generated a dendrogram and calculated an FD value that represents the full spectrum

of functions for the biome. Although it is not possible to guarantee that all species were included on that assemblage, we consider it as our complete medium- and large-sized mammal's assemblage for the Atlantic Forest biome. We used the FD value of the complete assemblage to standardize values for all other assemblages, ranging from 0 to 1. Standardization provides an idea of the proportion of functional relationships exerted by species in each forest remnant, allowing the assessment of the ecological importance of the assemblages and studied areas.

Trait selection

We selected traits based on resource use, such as physical and dietary data. We also included behavioral traits because they may influence how species acquire resources from the environment (Flynn *et al.*, 2009). The environmental sensitivity trait relates the tolerance of species to habitat modification, resource availability and anthropogenic pressure, which limits the occurrence of sensitive species; here we considered it an important trait, especially to differentiate assemblages in forest remnants with distinct structural characteristics and landscape configuration. The selected traits were commonly used in previous studies of FD with mammals (e.g. Flynn *et al.*, 2009; Carvalho *et al.*, 2010; Safi *et al.*, 2011). We compiled information on species traits from specialized literature (Table 1; for more details see Table S3).

FD and patch size

First, we assessed the spatial autocorrelation (Fortin & Dale, 2005) of our data using the 'mantel.rtest' function (Monte-Carlo test, using 9999 repetitions) of the 'ade4' package (Dray & Dufour, 2007). The spatial correlation was nearly zero ($r = 0.037$; P -value = 0.2439), which indicates that our data were not spatially autocorrelated. Our models assumed normally distributed residuals. We extracted the residuals using the function 'residuals' in program R (R Core Team 2014) and tested the validity of our assumption using a Shapiro-Wilk test implemented in the function 'shapiro.test' in R, which failed to reject the hypothesis that the residuals were normally distributed ($w = 0.9748$, $P = 0.3585$).

Table 1 Trait data used to calculate functional diversity of medium- and large-sized mammal assemblages at Atlantic Forest domain, Brazil

Trait type	Trait	Range or categories
Physical	Body mass (kg) ^a	0.15 to 260
	Locomotion form ^b	Terrestrial, fossorial, aquatic, arboreal
Behavior	Periods of activity ^b	Diurnal, nocturnal, crepuscular
	Social behavior ^b	Yes or no
Dietary	Trophic guild ^b	Carnivorous, insectivorous, frugivorous, omnivorous, herbivorous
	Food type ^b	Small-, medium- and large-sized vertebrates, invertebrates, fish, fruit, grasses, plants, leaves, seeds
Environmental sensitivity	Foraging substrate ^b	Water, trees, ground vegetation, ground
	Species sensitivity ^b	Low, average, high

^aContinuous data.

^bBinary data.

We used a linear regression model to test whether FD was linearly related to the logarithm of patch size. We used the coefficient of determination (adjusted- R^2) and the significance of the regression coefficients for the evaluation of our results. We performed all analysis in R 3.1.2 (R Core Team, 2014).

FD threshold analysis

To check for the existence of thresholds using our database with mammals' assemblage, we sampled 10 000 bootstrap replicates, with replacement and sample size of 53. For each subset, we estimated the parameters of linear regressions and two breaking points. In this study, the response variable was the FD values and the explanatory variable was the patch size.

Next, for each of our 10 000 subsets, we estimated the breaking points in contrast to linear regression. This was done using the 'segmented' function from the package of the same name (Muggeo, 2008). This function estimates parameters for linear regression models, allowing for the identification of one or more breaking points at once. For the analysis, we used the function 'rnorm' of the 'stats' package to establish two breaking points using the settings 'rnorm [1, mean = 100, standard deviation (sd) = 50]' for the first breaking point, and 'rnorm (1, mean = 500, sd = 200)' for the second breaking point. The starting seed (mean values for the 'rnorm' function) were determined according to Ribeiro *et al.* (2009), because Atlantic Forest remnants with less than 100 ha represent 92.1% of the remaining fragments, and remnants larger than 500 ha represent about 1.1% of the remaining fragments, two distinct situations. The breaking points are required as input (a.k.a. seeds) for the 'segmented' function. We stored the estimated breaking point values so that both the first and the second breaking points were obtained for 10 000 replicates.

Subsequently, for each of our 10 000 subsets, we classified the segments (below the first, between first and second, and above the second breaking points) into three groups based on threshold values: (1) assemblages with low functional representation; (2) assemblages that exhibit an increase in FD values in response to increased patch size; (3) assemblages with high FD values in a more stable situation. We used the one-way analysis of variance (ANOVA) and Tukey's post hoc test to determine differences between the groups established. We performed all analysis in R 3.1.2.

Model comparison: neutral versus threshold hypothesis

We made a comparison between the linear and the threshold models generated from FD values and patch size relationship. For each subset of the 10 000 subsets, we used the Akaike information criterion corrected (AICc) for small samples (Burnham & Anderson, 2002) to compare neutral and threshold models. We stored and used Akaike's weights (wAICc) in model comparisons. We considered the best

model the one that presented an AICc ≤ 2 and a high weight for each of the 10 000 subsets. We conducted AIC analysis using the 'bbmle' package (Bolker, 2008) available in R 3.1.2.

Results

Patch size and FD

By analyzing the dendrogram, which describes the full spectrum of functional relationships among all species of medium- and large-sized mammals in Atlantic Forest (Fig. 3), we observed a gradual increase in FD values with increased patch size (Fig. 4). This indicates a positive relationship between FD and fragment area (adjusted- $R^2 = 0.8048$, $F = 215.4$, $P < 0.0001$).

Assemblages with the same number of species (such as richness = 12, 14, 15, 21 and 27, Fig. 5) indicated in some cases a proportional increase in FD values related to increasing patch size. Conversely, some assemblages within larger forest patches presented lower FD values when compared with assemblages in smaller patches (e.g. Passamani, Dalmaschio & Lopes, 2005; Silva Jr. & Pontes, 2008 [500 ha]; Abreu Jr. & Köhler, 2009; Sacilotto, 2009; Penido & Zanzini, 2012).

FD thresholds

We identified two thresholds between FD and patch size relationship, which occurred at 60 ha (lower limit) and at 2050 ha (upper limit), forming three distinct levels (Fig. 6). The first threshold indicated that assemblages located in forest remnants with areas of less than 60 ha (group A) had lower FD values (mean = 0.15, SD = 0.11). The range of FD values in this group was high (from 0.03 to 0.42) and the curve, which initially shows low slope, becomes more pronounced when values approached the first threshold (i.e. the first breaking point). For group A, the FD increase occurred mainly for assemblages within forest remnants with patch sizes that approached or reached the first threshold [i.e. fragments F1, F3 and F4 with area of 44.9, 59.5 and 64.7 ha (Magioli, 2013)].

Assemblages found between the two thresholds (group B) had intermediate FD values (mean = 0.43, SD = 0.12) with a wide range (from 0.24 to 0.70). The curve in Fig. 6 maintained a high slope, indicating that FD values increased significantly with increasing patch size.

As we expected, forest remnants above the second threshold (group C) supported assemblages with higher FD values (mean = 0.62, SD = 0.07) when compared with groups A and B. This indicates a higher number of functions maintained on larger forest blocks, when compared with small and intermediate patch sizes. We observed a small range of FD values (from 0.47 to 0.67) for group C. From the second threshold the curve exhibits a low slope (Fig. 6), though FD values above this threshold still increase slightly with patch size.

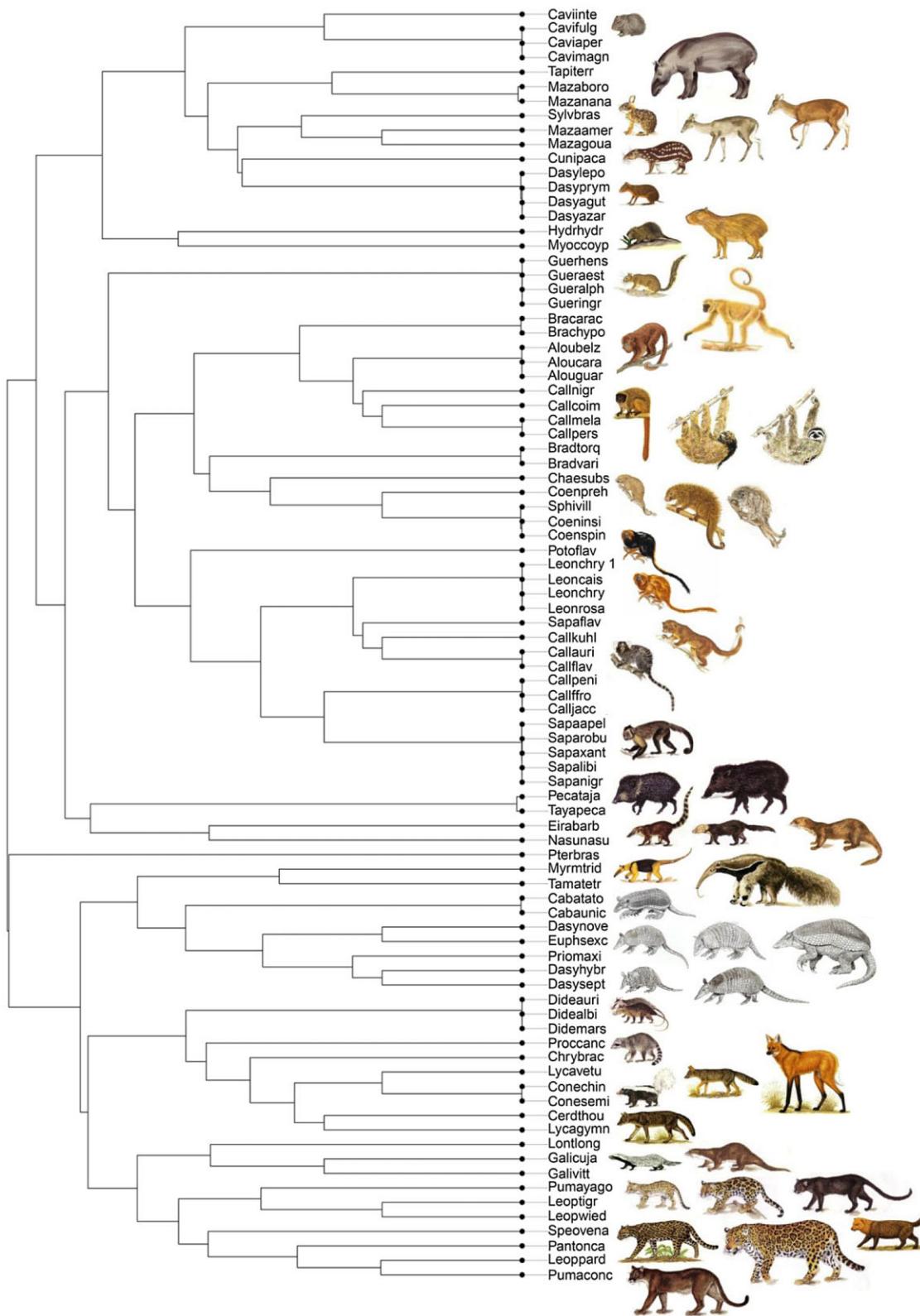


Figure 3 Dendrogram grouping all medium- and large-sized mammals based on species traits within Atlantic Forest domain, Brazil.

Some assemblages in group B presented FD values that were similar to or higher than those presented in group C, such as Gaspar (2005), F8, F2, and Passamani, Mendes & Chiarello (2000) and Srbek-Araujo & Chiarello (2008). Other assemblages showed FD values that were similar to or lower than those in group A, such as Modesto *et al.* (2008), Passamani *et al.* (2005) and F5. The three identified groups (A, B, C) were significantly different (ANOVA, $F = 57.61$, $P < 0.0001$; Tukey's Honestly significant difference test, $P < 0.01$; Fig. 6), strengthening our finding that groups are functionally distinct.

Model comparison: neutral versus threshold hypothesis

By analyzing the 10 000 bootstraps replicates of FD values as function of patch size, where we compared neutral versus threshold hypothesis, the threshold model best explained the pattern ($AIC_c = 0$, $wAIC_c = 1$), while the linear model was less well supported by the data ($\Delta AIC_c = 35.8$, $wAIC_c < 0.001$). This confirms our

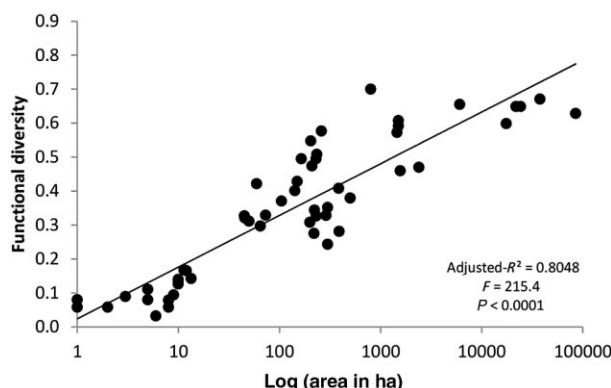


Figure 4 Positive relationship between functional diversity (FD) values of medium- and large-sized mammalian assemblages and patch size within Atlantic Forest, Brazil.

threshold hypothesis that assumed the existence of two breaking points on the relationship between FD values and patch size.

Discussion

FD and patch size

The increase in FD values as patch size increases could be related to the greater structural complexity of the vegetation in larger patches as FD calculation is based on traits that represent the use of environmental resources by species (Cadotte, Carscadden & Mirochnick, 2011). A more complex vegetation structure offers a high availability and variety of resources, resulting in more diverse mammal assemblages (August, 1983; Robinson & Redford, 1986). Therefore, high species diversity in larger areas (e.g. $> 10\,000$ ha) is more expected than for smaller patches, as observed in studies with mammals (Chiarello, 1999; Michalski & Peres, 2007; Galetti *et al.*, 2009), plants (Tabarelli, Mantovani & Peres, 1999), amphibians, reptiles (Cabrera-Guzmán & Reynoso, 2012) and birds (Banks-Leite, Ewers & Metzger, 2010; Morrison *et al.*, 2010).

However, some mammal assemblages in forest remnants with intermediate size (> 200 ha; e.g. Passamani *et al.*, 2005; Abreu Jr. & Köhler, 2009; Saciloto, 2009) presented low species richness and diversity, resulting in low FD values. This could be attributed to other landscape metrics like intense edge effects (Zurita *et al.*, 2012; Vespa, Zurita & Bellocq, 2014), isolation, matrix permeability (Ferraz *et al.*, 2012) and low structural connectivity (Ribeiro *et al.*, 2009); and also to high levels of human disturbance and hunting pressure (Peres, 2001).

FD thresholds

The low quality of the forest remnants in group A, because of a high degree of environmental degradation, human

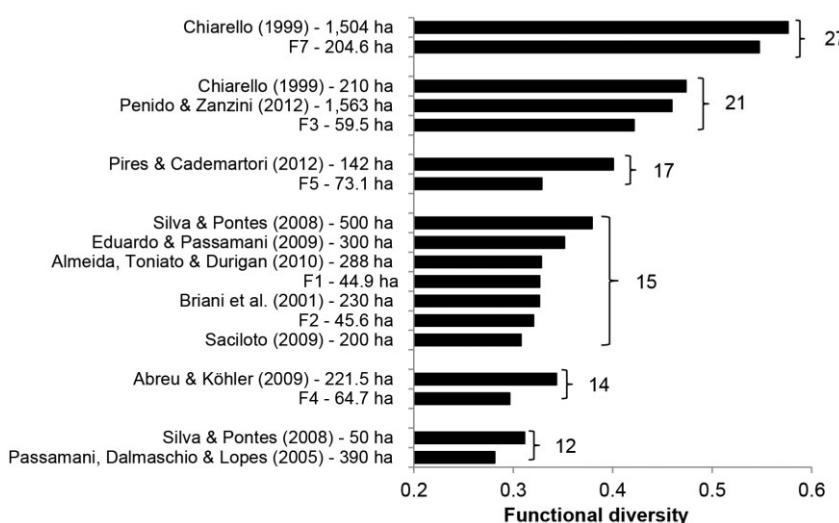


Figure 5 Variation in functional diversity (FD) values between mammal assemblages with the same species richness; the brackets are grouped by species richness, which is indicated by values at right.

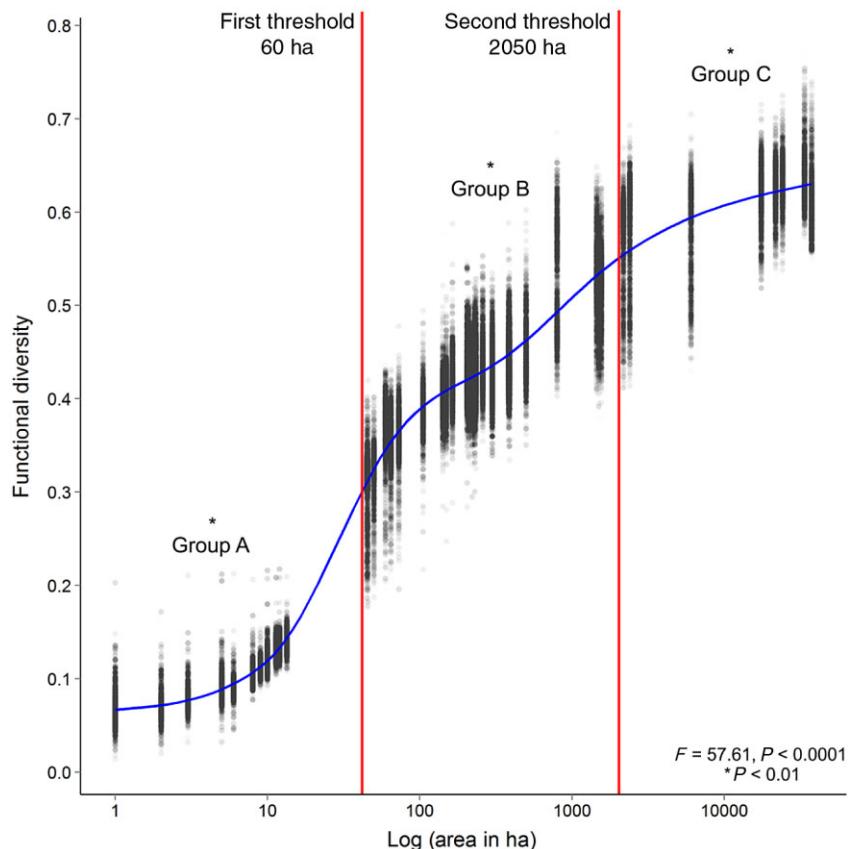


Figure 6 Relationship between functional diversity (FD) and patch size, with the three thresholds identified for the medium- and large-sized mammals within 53 assemblages of the Atlantic Forest, Brazil. The red lines are the two breaking points estimated after 10 000 bootstraps from the mammal assemblages' database. Groups A, B and C indicate the low, intermediate and high functional diversity, and exhibited significant differences between each other.

disturbance and changes in landscape configuration acts as an environmental filter for biodiversity (Ceballos & Ehrlich, 2002; Fahrig, 2003; Ferraz *et al.*, 2012). We can also consider that the simplified vegetation structure and floristic composition of the forest remnants cause differentiation in the composition of mammal assemblages (Haugasen & Peres, 2005). In addition to intense edge effect (Zurita *et al.*, 2012; Vespa *et al.*, 2014), connectivity loss and isolation of the forest remnants (Ribeiro *et al.*, 2009; Martensen *et al.*, 2012), the availability and variety of food resources is compromised (Tabarelli *et al.*, 2010). In particular fruits are essential to the persistence of mammalian species (Chiarello, 1999; Galetti *et al.*, 2009), and their lack could augment biodiversity erosion in modified environments (Michalski & Peres, 2007; Tabarelli *et al.*, 2010). We observed similar results regarding environmental simplification and the intensification of land use and occupation in studies of FD for birds (Petchey *et al.*, 2007) and mammals and birds (Flynn *et al.*, 2009).

Besides the wide range of FD values we observed in group B assemblages, the increase of functional diversity highlights the importance of these areas in the context of conservation of mammal populations and ecosystem services. The wide range of values is mainly related to all previously mentioned factors related to changes in habitat quality and landscape configuration. Some of the smaller forest remnants retain high species richness and/or those taxa

threatened with extinction [e.g. fragments F6, F7 and F8 (Magioli, 2013)]. But the viability of mammal populations may be at risk because of restrictions on size, quality (Galetti *et al.*, 2009) and hunting pressure (Canale *et al.*, 2012) in these areas. Therefore, small forest remnants have great ecological value (Turner, 1996), and actions promoting restoration and maintenance of these areas are necessary and should be encouraged (Galetti *et al.*, 2009).

Group C assemblages are present in forest remnants with highest environmental heterogeneity and low levels of human disturbance. These areas present more diverse species composition, especially of more sensitive species (e.g. *Tapirus terrestris*, *Callithrix aurita*, *Speothos venaticus*, *Panthera onca*, *Tayassu pecari*), resulting in high FD values. The low increase in FD values with increasing patch size is evident in this group, as most of ecological functions are present in many remnants. This situation underscores the importance of large forest blocks for the maintenance of the entire chain of ecosystem services performed by medium- and large-sized mammals. In addition, these areas play an essential role in the maintenance and conservation of mammalian populations.

Implications for species conservation

The formation of three distinct groups based on FD thresholds allows us to indicate specific strategies of action

for conservation planning. For group A, we notice that increasing forest coverage of the remnants (through reforestation) adds little to the functional characteristics of an assemblage. Even with the addition of new species, the functional gain would not be significant if considered the structural limitations of these forest remnants and the disturbance regime. In landscapes with reduced forest coverage and connectivity, actions for conservation are expensive, and the benefits for biodiversity are small compared with the effort that will be undertaken (Hobbs, Higgs & Harris, 2009).

However, these areas represent important points of connection (stepping stones) between forest remnants in better condition (Ribeiro *et al.*, 2009). Therefore, we strongly recommend compliance with the current environmental legislation (Forest Code, Federal Law No. 12.651/2012) in the foreground, with a focus on restoration and conservation of the 'permanent preservation areas' and 'legal reserves'. Following these guidelines will contribute significantly to biodiversity maintenance, by improving landscape structural connectivity and maintaining important ecosystem services (Tambosi *et al.*, 2014), such as seed dispersal (Pereira, Oliveira & Torezan, 2013), water production and protection (Ferraz *et al.*, 2014), carbon storage (FAO, 2010; Pütz *et al.*, 2014), and local climate regulation (Ewers & Banks-Leite, 2013).

Group B assemblages are located in forest remnants that represent approximately 46% of the remaining forest area (Ribeiro *et al.*, 2009), occupying most range of the actual Atlantic Forest biome. Thus, we encourage actions aiming biologic restoration and improvements in landscape configuration of these areas. Investments should primarily include the recovery of the quality of forest remnants in a landscape perspective, increasing connectivity and the effective area of existing forest remnants, reducing pressure on edges and controlling invasive species (Rodrigues & Gandolfi, 2007). These actions will contribute not only to assemblages' functional enrichment, but also for forest structure and floristic composition, and as consequence incrementing mammalian species composition.

Considering aspects of conservation for the entire Atlantic Forest, assemblages of group C are extremely important for maintaining ecological functions on a biome-level. In areas with high forest coverage and connectivity, we mainly suggest the establishment of new protected areas or, at least, the maintenance of the existent ones. The large forest remnants, considered here as reference areas, are essential to the conservation of mammal populations (Chiarello, 2000b; Michalski & Peres, 2007; Tabarelli *et al.*, 2010; Canale *et al.*, 2012).

Currently, only 9.3% of Atlantic Forest vegetation coverage is under protection (Ribeiro *et al.*, 2009). One should also consider that only 0.03% of the large forest remnants are still present in the Atlantic Forest, but these remnants represent approximately 25% of the existing forest cover. We also recommend conservation actions aiming at restoring connectivity between nearby smaller areas, which

may favor the flow of species, genes and functional traits to assemblages of groups A and B.

Conclusions

Our approach allowed identification of FD thresholds for medium- and large-sized mammal assemblages, confirming our threshold hypothesis. We were able to identify situations that were more stable and critical to mammal assemblages, allowing us to propose specific strategies for better planning the actions for conservation, landscape management and prioritize areas for restoration.

The combination of functional diversity and threshold analysis has potential to be replicated for other taxonomic groups and in distinct ecosystems, especially because of functional diversity's flexibility. We conclude that, by stimulating the use of our approach, the chance of maintaining faunal ecological functions within ecosystems increases, improving conservation planning.

Finally, the prioritization of new areas to be protected, allocation of funds and planning for biological restoration contributes to the maintenance of ecological and ecosystem processes. However, decision making involving conservation strategies still causes much debate, and the search for good indicators that are ecologically well-grounded, particularly when using simple and robust methods, is a constant challenge.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Description of the secondary data used to create the database of medium- and large-sized mammal assemblages at Atlantic Forest Domain, Brazil.

Table S2. Mammal species selected to calculate functional diversity at Atlantic Forest Domain, Brazil.

Table S3. Trait data used to calculate functional diversity of medium- and large-sized mammal assemblages at Atlantic Forest Domain, Brazil.