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Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests

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Running head: Functional impacts of forest fragmentation

Summary

1. Fragmentation of tropical forests is one of the greatest threats to global biodiversity. Understanding how biological and functional attributes of communities respond to fragmentation and, in turn, whether ecosystem functioning is impacted upon are critical steps for assessing the long-term effects and conservation values of forest fragments. Ecosystem functioning can be inferred through functional diversity metrics, including functional richness, evenness, and divergence, which collectively quantify the range, distribution, and uniqueness of functional traits within a community.

2. Our study was carried out in forest remnants of the Brazilian Atlantic rainforest, which is a global hotspot of threatened biodiversity that has undergone massive deforestation and fragmentation. We focus on trees, which play critical functional roles in forest structure, food provisioning, and carbon storage, to examine community organisation and functional diversity across a gradient of fragmentation, from small to large fragments and at edge versus interior habitats.

3. The interiors of small fragments have marginally higher species richness, but similar community structures, to the interiors of bigger fragments. In contrast, fragment edges suffered significant losses of species and changes in community structure, relative to fragment interiors.

4. Despite shifts in community organisation, functional richness was not impacted by fragmentation, with the same number of functions provided independent of fragment size or proximity to edge. However, functional evenness and functional divergence both increased with decreasing fragment size, while fragment edges had lower functional evenness than interiors did, indicating that the abundance and dominance of functional traits has changed, with negative implications for functional redundancy and ecosystem resilience. At fragment edges, large-fruited trees, critical as resources for fauna, were replaced by early successional, small-seeded species. The influence of fragment size was smaller, with a reduction in very large-fruited trees in small fragments counterbalanced by increased numbers of fleshy-and medium-fruited trees. Wood density was not impacted by fragmentation.

5. *Synthesis.* These results suggest that the interiors of even small fragments can contain important biodiversity, ecosystem functions, and carbon stores, offering potential opportunities for co-benefits under existing carbon markets. Retaining forest fragments is an important conservation strategy within the highly threatened Brazilian Atlantic forest biome.

Key-words: carbon, fauna resources, fragmented landscape, functional diversity, functional trait attributes, species richness, Tableland Atlantic Rain Forest, wood density

Introduction

The ongoing fragmentation of tropical forests is one of the greatest threats to global biodiversity (Fahrig 2003; Laurance *et al*. 2006a,b). These threats are arising primarily from rapid habitat loss (Schroth *et al*. 2004), with some 83 million hectares of tropical forest cleared for agriculture in the 1980s and 1990s alone (Gibbs *et al*. 2010). Such clearance isolates remnant blocks of forest and divides them into smaller parcels, driving reductions in wildlife populations, the severity of which is determined by the size, shape, isolation and edge effects of fragments (Murcia *et al*. 1995; Fahrig 2003; Santos *et al*. 2010; Laurance *et al*. 2011). While the biggest blocks of primary forest are irreplaceable for biodiversity conservation (Gibson *et al*. 2011), the sheer scale of forest fragmentation means that understanding how the biological, functional and ecosystem attributes of fragmented communities are being affected is critical.

Many studies have highlighted the changing patterns of species richness, diversity and community composition between contiguous forest and fragments, across gradients of forest fragment sizes, and from forest edges to interiors. Intense landscape-level fragmentation can impact severely upon species richness compared to intact forests, with larger fragments typically harboring communities that are more similar to those in contiguous forest (e.g. Laurance 1994; Benítez-Malvido & Martínez-Ramos 2003; Watson *et al*. 2004; Benedick *et al*. 2006; Hillers *et al*. 2008; Arroyo-Rodríguez *et al*. 2008; Pardini *et al*. 2010; Tabarelli *et al*. 2010; Laurance *et al*. 2011). There are severe abiotic changes at fragment edges, such as desiccation, wind disturbance, light and temperature increase, and decrease in air humidity, which are likely to cause some of the biological edge-effects that occur after fragmentation (Fagan *et al*. 1999; Laurance *et al*. 2002, 2011; Tabarelli *et al*. 2010; Pütz *et al*. 2011). At forest edges, forest-specialist species (e.g., shade-tolerant trees) are typically replaced by generalist or pioneer species, promoting losses of species richness, changes in community structure, and shifts in forest dynamics (Oliveira *et al*. 2004; Tabarelli *et al*. 2010; Laurance *et al*. 2006ab). Furthermore, the impacts of size and edge often co-occur and can act synergistically, confounding assessments of the relative importance of these factors in driving biological change (Ewers & Didham 2006; Fletcher *et al*. 2007). Nevertheless, given the high species richness and spatial turnover in intact tropical forests, fragments that have apparently undergone severe declines in species richness can still retain a subset of species with high conservation value (Hill *et al*. 2011; Arroyo-Rodríguez *et al*. 2008; Gardner *et al*. 2009; Pardini *et al*. 2010; Santos *et al*. 2010).

Our understanding of the impacts of forest fragmentation on the functional roles performed by species, and thus on ecosystem functioning, is much more limited (Chapin 2003; Gardner *et al*.

2009). As an example, the sizes and dispersal types of fruits and seeds can be used to evaluate resource availability and the diversity of interactions between animals and plants (Moran & Catterall 2010). Most assessments use simple indices, such as the Shannon and Simpson diversity indices (e.g. Metzger 2000; Girão *et al*. 2007) or the number of functional groups observed per plot (Mayfield *et al*. 2005), to infer that communities have significantly lower functionality in fragments than in intact tropical forests (see Metzger 2000; Mayfield *et al*. 2005; Girão *et al*. 2007; Tabarelli & Peres 2002; Laurance *et al*. 2006ab; Michalski *et al*. 2007). However, these methods of quantifying the impacts of disturbance on functional roles are incapable of combining a variety of functional traits into a single overall measure of functional changes (Petchey & Gaston 2002). Further, they fail to consider variation in the functional impacts of other traits that vary within a particular functional group, for instance, large-fleshy fruits that contain one large to many small seeds.

An alternative approach to evaluating the effects of forest fragmentation on the functional roles performed by species is to examine functional diversity (Loreau 2001; Petchey & Gaston 2002; Villéger *et al*. 2008; Kooyman *et al*. 2013). Functional diversity quantifies a range of functional traits within multi-dimensional niche space, typically focusing on the physiological and morphological traits that define a species' ecological role in a community (Petchey & Gaston 2006; Villéger *et al*. 2008) and yielding a single continuous measure. This also allows one to assess how regularly species are distributed within functional space, weighted by relative abundances, and how the relative abundance of species are distributed within functional space, relative to the centre of gravity (Villéger *et al*. 2008). Such assessments can help us to understand the effects of disturbance on ecosystem functioning, particularly in the context of conservation of tropical biodiversity (Laliberté *et al*. 2010; Villéger, *et al*. 2010; Pakeman *et al*.

2011; Baraloto *et al*. 2012; Edwards *et al*. 2013). Furthermore, functional diversity indices are typically more able to discern impacts of environmental disturbance than are basic measures of species diversity (Loreau *et al*. 2001), due to differences in functionality assigned to each species (Petchey & Gaston 2002).

In this study, we focus on forest fragmentation in the Brazilian Atlantic forest and on trees, which play critical functional roles in ecosystems for instance, by providing shelter and food resources for fauna (Moran & Catterall 2010), considerable primary production (Barber 2007) and carbon storage (Laurance 2004; Nascimento & Laurance 2004). The Brazilian Atlantic forest is a hotspot of imperiled biodiversity (Myers *et al*. 2000); around 300 tree species are found in just one hectare of Atlantic Forest (Rolim & Chiarello 2004; Saiter *et al*. 2011), making it one of the biologically most important biomes on Earth. Yet deforestation has been so widespread in the Atlantic forest that just 11% of forest cover remains and 80% of the forest that does persist is within fragments smaller than 50 hectares (Ribeiro *et al*. 2009). We examined community organisation and functional diversity across a gradient of fragmentation, from small to large fragments and at edge versus interior habitats.

Material and methods

STUDY AREA

This study was based in the state of Espírito Santo, in Southeast Brazil. Within the region, we focused on the municipalities of Sooretama, Linhares and Jaguaré ($18^{o}54'$ to $19^{o}15'$S and $39^{o}54$ to $40^{o}15'$W, 28- 65 m.a.s.l) (Fig. 1), which contain a landscape matrix composed mainly of grasslands, and *Eucalyptus* spp., coffee, and papaya plantations (Rolim *et al*. 2005). The climate is tropical wet (Köppen classification), with an annual precipitation of 1,403 mm and a distinct dry season from May to September, when precipitation is just 33 mm per month (Peixoto & Gentry 1990). The predominant soil in the study region is Yellow Podzolic (IBGE 1987).

This region is part of the phytogeographic domain Atlantic Forest and is officially classified as Lowland Rain Forest (IBGE 1987) or Tertiary Tablelands Forest (Peixoto & Silva 1997). The study area is of high conservation importance due to the presence of two forest fragments larger than 20,000 hectares, which contain a high diversity of plant and animal species (Peixoto & Silva 1997; Chiarello 1999; Masden *et al*. 2001).

TREE SAMPLING

Fieldwork was conducted from January 2011 to January 2012. We created permanent plots along transects within 9 fragments ranging from 13.2 to 1318.3 ha in area (mean=333.9 ha) and within 2 control-forest blocks larger than 20,000 ha in Reserva Natural Vale (RNV) and Reserva Biológica de Sooretama (REBIO) (Table S1). Our sampling unit was a transect that contained ten 10 x 10 m plots at 20 m intervals, and we sampled each fragment with one edge and one interior transect. A major review of 33 abiotic and biotic edge parameters showed that 10 parameters penetrated less that 25 m from forest edge and that all but one parameter penetrated less than 300 m (Laurance *et al*. 2002). We thus stationed edge transects ~5 m inside the fragment and parallel to the forest edge to capture all edge parameters, and interior transects with distance ≥300 m from the nearest edge (noting that the smallest fragments did not permit a longer minimum distance from edge). We also allocated six transects within control areas: one edge and one interior transect in RNV, and two edges and two interior transects in REBIO, with a mean distance of 17.1 ± 10.4 km between transects. All plots were on the same soil type (Yellow Podzolic).

Within each plot, we sampled every living tree with a diameter-at-breast height (DBH) ≥4.8 cm at 1.3 m height, and collected samples from each individual. We identified this material with reference to collections at the CVRD Herbarium of the Vale and the VIES Herbarium of the Federal University of Espírito Santo, and with aid from taxonomic experts in plant species identification in specific families (e.g. Myrtaceae and Sapotaceae). Botanical material collected in the fertile stage was deposited in the collection of Vale Herbarium of the Reserva Natural Vale in Linhares, ES.

FUNCTIONAL TRAIT MATRIX

We use functional traits that are relevant to the morphological and physical adaptations of trees in their role as food resources, their dispersal, and in carbon storage and forest structure (Tabarelli & Peres 2002; Bolmgren & Eriksson 2005; Laurance *et al*. 2006ab; Bongers *et al*. 2009; Moran & Catterall 2010; Tabarelli *et al*. 2010). Within these three broad types of functional role, we had five categorical traits and one continuous trait, classified as: (1) fruit size, (2) seed size, (3) fruit type, (4) fruit dispersal syndrome; (5) successional group, and (6) wood density (continuous variable).

Food Resources: Fruit and seed sizes for each of the species identified were classified into four categories according to Tabarelli & Peres (2002): small (<0.6 cm in length), medium (0.6-1.5 cm), large (1.6-3.0 cm), and extremely large (>3.0 cm). We used fruit and seed sizes as categorical variables because both metrics are poorly explored within the Brazilian Atlantic forest, such that many species lack sufficient precision to use as a continuous variable. To place species into categories, we used a combination of reliable measurements for the subset of fruits within the CVRD herbarium and literature, supplemented by observational records (e.g. of seed scar size in fruits), descriptions from the literature, and botanical knowledge (e.g., consistent family traits and from botanists at the CVRD herbarium). We also categorized the fruits into two types: (i) fleshy fruits (i.e., the pericarp can accumulate water and many organic compounds; see Coombe (1976)) and non-fleshy fruits.

Fruit dispersal syndrome: Fruits were classified as zoochoric or non-zoochoric following Van Der Pijl (1982). A zoochoric tree produces diaspores surrounded by fleshy pulp, an aryl, or other features that are typically associated with dispersal by animals, and a non-zoochoric tree has characteristics that indicate dispersal by abiotic means, such as winged seeds, feathers, or a lack of features that indicate dispersal via methods other than downfall or explosive indehiscence.

Carbon storage and forest structure: We classified species into the successional groups defined by Bongers *et al.* (2009). We considered as pioneers those trees that develop in conditions of high light and generally do not occur in the understorey, as early secondary those trees that develop in intermediate shading conditions, and as late secondary those trees that develop exclusively in permanently shaded understorey. Species were classified using the database by Jesus & Rolim (2005) from the Reserva Natural da Vale. Data for wood density in dry weight (g/cm^3) were obtained from The Global Wood Density (GWD) database in the subsection Tropical South America (http://hdl.handle.net/10255/dryad.235, Chave *et al*. 2009; Zanne *et al*. 2009). We made two adjustments (following Flores & Coomes 2011; Hawes *et al*. 2012): for morphospecies only identified to the family or genus level, we used the average wood density of the taxonomic group; and for species not in the GWD database, we used the average wood density for the species' genus.

Species identified at morphospecies level represented only 1.1% of species richness and 0.2% of total abundance. These species were not treated in any of the functional traits described above, being considered only in the analysis of species richness and community structure.

DATA ANALYSIS

We used Nonmetric Multidimensional Scaling (NMS) ordination analysis in the PC-ORD 6 package (McCune & Mefford 2011) to identify changes in community structure between different-sized fragments, and between edge and interior habitats. We used the raw species abundance data from each plot and the Sørensen (Bray-Curtis) distance. We considered the NMS results arising from tree species abundance data as a measure of community structure (Barlow *et al*. 2010), with the number of individuals representing abundance.

To analyze functional diversity we used three indices proposed by Villéger *et al.* (2008): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). FRric represents the volume of space of a functional convex hull occupied by the community, FEve the regularity of the distribution in abundance on this volume, and FDiv the divergence in the distribution of species characteristics within the volume occupied by each functional trait. To calculate these three indices we used methods and scripts from Villéger *et al.* (2008), in R version 2.15.1 (R Development Core Team 2012).

To investigate fragmentation effects on community structure and functionality of tree species, we considered two explanatory variables: (i) fragment size as a continuous variable and (ii) habitat type with two levels (interior and edge). We also applied an interaction between size and habitat type to investigate possible differences in the relationship with fragment size at edges and interiors. We used the raw species abundance data from each transect, and Generalized Linear

Mixed Models were carried out using the glmmadmb function from the glmmADMB package. We used Negative Binomial error distributions for count data, since our data showed significant overdispersion, and a Gaussian error distribution for the remaining data. The sites (each fragment) were codified as a random variable in all analyses (Bolker *et al*. 2009). We used the dredge function from the MuMIn package to test all possible combinations of the variables included in the global model. To determine which of these explanatory variables were the most decisive in possible changes in species richness, community structure, functional diversity and functional trait attributes we used an information theoretical approach based on the Akaike Information Criterion of Second Order (AICc), which is indicated for small sample sizes and the best model was indicated by the AICc lower value (Burnham *et al*. 2011). All analyses were performed in the R version 2.15.1 (R Development Core Team 2012).

Results

FRAGMENTATION AND COMMUNITY ORGANISATION

Across all fragments, we sampled a total of 4,140 tree individuals belonging to 443 species (Table S2). Considering only the best model selected on the basis of their AICc values, species richness at the transect level was significantly influenced by the interaction between fragment size and edge versus interior habitat (GLZ: Z=2.52; P=0.03), where increasing fragment size had a significant negative effect on species richness in interiors (F=6.95: P=0.02; Fig. 2A) but no significant effects near edges (F=1.89: P=0.1982; Fig. 2A). Species richness was significantly higher within fragment interiors than at fragment edges (GLZ: Z=2.79; P =0.02, Fig. 2B).

NMS analysis of species composition and abundance (community structure) parameters indicated significant changes in community structure for the axes 1, 2, and 3 (P=0.02; Fig. S1).

However, GLZ models revealed that only axis 1 and 2 of tree community structure were significantly influenced by fragments' size and by edges. The best model selected by AICc for axis 1 indicated that changes in community structure were strongly influenced by the creation of an edge habitat (GLZ: Z=3.84; P<0.01; Fig. 2C). For axis 2, the best model included the interaction between fragment size and habitat (GLZ: Z=-4.05; P<0.01; Fig. 2D), with changes significantly related to fragment size in the interior (F=95.95: P=0.01; there was no significant effect of edge versus interior habitat, F=7.76: P=0.37).

FRAGMENTATION AND FUNCTIONAL DIVERSITY

We found no significant effects of edge versus interior habitat (GLZ: Z=-0.46; P=0.66), fragment size (GLZ: Z=-0.78; P=0.45), or the interaction between habitat type and fragment size (GLZ: Z=0.38; P=0.71) on functional richness, indicating that forest fragmentation causes no overall loss in functional richness in this landscape. Functional evenness was, however, significantly negatively related to fragment size (GLZ: Z=-2.23; P<0.05; Fig. 3A), indicating that the evenness of traits is less heterogeneous in larger than smaller fragments. Functional evenness was also significantly higher in fragment interiors versus edges (GLZ: Z=4.8; P<0.001, Fig. 3B). Functional divergence showed a significant negative relationship with fragment size (GLZ: Z=2.1; P<0.04; Fig. 3C), demonstrating that smaller patches are more divergent (i.e., have less functional redundancy) than larger fragments in the landscape. There was no effect of edge versus interior on functional divergence (GLZ: Z=-0.87; P=0.4). Changes in functional evenness and functional divergence thus indicate that, despite finding no significant impact of fragmentation on functional richness, there are shifts in the provision of different functional trait attributes following fragmentation.

We investigate this variation in our fifteen functional trait attributes using two metrics: the richness of species exhibiting a particular functional trait attribute, and the abundance of individuals exhibiting a particular functional trait attribute. For the richness of species exhibiting particular functional trait attributes, we find that edge versus interior habitats had the largest effect, being a significant predictor in 6 of 15 of the best models proposed by AICc (Table 1). Proximity to forest edges had a significant negative influence on the richness of tree species with zoochoric dispersion, fleshy fruits and later secondary species (i.e., these traits had higher species richness in interiors), and a significant positive influence on the richness of non-zoochoric dispersed, pioneer, and initial secondary species (Table 1). Fragment size, and the interaction between size and habitat, had a significant negative effect on the richness of tree species with very large fruits (Table 1 and Fig. S2), with the other 14 functional trait attributes not selected in size and size*habitat best models.

Edge versus interior was also prominent for the abundance of individuals exhibiting a functional trait attribute (significant predictor in 9 of the 15 best models), negatively influencing the abundance of zoochoric dispersion, fleshy fruits, very large, medium and small fruits, medium seeds, and late secondary species, and positively influencing the abundance of non-zoochoric dispersers and pioneers. Fragment size (significant predictor in six of the 15 best models) showed a negative influence on the abundance of very large fruits trees species and a positive influence on zoochoric dispersion, fleshy fruits, medium fruits, and large and medium seeds trees species. The interaction between fragment size and edge versus interior habitat had a significant, positive influence on the abundance of very large fruits and initial secondary species (Table 1, Fig. S3), with the remaining 13 functional trait attributes not selected. Wood density did not respond significantly to fragment size, edge versus interior habitats, or the interaction between size and habitat (Table 1).

Discussion

It is important to understand how forest fragmentation affects the functional attributes of tree communities and, in turn, ecosystem functioning. Our results suggest that functional richness is not impacted by fragmentation in the Brazilian Atlantic forest, indicating that a similar number of functions are provided regardless of fragment size or proximity to edge. However, functional trait attributes do vary: edges were particularly severe in driving functional change (e.g., replacing large-fruited species consumed by fauna with early successional, small-seeded trees), whereas functional divergence and functional evenness increased in small versus large fragments, suggesting a loss of functional redundancy of tree communities and ecosystem resilience in small fragments. Wood density, however, was not impacted by fragmentation. The interiors of even small fragments thus represent important reservoirs of biodiversity and sustain functionally important tree groups for fauna and carbon storage, at least in the short term, and potentially for a century after fragmentation (Kooyman *et al*. 2013). Our results also suggest important potential co-benefits between carbon markets, ecological services and biodiversity protection in fragments.

FRAGMENTATION AND COMMUNITY ORGANISATION

Tree species richness in the interiors of smaller fragments was greater than that in the interior of larger fragments of Brazilian Atlantic forests in our study, and a similar pattern was apparent for the richness of tree genera in forest fragments in Amazonia (Michalski *et al*. 2007). This contrasts with other studies that showed that while larger fragments typically retain the highest overall species richness (e.g., Laurance *et al*. 2002, 2011), there was no difference between fragment size and species richness per unit of sample area (Laurance *et al*. 2006b). One possibility is that there is a lot of spill-over of species into the interiors of small fragments, both from the non-forest matrix (Cook *et al*. 2002) and from large fragments or contiguous forest sources (Brudvig *et al*. 2009), the latter spillover determined in part by landscape configuration and connectivity (Brudvig *et al*. 2009). In our study, the small- and medium- sized fragments were often close to large fragments and the continuous forest blocks, and there was high connectivity among them (Fig. 1). Another reason for high species richness in small fragments was that they contained species typical of both forest interiors and matrix areas (e.g., equivalent abundances of zoochoric species and non-zoochoric dispersion species), whereas larger fragments were dominated by zoochoric species.

Across all fragment sizes, we found lower species richness at fragment edges than interiors, a pattern found in other fragments of Brazilian Atlantic forest (Oliveira *et al*. 2004; Lopes *et al*. 2009) and in other tropical regions (Saunders *et al*. 1991). It is likely that changes in abiotic conditions at fragment edges, such as increased wind speed and air temperature, and decreased humidity (Laurance *et al*. 2002, 2011), explain these biological edge-effects.

We observed significant shifts in community structure near fragment edges and in fragments of varying sizes. These shifts are likely related to the abundance of pioneer and early secondary species, which can lead to a rapid change in forest structure, species composition and ecological functionality (Laurance *et al*. 2006ab; Bongers *et al*. 2009; Tabarelli *et al* 2010), and are apparently driven by proximity to forest edge rather than by fragment size per se (Table 1). For instance, Amazonian forest fragments tend to have a greater number and abundance of successional species near edges than in interiors of even small fragments (Laurance *et al*.

2006ab; Michalski *et al*. 2007), and these influence the structure and dynamics of forest patches (e.g. Laurance *et al*. 2006ab; Tabarelli *et al*. 2010).

FRAGMENTATION AND FUNCTIONAL DIVERSITY

Among the three indices that describe functional diversity, those accounting for the abundance of species (functional evenness) and the dominance of a functional group over other functional groups (functional divergence) were more sensitive to fragmentation effects than was functional richness, which is more influenced by species richness (see Villéger *et al*. 2008; Mouchet *et al*. 2010). In our study, functional richness remained constant with fragment size and at edges versus interiors; thus fragmentation does not appear to alter the volume of functional space occupied by species within different communities. Small fragments of forest in the Australian subtropics also retained similar levels of functional richness to large fragments (Kooyman *et al*. 2013). However, in our study, the retention of functional richness with fragmentation is underpinned by species that exhibit different functional trait attributes (Table 1, see below), indicating shifts in ecological functionality that can modify the diversity of interactions between plants and animals (Moran & Catterall 2010).

A high intensity and frequency of disturbances at fragment edges (Murcia 1995) may explain reductions in functional evenness compared to fragment interiors. Declines in functional evenness indicate that some parts of the functional space within edges decline or disappear (e.g. Mouchet *et al*. 2010). At fragment edges, the reduction of functional evenness was related to the loss of important functional groups, such as zoochoric dispersion, fleshy fruits and later secondary species, balanced to some degree by an increase in non-zoochoric and pioneer species. Such shifts are likely to make edges functionally more homogeneous, leading to declines in food resources for frugivorous birds and mammals, and reducing forest regeneration potential via dispersal (Bolmgren & Eriksson 2005; Moran & Catterall 2010). In turn, a loss of ecological functionality is likely to have secondary consequences for faunal and floral richness (Fig. 1; Tabarelli & Peres 2002; Laurance *et al*. 2002; Oliveira *et al*. 2004; Laurance *et al*. 2006b).

Lower functional divergence and functional evenness in the interiors of large versus smaller fragments suggest niche homogenization between species (Mouchet *et al*. 2010), with most abundant species being functionally similar and exhibiting higher competitiveness, coupled with low prevalence or absence of some parts of functional space. Reductions were accompanied by an increase in the abundance of fleshy fruit, zoochoric dispersed species, and a decrease in abundance of initial secondary species, implying greater resources and interactions with fauna in large fragments (see Bolmgren & Eriksson 2005; Bongers *et al*. 2009). Indeed, in our study landscape, mammal communities shifted from one dominated by medium- and large-bodied frugivorous species in large fragments to one dominated by herbivorous mammals in small fragments (Chiarello 1999). Low functional divergence also suggests that there is higher functional redundancy in large versus smaller fragments. This means that there is a degree of resilience for key ecosystem functions in large fragments, since there is likely to be a functionally equivalent species in the tree community if another is lost (Laliberté *et al*. 2010). However, reductions in patch size apparently reduce functional redundancy and thus resilience, with the potential for the long-term erosion of ecosystem functions in small fragments.

Despite significant increases in the species richness and abundance of early successional trees at forest edges and in the interior of smaller fragments, we found no significant effects of fragmentation on wood density. Thus the apparent lack of response of wood density to fragmentation suggests that even small fragments or fragment edges can be managed to play an important role in carbon storage. However, since wood densities of species can be affected by environmental changes due to fragmentation (e.g. Laurance *et al*. 2006; Thomas *et al*. 2007; Nock *et al*. 2009), the average wood densities we used from the literature (Chave *et al*. 2009; Zanne *et al*. 2009) would miss any such variation. Our functional diversity analyses could be refined in future analyses by using wood densities derived from in situ measurements, and, when herbarium collections permit, fruit and seed sizes as continuous rather than categorical variables.

CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

The changes in functional diversity, functional trait attributes, species richness and community structure at forest edges and in smaller fragments have important implications for conservation in fragmented landscapes. Although our fragments are typically ~40 years old, we cannot rule out the possibility that there remains an extinction debt in smaller fragments and at edges, especially given the longevity of many tree species in tropical rain forests (Chambers *et al*. 1998; Laurance *et al*. 2004), that could further degrade the functional value of these habitats over far longer timescales (but see Kooyman *et al*. 2013). Additionally, tree populations in smaller fragments may be sustained to some extent by seed dispersal from larger blocks of natural habitat, and we highlight understanding the impacts of landscape connectivity on ecosystem functioning in fragmented systems as a key research frontier. Hence the functional diversity of small fragments and edges may change over time or if other forest fragments were removed from the landscape. Consequently, protecting large forest fragments from conversion and interiors from degradation must remain top conservation priorities.

Nonetheless, our results support previous studies suggesting that even small forest patches can retain high conservation value, especially within highly threatened biomes, such as the Brazilian

Atlantic forest (e.g. Arroyo-Rodríguez *et al*. 2008; Gardner *et al*. 2009; Santos *et al*. 2010). First, we found similar communities in the interior of small and large fragments, suggesting that small fragments could represent important reservoirs of forest specialist trees and aid seed dispersal or connectivity across landscapes. Second, the retention of functional diversity within small fragments and edges was maintained by non-zoochoric, pioneer and initial secondary tree species. These species are excellent dispersers and, in the event of agricultural abandonment or land purchases to reconnect forest fragments (Martínez-Garza & Howe 2003; Cortines & Valcarcel 2009; Simmons *et al*. 2011; see also savingspecies.org), they could play important roles as sources of seeds in the recovery of early secondary forests. Third, the apparent absence of change in wood density across the fragmentation gradient suggests that even small fragments can be important carbon stores, with potential co-benefits between carbon market payments, ecological services and biodiversity protection (Díaz *et al*. 2009; Phelps al. 2012).

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Figure legends

Fig. 1. Study area and forest fragments sampled in Southeastern Brazil. Names and information about fragments are given in Table S1.

Fig. 2. Taxonomic changes as a function of fragments size and habitat. (A) The effect of the interaction between fragments size and habitat on total species richness, partial residuals plots; (B) the effect of habitat on total species richness; (C) the effect of habitat on tree community structure (Axis 1 scores from NMS analysis); and (D) the effect of the interaction between fragment size and habitat on tree community structure (Axis 2 scores from NMS analysis), partial residuals plots. Filled (forest edge) and empty (forest interior) circles represent values obtained after summation of raw residuals with the expected values for each variable, assuming average values for other covariates. Errors bars represent standard errors.

Fig. 3. Graphs of best models of functional diversity in relation to the size and habitat of the fragments. (A) The effect of fragment size on Functional Evenness (FEve), partial residuals plots; (B) the effect of habitat on Functional Evenness (FEve); and (C) the effect of fragment size on Functional Divergence (FDiv), partial residuals plots. Filled circles represent values obtained after the summation of raw residuals with the expected values for each variable, assuming average values for other covariates. Errors bars represent standard errors.

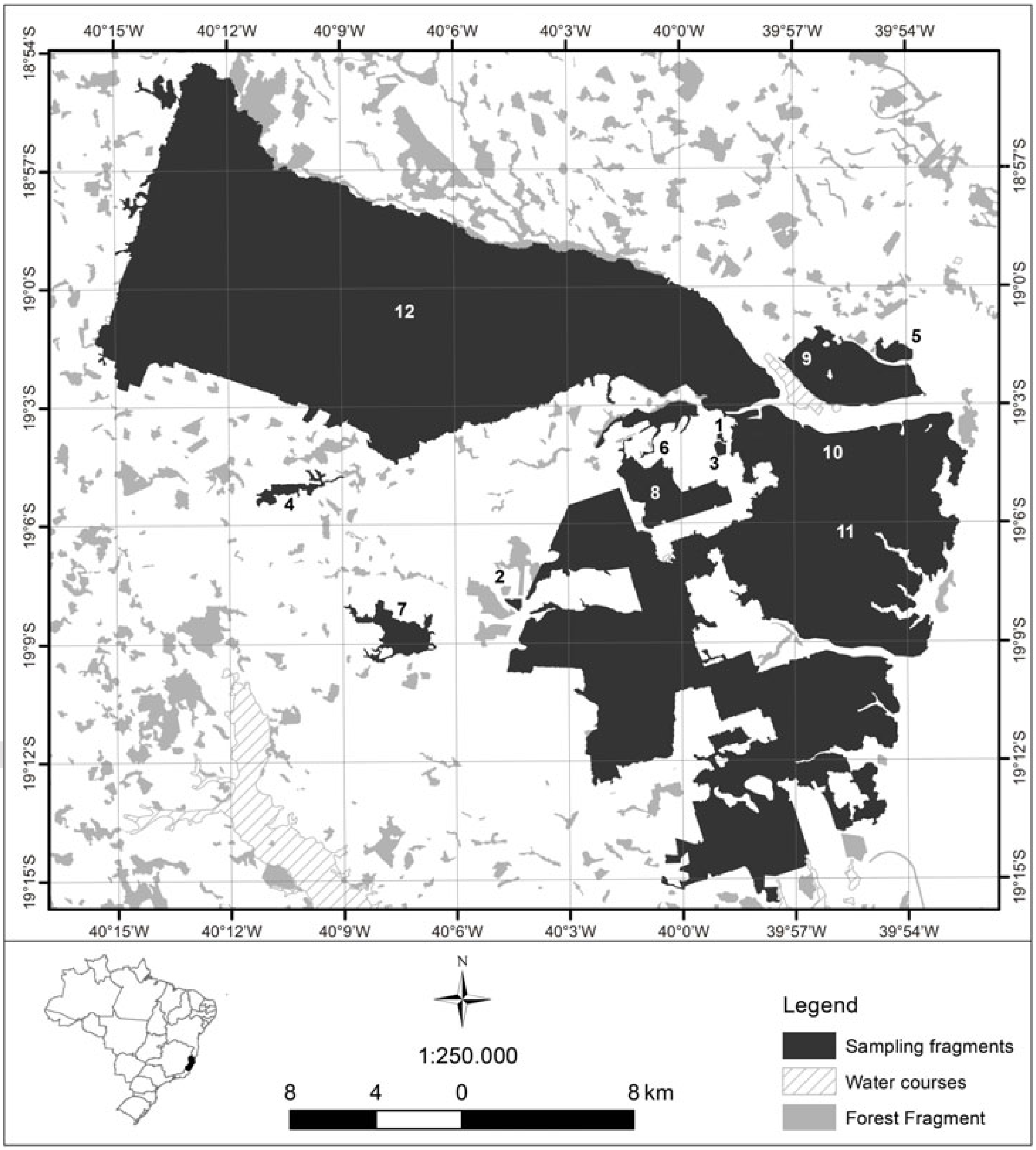
Tables

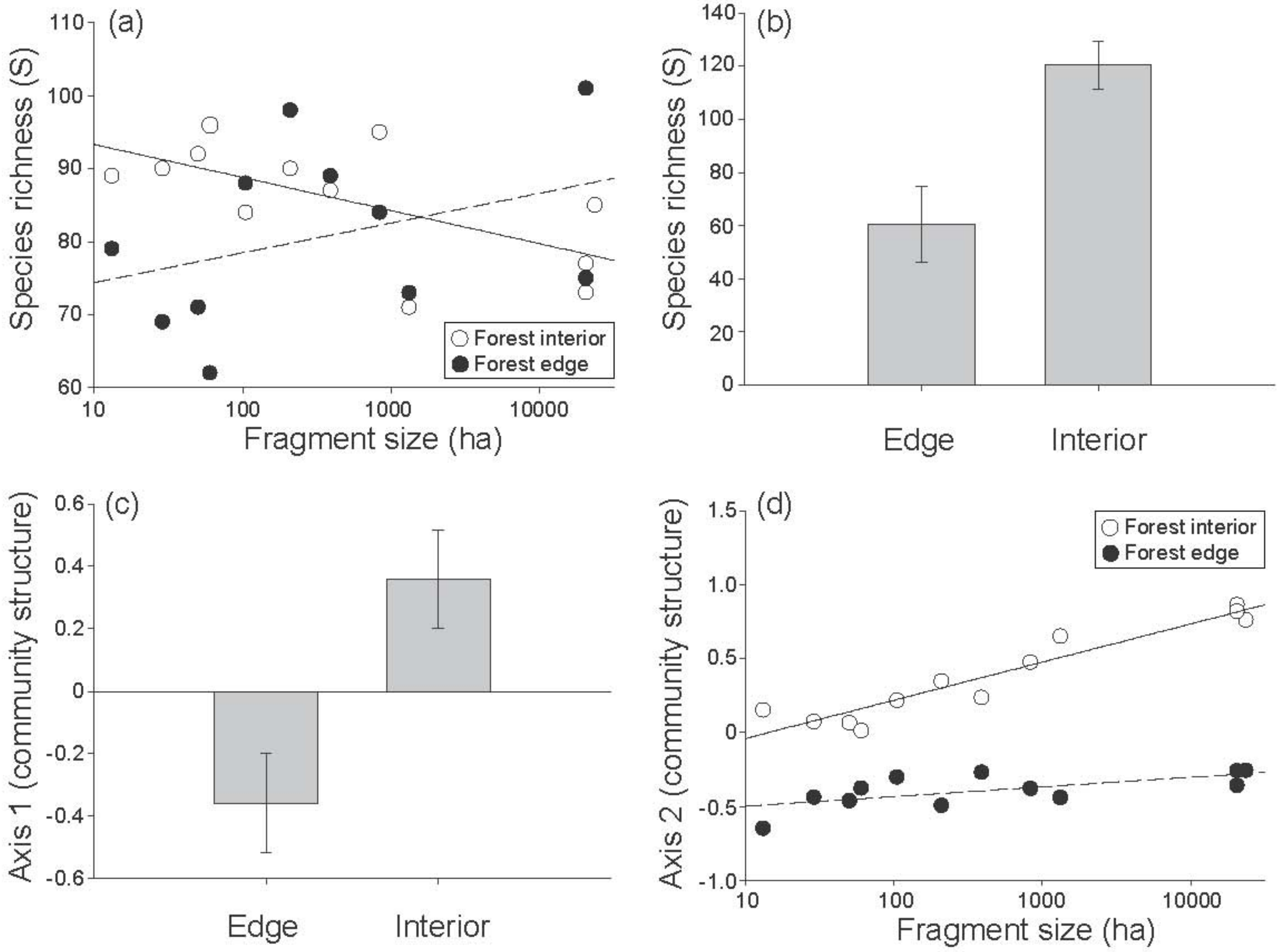
Table 1. Results from Generalized Linear Mixed Models for the effects of fragment size, edge versus interior habitat, and the interaction between size and habitat on species richness and abundance of different functional groups. Only the best models according to their AICc values are shown. Values show coefficient estimates and standard errors.

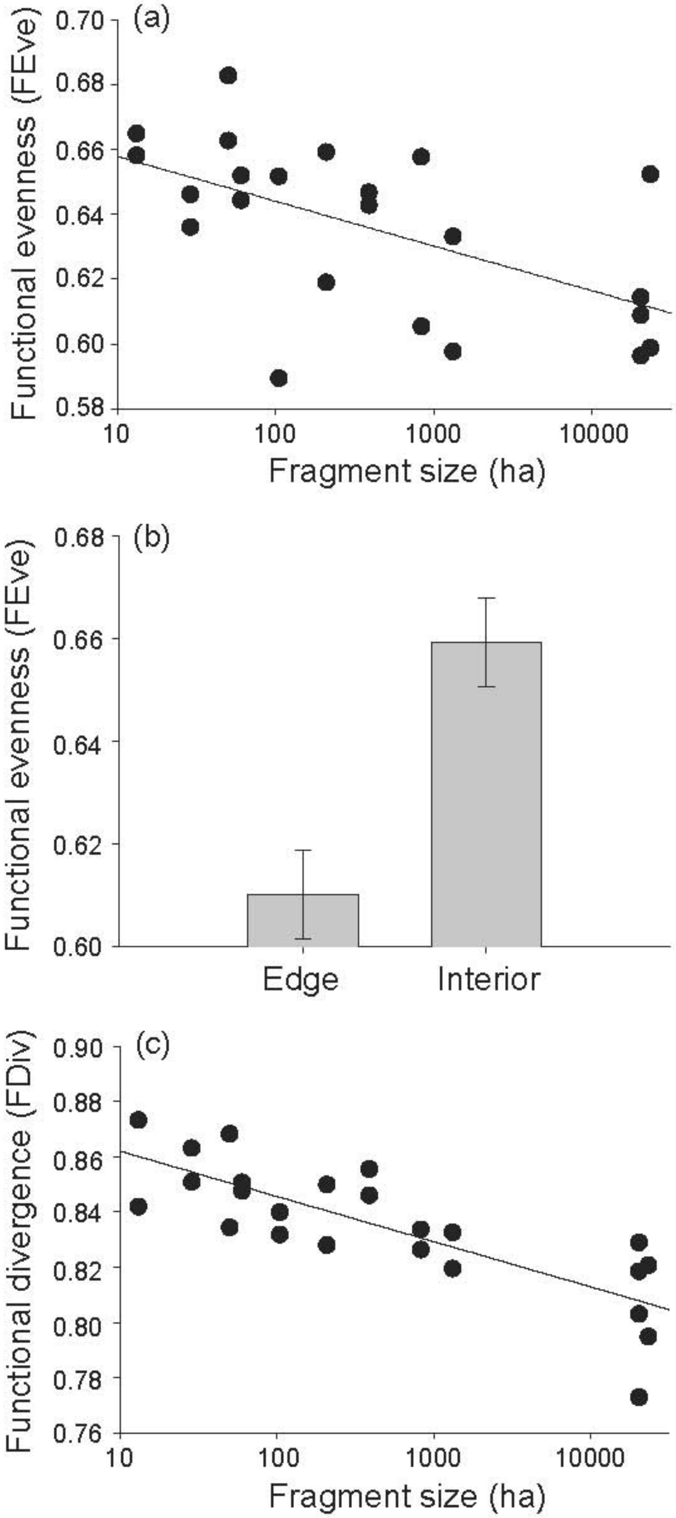
Functional trait	Fragment size (log)	Habitats (Edge)	Size*habitats
Species richness			
Zoochoric dispersion		-10.08 (3.65)**	
Non-zoochoric dispersion		5.58 (1.94)**	
Fleshy fruits		-9.08 (-3.26)*	
Non-fleshy fruits		4.58 (2.57)ns	
Very large fruits	-4.05 (1.2)***	-8.55 (4.91)ns	4.24 (1.7)*
Large fruits		-4.92 (2.3)ns	
Medium fruits		-3.25 (1.7)ns	
Small fruits		0.92 (0.77)	
Very large seeds	-0.73 (0.47)ns		
Large seeds		-4.91 (2.3)ns	
Medium seeds		-5.25 (2.74)ns	
Small seeds		1.08 (1.92)ns	
Pioneers		2.17 (0.93)*	
Initial secondary		7.75 (2.3)**	
Later secondary		-14.42 (2.7)***	
Abundance			
Zoochoric dispersion	0.09 (0.02)***	-0.32 (0.06)***	
Non-zoochoric dispersion		0.41 (0.09)***	
Fleshy fruits	0.12 (0.03)***	-0.27 (0.07)***	
Non-fleshy fruits	-0.04 (0.07)ns		
Very large fruits	-0.15 (0.06)**	-0.53 (0.22)*	0.25 (0.08)***
Large fruits		-0.15 (0.1)ns	
Medium fruits	0.11 (0.05)*	-0.19 (0.09)*	
Small fruits		-0.39 (0.16)*	
Very large seeds		0.28 (0.21)ns	
Large seeds		-0.14 (0.08)ns	
Medium seeds	0.1 (0.03)**	-0.22 (0.08)**	
Small seeds		-0.07 (0.08)ns	

Pioneers		1.05 (0.32)**	
Initial secondary	0.13 (0.05)**	-0.14 (0.25)ns	0.25 (0.09)**
Later secondary	0.06 (0.04)ns	-0.48 (0.07)***	
Wood characteristic			
Wood density		-0.02 (0.01)ns	

Note that the positive parameters indicate positive effects and negative parameters indicate negative effects. N=12; * p> 0.05, ** p> 0.01, *** p> 0.001, ns = not significant.




(a)
Species richness (S)
110
100
90
80
70
60
10
100
1000
10000
Fragment size (ha)
○ Forest interior
● Forest edge
(b)
Species richness (S)
140
120
100
80
60
40
20
0
Edge
Interior
(c)
Axis 1 (community structure)
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Edge
Interior
(d)
Axis 2 (community structure)
1.5
1.0
0.5
0
-0.5
-1.0
10
100
1000
10000
Fragment size (ha)
○ Forest interior
● Forest edge


(a)
Functional evenness (FEve)
0.70
0.68
0.66
0.64
0.62
0.60
0.58
10
100
1000
10000
Fragment size (ha)
(b)
Functional evenness (FEve)
0.68
0.66
0.64
0.62
0.60
Edge
Interior
(c)
Functional divergence (FDiv)
0.90
0.88
0.86
0.84
0.82
0.80
0.78
0.76
10
100
1000
10000
Fragment size (ha)