Special Issue: Defaunation's impact in tropical terrestrial ecosystems

No changes in seedling recruitment when terrestrial mammals are excluded in a partially defaunated Atlantic rainforest

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ABSTRACT

One of the most intriguing questions in ecology is how to identify which and how many species will be able to inhabit human-modified landscapes. Large-bodied mammals structure plant communities by trampling, herbivory, seed dispersal and predation, and their local extinction may have pervasive consequences in plant communities due to the breakdown of key interactions. Although much attention has been given to understanding the effects of defaunation on plant communities, information on the potential impacts on plant functional groups (seed dispersal, seed size and seedling leaves defense) inhabiting continuous forests after defaunation is scarce. We conducted mammal surveys (line transects and camera trapping) to determine the defaunation status of a continuous Atlantic forest in Brazil. Then, we evaluated the effects of defaunation on seedling diversity, richness and abundance of functional groups using 15 plot-pairs (each pair with one open and one exclusion plot) monitored over 36 months. We found that the studied area is partially defaunated because it exhibits high abundance of primates, while terrestrial mammals, such as large rodents and ungulates, are rare. We found no significant changes in either seedling richness and diversity or in the seedling composition of plant functional groups in response to mammal exclosure. Seedling mortality and recruitment were similar between plot types. Our findings suggest that at semi-defaunated areas, where arboreal species are still present, terrestrial mammals have low impacts on the plant community reassembly.

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1. Introduction

Naturalists and ecologists have long endeavored to understand the mechanisms that explain tropical forest diversity and to tease apart the roles of abiotic, biotic and historical factors in the control of community composition and diversity (Chase, 2003; Hubbel, 1979; Janzen, 1971; Terborgh, 1988; Tilman and Pacala, 1993; Wright, 2002). Large-bodied mammals play a key role in structuring plant communities because they are important dispersers and predators of seeds, affecting the distribution, abundance and recruitment of numerous plant species (Beck 2005, 2006, 2007; Beck et al., 2013; Dirzo and Miranda, 1991; Keuroghlian and Eaton, 2009; Roldán and Simonetti, 2001; Silman et al., 2003; Stoner et al., 2007a; Terborgh et al., 2008; Wright, 2003). While most temperate ecosystems face dramatic explosions of ungulate populations due to the extinction of top predators (Côté et al., 2004), tropical ecosystems are experiencing increased defaunation because of overexploitation, which is leading to a lack of both top predators and large-bodied herbivores (Giacomini and Galetti, 2013; Peres and Palacios, 2007; Wright et al., 2000).

Most of the studies addressing the effects of vertebrate extirpation on plant recruitment have contrasted forest areas at the extremes of the defaunation spectrum, i.e., they compare so-called "empty forests" (sensu Redford, 1992) with pristine areas retaining complete mammal assemblages (Dirzo and Miranda, 1991; Kurten, 2013; Terborgh et al., 2008; Wright et al., 2007). However, some mammalian species are resilient and persist even in areas that suffer heavy hunting (Cullen et al., 2000; Galetti et al., 2009; Peres and Palacios, 2007). The persistence of these subsets of the original assemblages generates "half-empty forests" (Wilkie et al., 2011), and therefore such forest become a relevant subject of research. Donatti et al. (2009) found that small mammals (<1 kg), such as small rodents, do not adequately perform the ecological roles of large mammals (>1 kg) when the latter are experimentally excluded from areas of pristine forest. However, no study thus far has tested whether, in partially defaunated forests, persistent large- and medium-sized animals are able to perform the ecological roles of locally extinct species and serve as a tool for adequate long-term conservation of natural habitat.

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In this study, through an exclosure experiment, we investigated the consequences on the plant community (seedlings and saplings) of the extinction of the remaining large- and medium-sized mammals in a continuous Brazilian Atlantic forest. Our objective was to assess how the loss of ungulates and large rodents (simulated by the experimental exclosure plots) affects plant survival and recruitment and how this translates into changes in species richness and diversity or changes in abundance of plant functional groups. We expected that in the total absence of medium- and large-bodied mammals, we would detect some loss of plant richness and diversity due to the prevalence of more competitively dominant plant species (Dirzo and Miranda, 1991; Wright, 2003).

We tested the effects of the exclusion of terrestrial mammals on abundance of three aspects of functional group of seedlings: seed dispersal syndrome, seed size and seedling leaf defense. The abundance of plants dispersed by large vertebrates is expected to decrease in defaunated forests, with a subsequent increase in species dispersed by abiotic factors or non-hunted animals (Stoner et al., 2007b; Terborgh et al., 2008; Wright et al., 2007). However, in our study, we did not expect great alterations in response to seed dispersal syndrome because our plots did not exclude seed dispersal by arboreal mammals, such as primates, the main large-bodied seed dispersers in the Atlantic rainforest (Bueno et al. 2013).

Seed size, in addition to being related to dispersal, can influence the chance of predation by invertebrates, small rodents and large mammals (Bodmer, 1991; DeMattia et al., 2004; Dirzo et al. 2007; Galetti et al., 2010; Vieira et al., 2003). We expected that if large- and medium-sized mammals were important seed predators in our study site, the abundance of functional groups with large and medium seeds would increase in the exclosure plots (see the seed size classification in Section 2.4) because these seeds are preferred by large species (Bodmer, 1991; Galetti et al., 2010).

For seedling leaf defense against herbivores, we expected to find more seedlings of fast-growing species (i.e., seedlings without active defenses), which are preferred by vertebrate herbivores, within the exclosure plots (Barrett and Stiling, 2006; Bee et al., 2009; Jefferies et al., 1994; Salas and Fuller, 1996). There is a well-documented trade-off in plants between investment in leaf defenses and growth rate. Plants with defenses against herbivores resist herbivory and tend to grow more slowly than plants without anti-herbivore defenses, which tolerate herbivory through compensation or even overcompensation of consumed tissues (Coley, 1983; Coley et al., 1985).

2. Materials and methods

2.1. Study site

We carried out our experiments at the Carlos Botelho State Park (CBSP) in São Paulo, Brazil (37,664 ha; 24°08′S; 47°58′W) (Fig. 1). This park is located in a 360,000-ha continuous forest block in the Paranapiacaba massif, one of the largest remaining patches of Atlantic forest (Ribeiro et al., 2009). The altitude in the study area ranges between 715 and 810 m above sea level, and the climate is subtropical. The annual average temperature varies from 15 to 19 °C, and the annual rainfall varies from 1700 to 2000 mm. The region lacks a distinct dry season, but less precipitation occurs during the austral winter (Instituto Florestal, 2008). The forest is composed mainly of primary and mature secondary successional stages, with a high abundance of Lauraceae, Myrtaceae and palmito palm (Euterpe edulis) (Brocardo et al., 2010; Lima et al., 2011).

2.2. Mammal abundance

To estimate the defaunation level of large- and medium-sized mammals (species ⩾ 1 kg, see Galetti et al., 2009) in the study area, we used two methods: camera trapping and diurnal line transect surveys. Camera trapping was used to obtain records of elusive species that are rarely detected during a line transect census (Srbek-Araujo and Chiarello, 2005; Trolle, 2003; Trolle et al., 2008). Surveys were carried out between September 2009 and June 2010, with six Reconyx™ cameras (model RC55 RapideFire, www.reconyx.com), configured for very high sensitivity and without interval delay. The cameras were used monthly (10–15 days per month), with a minimum between-camera distance of 200 m. The cameras were installed in areas adjacent to the experimental plots (within a 20-m radius); therefore, they were also used to verify which mammal species occurred in the experimental areas.

The total effort was 497 camera trap days (camera traps × number of days sampled; 1 day = 24 h). To estimate the relative abundance of each mammal species we used the following equation (adapted from Srbek-Araujo and Chiarello, 2005): $A = Ic/E \cdot 10$, where A = relative abundance, given by the number of independent captures per sampling effort (10 camera trap days); Ic = independent captures (photos taken at intervals of at least 30 min for each camera trap); and E = survey effort (total number of camera trap days).

We also conducted diurnal line transect surveys to include diurnal and arboreal species in our sample (Chiarello, 1999; Peres, 1999), following standardized protocols (Cullen and Rudran, 2006; Peres, 1999). The surveys were conducted monthly between August 2009 and June 2010 along four transects: 1.2 km, 3.85 km, 4.0 km and 5.0 km. The sampling along transects was conducted from 05:30 to 12:00 and from 13:30 to 19:00 at an average speed of 1 km/h. Sampling was not conducted when it was raining. We sampled a total length of 430.35 km. To estimate the relative abundance of species from the results of our line transect surveys, we used the encounter rate (E_r) of animals (ind) every 10 km walked (where km_t = total distance traveled) (see Galetti et al., 2009): $E_r = ind/km_t \cdot 10$.

To complement the estimate of mammalian species richness, we used records of signs (tracks, burrows, feces) and casual observations collected between July 2009 and July 2010.

2.3. Defaunation impact on plant recruitment

Exclusion treatments have been widely used to better understand the effects of mammals (or their loss) on forest structure (Asquith and Mejia-Chang, 2005; Beck et al., 2013; DeMattia et al., 2006; Dirzo and Miranda, 1991). To assess how forest regeneration responds to the loss of medium- and large-bodied mammals, we used a paired design of 15 fenced and control forest plots. The fenced plots excluded any activity (seedling herbivory, trampling, defecation or deposition of urine) of large- and mid-size (over 1 kg) ground-dwelling mammals, allowing us to estimate the impact of these animals on plant recruitment when compared with the control plots (open to all animals).

The exclosure plot fences (5 × 3 m in area and 1.2 m in height) were constructed with wire mesh firmly attached to six wooden stakes. Small rodents (e.g., Guerlinguetus and Trinomys), marsupials and invertebrates were not excluded by the wire mesh (mesh size of 5 by 7 cm). The control plots had the same dimensions as the exclosure plots. The control plots were located no more than 5 m from their paired exclosure plots, and their four corners were marked with wooden stakes. The minimum distance between pairs of plots was 200 m. The exclosure and control plots were subdivided into eight 1 m² subplots to perform different experiments, and we left a 0.5-m-wide buffer zone around each plot, which
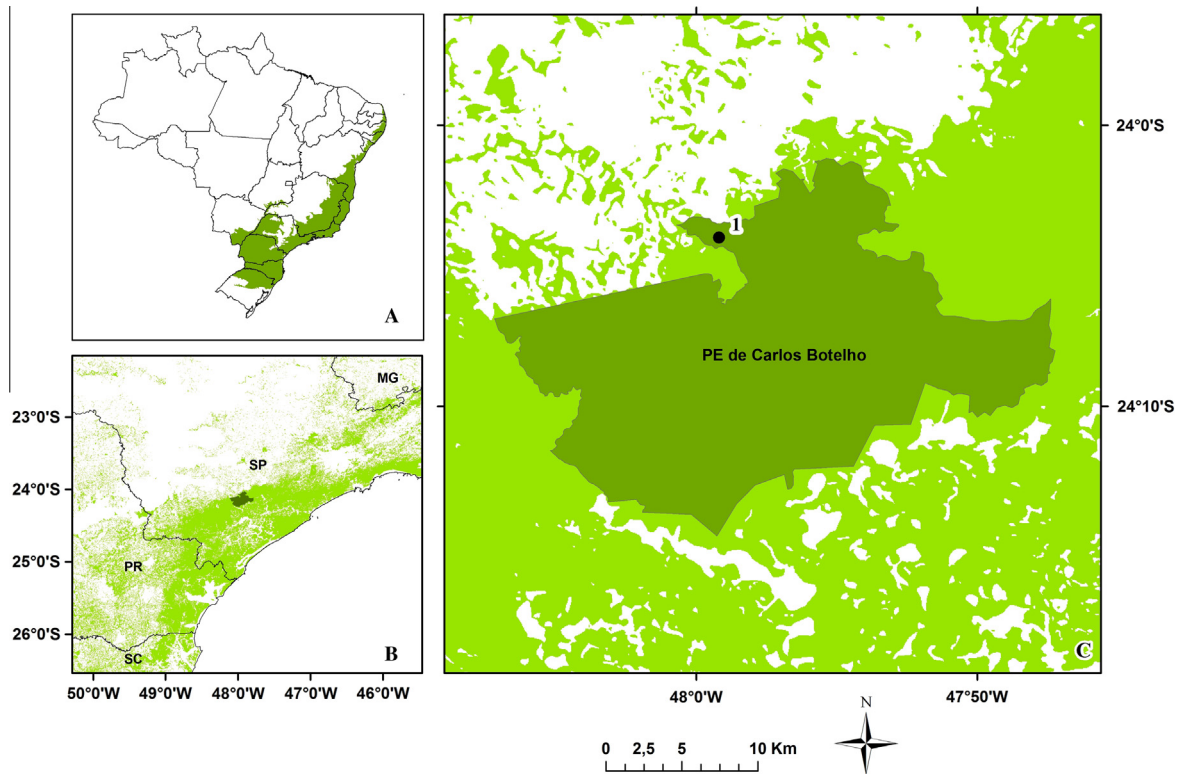
Fig. 1. Original distribution of the Atlantic rainforest in Brazil and the location of Carlos Botelho State Park, a 37,664 ha protected areas in Serra de Paranapiacaba massif, in south-east Brazil (A–C). (C) The location of our study area and plots (1).

minimized the effects of seeds deposited in the experimental sub-plots by birds perching on the stakes and allowed us to walk around fenced plots without trampling seedlings and saplings. Three subplots in each plot, selected at random, were used to analyze the survival of seedlings and saplings and recruitment of new seedlings. All seedlings and saplings of woody and herbaceous species (hereafter collectively referred to as seedlings) with heights less than one meter and greater than 10 cm were individually marked (modified from DeMattia et al., 2006). Although most studies of defaunation effects have been focused only on woody species, we decided to include herbaceous species because of their importance in forest regeneration (see Royo and Carson, 2005). The experimental plots were revisited every 6 months from the initial marking to record individual mortality and recruitment. The experiment began in July 2009 (austral winter, June–September), and the last visit occurred in July 2012 (austral winter), providing a total of 36 months of experimentation.

2.4. Richness, diversity and functional groups

Seedling species richness and diversity were calculated for each plot. We identified the seedlings in each plot at the species, genus or morphospecies level on the basis of leaf characteristics. In addition, we classified each marked plant according to three functional groups defined by: *seed dispersal syndrome*, *seed size* and *leaf defense*. In the cases of genus or morphospecies (identified to the family level) we used the functional group more common in the genus or family. When it was not possible to classify a seedling in one functional group, we excluded it from our analysis.

Seed dispersal syndrome was based on a dataset of fruit syndromes of the Atlantic forest (Almeida-Neto et al., 2008). Considering the barrier to seed dispersal that could be caused by our exclosure treatment, the species were classified into the following categories:

(a) Bird or bats dispersal: plants with small seeds that are dispersed primarily by birds or bats. This category includes several species of the Moraceae, Piperaceae, and Rubiacae families. Dispersal is not affected by exclosure treatment but their abundance may increase in exclosure plots.

(b) Mammal dispersal: plants for which non-volant mammals are the primary dispersers. These species have larger seeds than those in the previous category and are represented mostly by Myrtaceae, Sapotaceae and Chrysobalanaceae. Only dispersal by terrestrial mammals (not arboreal mammals) is affected by the exclosure treatment.

(c) Non-vertebrate dispersal: plants with seed dispersal achieved by autochory, abiotic factors, or myrmecochory (ants). Dispersal is not affected by the exclosure treatment.

(d) Mixed dispersal: seedlings with mixed dispersal (birds, bats and large mammals). Again, only dispersal by terrestrial mammals is affected by the exclosure treatment

Seed size – We classified the seedlings according to seed size (in the shortest dimension) as follows:

(a) Small seeds: species or genera with seeds $\leqslant 1$ cm (diameter), which are rarely predated by large mammals, including larger rodent species (Bodmer, 1991; Galetti et al., 2010).

(b) Medium seeds: species or genera with seed sizes ranging from >1 to $\leqslant 2$ cm. These seeds are preyed upon by large and small mammals (rodents), and an increase in predation of seeds in this size range is expected in defaunated forests if density compensation effects occur (Bodmer, 1991; Dirzo et al., 2007; Galetti et al., 2010; Vieira et al., 2003).

(c) Large seeds: Seed size > 2 cm. These seeds are preferentially preyed upon by medium and large rodents (*Dasyprocta* spp., *Cuniculus paca*, *Guerlinguetus ingrami*, *Trinomys* spp.), or, when not lignified, by peccaries (Bodmer, 1991; Galetti et al., 2010).

Leaf defense – We assigned every plant species growing in the experimental plots to one of two categories with respect to leaf defense:

(a) Anti-herbivory defense: seedlings known to exhibit any apparent defense against herbivores, such as latex, secondary compounds (from the literature), or presence of thorns or trichomes.
(b) Anti-herbivory non-defense: seedlings with no apparent defensive structures or substances (from the literature) against vertebrate herbivory.

2.5. Data analysis

We generated the richness and functional group abundances for each plot by summing the subplots values, but the subplots served to randomize our sampling within each plot. Diversity was calculated using the Shannon index. Mortality and recruitment were also estimated by summing the subplot values to generate data for each plot. For mortality and seedling recruitment, respectively, we only counted the number of dead seedlings and the number of established new seedling, and we included these values in the analysis because our objective was to verify whether treatment would affect the establishment and/or mortality of seedlings (independent of the time since a seedling arrived in the sample). Linear mixed-effect models were used with repeated measures to test the effects of exclusion on metrics of diversity, richness, abundance of functional groups, mortality and new established seedlings. The response variable was the difference between the exclosure and the open treatment of each pair of plots at each sampling period (N = 105, 15 pairs of plots and seven sampling times). In this manner, we controlled for landscape heterogeneity. In the fixed component of the model, we tested the effect of time (regression). Because of the paired nature of the experiment, any departure from zero for the time factor implies a direct effect of exclosure treatments. In the random component of the model, we modeled the repeated measurement nature of the experimental design within each pair of plots. We tested for differences at the starting conditions between pairs of plots, based on the intercept of the models.

All of the statistical analyses were performed using the software *R* (Development Core Team, 2012), running mixed-effects models with the library nlme (Pinheiro et al., 2012).

3. Results

3.1. Mammal abundance

We recorded 21 mid- to large-bodied mammal species in our study site. Noteworthy are the records of top predators such as jaguars (*Panthera onca*) and pumas (*Puma concolor*), both endangered species, as well as the muriqui (*Brachyteles arachnoides*) and giant anteater (*Myrmecophaga tridactyla*), which are also threatened (Table 1). Primates were the most abundant order recorded during the line transects, while ocelots (*Leopardus pardalis*) and lowland tapirs (*Tapirus terrestris*) were the most abundant species recorded by camera trapping (Table 1). We did not record any deer (*Mazama* spp.) or collared peccaries (*Pecari tajacu*) using unbaited camera traps or the line transect census, but these species were detected through tracks (Table 1). The white-lipped peccary (*Tayassu pecari*) was not recorded, and interviews with park rangers confirm that

this species disappeared from the park in the 1980s (see Brocardo et al., 2012, for the most complete non-volant mammal inventory of the park).

3.2. Effects of large mammal exclosure on seedling richness, diversity, and abundance of functional groups

Initially (time 0), we marked 393 seedlings in the open control plots (269 identified to the species level, 70 to the genus level, 38 to the family level and 16 unidentified), and 466 in the exclosure plots (346 identified to the species level, 66 to the genus level, 27 to the family level and 24 unidentified). The mean abundance was 26.2 ± 3.37 (±s.e.) of seedlings in the open plots (3 m^2) and 31.06 ± 3.77 in the exclosure plots (3 m^2), with no significant difference between treatments (t = −0.96, p = 0.34). There was no initial (time = 0 months) difference in the average species richness (t = −0.15; p = 0.88) or average species diversity (t = 0.80; p = 0.43) between the open control and the exclosure treatment, with little change over time during the experiment (Fig. 2). There were no significant changes in seedling diversity and richness after large mammals were excluded (Fig. 2 and Table 2).

There were also no significant changes in the functional group abundances between treatments (Fig. 3 and Table 2). There were no differences in the number of newly established seedlings ($F_{1,68}$ = 0.08, p = 0.77) or in the number of dead seedlings ($F_{1,68}$ = 0.14, p = 0.70) in response to the exclusion of large mammals, i.e., recruitment and mortality did not differ between the controls and the exclosures throughout the sampling period.

4. Discussion

In this study, we did not detect changes in understory composition in the exclusion plots after 36 months. Our results indicate that patterns of seedling richness and diversity were unaltered by large terrestrial mammal exclusion and the same was true for the abundance of functional groups (seed dispersal syndrome, seed size and leaf defense). Although other studies that have used exclosure plots to measure the impact of vertebrates on seedling diversity have also failed to find drastic changes (Royo and Carson, 2005; Theimer et al., 2011; but see Beck et al., 2013; Ickes et al., 2001), natural experiments comparing defaunated and non-defaunated sites have shown that the loss of large vertebrates alters the seedling bank structure (Dirzo and Miranda, 1991; Nuñez-Iturri et al., 2008; Terborgh et al., 2008; Wright et al., 2007).

The long-term defaunation history and the composition of the resilient mammalian community in our study site may explain the lack of changes in seedling assemblage in the mammal-exclosure plots. If the seedling community has already faced a long history of low abundance of medium- and large-bodied herbivores, the composition reflects resilient species that were already selected in a defaunation scenario, and our exclosure plots did not capture changes in species composition.

Our results on mammal census confirm the low abundance of large terrestrial mammals and the local likely extinction of only one species, the white-lipped peccary (*Tayassu pecari*). While some highly threatened species exist in the area, such as jaguars, muriquis and tapirs, only primates are in great abundance in comparison to other areas of the Atlantic forest (Chiarello, 1999; Cullen et al., 2000; Galetti et al., 2009). Primates and tapirs are not particularly hunted in the Atlantic forest, unlike armadillos, ungulates and large rodents, which are considered the main targets of hunters (Cullen et al., 2000; Fragoso et al. 2011). Because white-lipped peccaries have the highest biomass in non-hunted communities in Neotropical forests, our studied area is partially defaunated in

Table 1
Presence and abundance of medium and large-bodied mammals in Carlos Botelho State Park, recorded between July 2009 and July 2011.

Species	Functional group	Bodymass[a] (kg)	Abundance	
			Camera trap (cap/10 cam.day)	Line transect (ind/10 km)
Big-eared opossum *Didelphis aurita*	Terrestrial omnivore	0.67–1.8	0.06	–
Naked-tailed Armadillo *Cabassous tatouay*	Terrestrial omnivore	5.35	0.06	–
Banded Armadillo *Dasypus* spp.	Terrestrial omnivore	1.5–3.65	P	P
Giant anteater *Myrmecophaga tridactyla*	Terrestrial insectivore	30.5	P	P
Brown Howler Monkey *Alouatta guariba*	Arboreal frugivore	5.6	–	0.51
Southern Muriqui *Brachyteles arachnoides*	Arboreal frugivore	10.75	–	2.78
Black-capuchin monkey *Sapajus nigritus*	Arboreal frugivore	3.5	–	1.28
Paca *Cuniculus paca*	Terrestrial herbivore	9.3	0.06	–
Agouti *Dasyprocta azarae*	Terrestrial herbivore	2.9	–	0.04
Crab-eating fox *Cerdocyon thous*	Terrestrial omnivore	6.5	P	P
Tayra *Eira barbara*	Terrestrial omnivore	4–10	0.02	0.02
Neotropical otter *Lontra longicaudis*	Semi-aquatic carnivore	6	P	P
Ocelot *Leopardus pardalis*	Terrestrial carnivore	8–11	0.60	–
Spotted cat *Leopardus* spp.[b]	Terrestrial carnivore	1.5–9	0.02	–
Coati *Nasua nasua*	Terrestrial omnivore	5.1	–	0.09
Crab-eating racoom *Procyon cancrivorus*	Terrestrial omnivore	5.4	0.12	–
Jaguar *Panthera onca*	Terrestrial carnivore	61–158	P	P
Puma *Puma concolor*	Terrestrial carnivore	22–70	0.12	–
Lowland tapir *Tapirus terrestris*	Terrestrial herbivore	260	0.34	0.04
Brocket deer *Mazama* spp.	Terrestrial herbivore	27	P	P
Collared peccary *Pecari tajacu*	Terrestrial herbivore	26	P	P

[a] From Paglia et al. 2012.
[b] Where it was not possible to distinguish *Leopardus tigrinus* or *L. wiedii* species identification; P = present; recorded in the study area through signals or casual visualizations without methodology for assess the abundance.
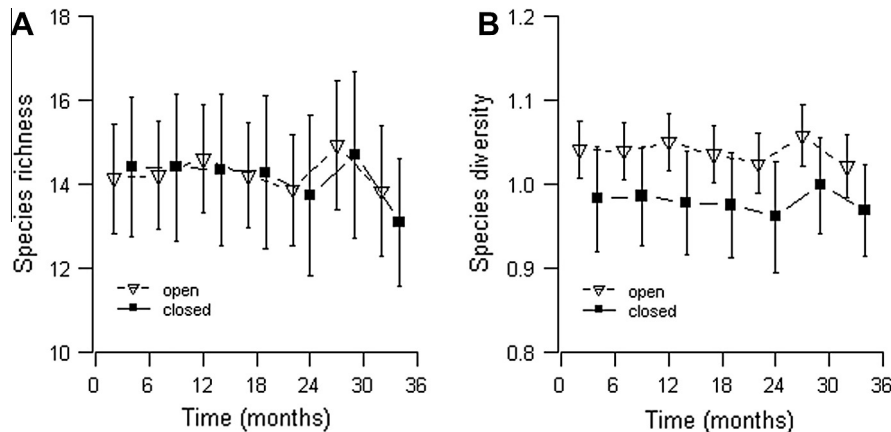
Fig. 2. (A) Average species richness and (B) average species diversity (H′) of seedlings in the plots of free access control (open) and exclosure treatment (closed), through 36-months sampling, at Carlos Botelho State Park (Atlantic forest). Vertical bars represent ± standard error, and points are offset to make symbols and error bars more visible.

Table 2
Statistical summary of repeated measurement with linear mixed-effects modeling to test the effects of large mammal exclusion on metrics of diversity, richness and abundance of functional groups of the seedling community in the Atlantic Forest.

Seedling assemblage attribute	d.f.	F	p
Diversity	1, 89	0.53	0.46
Richness	1, 89	<0.01	0.98
Birds or bats dispersed	1, 83	0.02	0.88
Mammals dispersed	1, 83	<0.01	0.99
Non-vertebrate dispersed	1, 83	<0.01	0.97
Mixed dispersed	1, 83	0.33	0.54
Large size seed	1, 83	0.41	0.52
Medium size seed	1, 83	0.26	0.61
Small size seed	1, 83	0.45	0.50
Defense foliar	1, 83	0.18	0.67
Non-defense foliar	1, 83	0.07	0.78

terms of biomass, but not in richness, in comparison to other large Atlantic forest remnants (Brocardo et al., 2012; Galetti et al., 2009).

We do not know the historical of abundance of the study area, but the protection of the study area is recent (1982). Even today, ungulates and large rodents are heavily hunted in the park (Pianca, 2004). In addition, the abundance of frugivorous primates, particularly muriquis, may be the major driver of seedling composition (Bueno et al., 2013). Because our plots did not exclude primates (and their seed rain generated by seed dispersal), for most large mammal-dispersed species, seeds fell continuously in our plots. Muriquis are known to deposit on average 72.5 seeds/scat and spreading them to most of our study area (Bueno et al., 2013). Although seed rain was slightly affected by the exclosure treatment and seed banks were controlled by the pairing of plots, it would be expected that herbivory and seed predation in open treatments, and consequently changes in seedling recruitment and survival, would modify seedling patterns (i.e., diversity, richness, and abundance of functional groups). However, this did not occur, since similar mortality and recruitment values were registered between plot types, along with similar seedling patterns in both plot types over time. These findings demonstrate that the
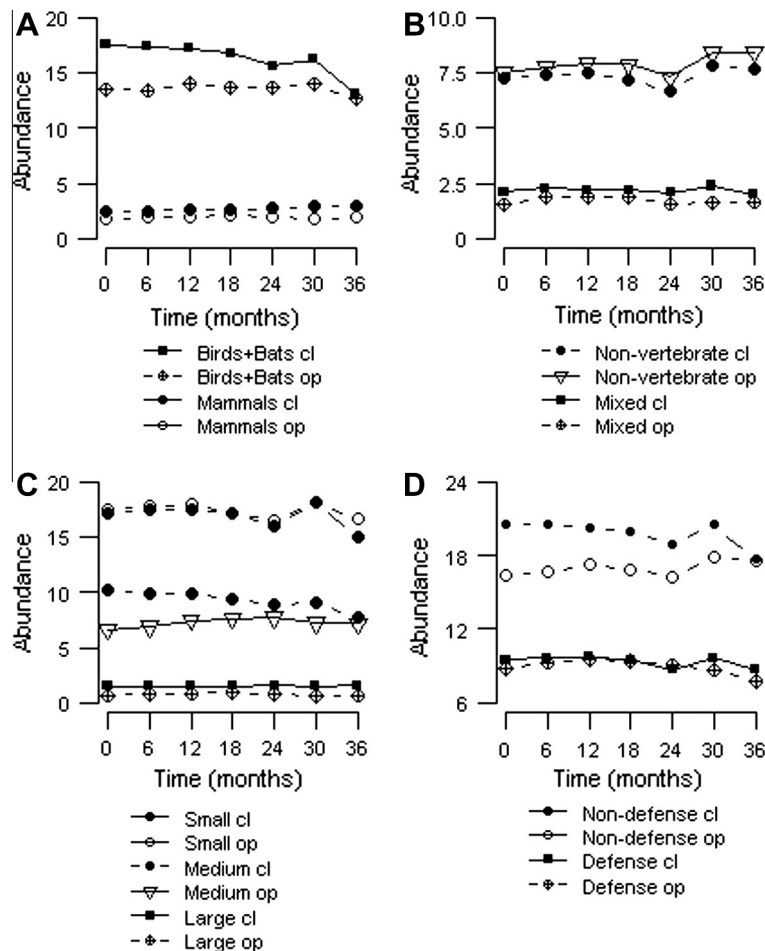
Fig. 3. Average seedling abundance of functional groups according to: (A and B) *Seed dispersal syndrome*, (C) *Seed size*, and (D) *Leaf defense* in closed plots (cl, exclosure) and control open plots (op) recorded every 6 months for the duration of the 36-months experiment. The error bars were omitted for clarity of data.

remaining medium- and large-bodied ground-dwelling mammals have little influence on the rates of seedling recruitment and mortality (top-down effects) in this partially defaunated forest.

The little effect of large terrestrial mammals on seedling mortality was reduced even in plots where the animals had access (open plots) probably because there is low abundance of some species, such as peccaries and deer in this forest. This implies that most of their ecological functions persist only at the basal level, such that they are "functionally extinct" (Dirzo and Miranda, 1991; Novaro et al., 2000; Redford, 1992). It is intriguing that apparently tapirs, the only ungulate that is common in our study site, did not influence seedling recruitment in open plots. Tapirs are important browsers and seed dispersers (Bueno et al., 2013; Hibert et al., 2011; O'Farrill et al., 2012). However, lowland tapirs tend to disperse their ingested seeds in latrines (Fragoso et al., 2003; Galetti et al., 2001), and none of our open control plots presented latrines, which means that we failed to capture seeds dispersed by this megafrugivore. Nonetheless, *Brachyteles arachnoides* disperses almost all the same plant species as tapirs do (Bueno et al., 2013). Moreover, lowland tapirs selectively browse on few species and plant parts, avoiding fibrous and toxic components (Hibert et al., 2011; Salas and Fuller, 1996). In our experiments, we were unable to find an increase in abundance of *anti-herbivory non-defense* functional groups in response to tapir exclusion from the exclosure plots.

Furthermore, the local extinction of *Tayassu pecari*, one of the most hunted and endangered mammals in the Neotropics, is very disquieting (Cullen et al., 2000; Jorge et al., 2013; Peres, 1996; Peres and Palacios, 2007). White-lipped peccaries form large herds, which increase their action in seed predation, herbivory and trampling on seedlings, causing major disturbances to the forest understory in the Neotropics (Antonik, 2005; Beck 2005, 2006, 2007; Keuroghlian and Eaton, 2008, 2009; Roldán and Simonetti, 2001; Silman et al., 2003; Wyatt and Silman, 2004). These animals are considered "ecosystem engineers" because they modify habitat conditions (Beck, 2005; Beck et al., 2010). In an Atlantic forest patch with *Tayassu pecari* present, Keuroghlian and Eaton (2009), for example, through an exclosure experiment, verified a significant increase in the establishment of new seedlings in exclusion plots, compared to open control plots, after 1 year. The researchers attributed the maintenance of habitat conditions in this site to white-lipped peccaries' activities. Curiously, Silman et al. (2003) detected alterations in the density and spatial distribution of the murumuru palm, *Astrocaryum murumuru*, when *T. pecari* were present versus when they were not. Thus, the reintroduction of white-lipped peccaries into large areas of Neotropics could lead to a restoration of an important top-down perturbation of the seedling bank (Jorge et al., 2013). It has already been demonstrated that the reintroduction of "ecosystem engineer" mammals provides benefits to ecosystems (James and Eldridge, 2007). However, before the reintroduction, it is necessary that programs focused on combating hunting in the destination area be adopted (Brocardo et al., 2012).

Finally, our findings allow us to conclude that the seed rain produced by primates, bats, birds and abiotic factors and the low level

of herbivory and seed predation by large terrestrial mammals explain the lack of differences in plant diversity and functional groups between the control and exclosure plots in our experiment. We suggest that continuous forests with a low biomass of terrestrial mammalian herbivores, but still intact arboreal ones, may already have experienced past community reassembly.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.04.024.

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