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