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Short communication

Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests

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ABSTRACT

Defaunation can trigger cascading events in natural communities and may have strong consequences for plant recruitment in tropical forests. Several species of large seed predators, such as deer and peccaries, are facing dramatic population collapse in tropical forests yet we do not have information about the consequences of these extinctions for seed predation. Using remote camera traps we tested if defaunated forests have a lower seed predation rate of a keystone palm (*Euterpe edulis*) than pristine areas. Contrary to our expectation, we found that seed predation rates were 2.5 higher in defaunated forests and small rodents were responsible for most of the seeds eaten. Our results found that defaunation leads to changes in the seed predator communities with potential consequences for plant–animal interactions.

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1. Introduction

Contemporary defaunation, the selective local extinction of large bodied species or populations driven by habitat fragmentation, poaching and illegal marketing (Dirzo et al., 2014), results in apparently impoverished ecosystems, the so-called “empty forest” (Redford, 1992). However, these forests are hardly “empty”; many species of small-bodied vertebrates still persist and carry on with their ecological activities to survive, grow and reproduce in scenarios in which usually the strongest competitors and most fierce predators have gone (Wright, 2003). The ecological and evolutionary consequences for forest dynamics brought about by contemporary defaunation have shown effects on biological systems, such as plant physiology (vegetative and reproductive performance), animal behavior (movement, foraging and dietary patterns) and ecosystem functioning (Dirzo et al., 2014; Galetti and Dirzo, 2013).

Large herbivores have been considered an important component to structure small mammal communities via direct impact (interference competition) or indirect (exploitative competition and habitat transformation) (Foster et al., 2014; Ripple et al., 2015). Experimental evidence suggests that areas with low abundance of large herbivores experience high abundance of small rodents (Galetti et al., in press; McCauley et al., 2006). In fact, most rodent species seem to be resilient to the main drivers of contemporary defaunation and tend to proliferate in areas where large mammals were extirpated (McCauley et al., 2006; Terborgh et al., 2001).

Rodents are predominantly seed consumers and are particularly diverse in Neotropical rainforests, not only in number of species and abundance but, also in sizes, diet, and behavior (Bonvicino et al., 2008). For instance, granivorous rodents can range from a small mouse (*Oligoryzomys* spp.) with less than 10 g to a paca (*Cuniculus paca*) weighing over 5000 g

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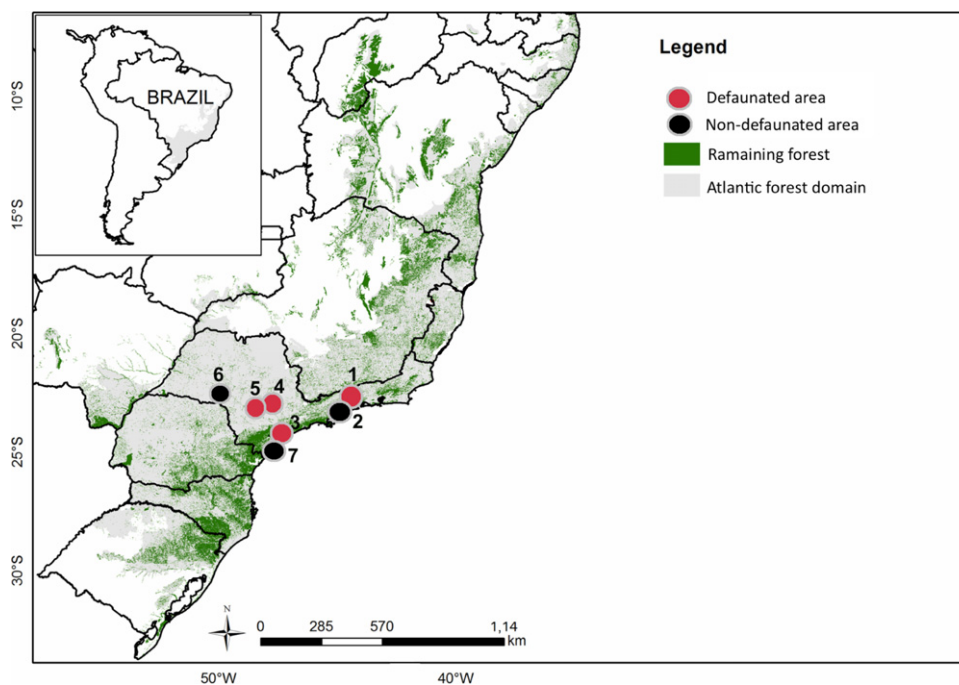


Fig. 1. Location of study areas in Atlantic Forest Brazil: (1) Serra do Mar State Park—Vargem Grande basis, (2) Serra do Mar State Park—Itamambuca basis, (3) Carlos Botelho State Park, (4) Mata Santa Genebra, (5) São José farm, (6) Caetetus Ecological Station, (7) Ilha do Cardoso State Park.

(Paglia et al., 2012). In addition, the populations of granivorous rodents are highly sensitive to food availability and may reach high densities when food sources are overabundant (Jaksic and Lima, 2003). Because post-dispersal seed predation by rodents is an important bottleneck for plant populations (Fleury et al., 2014), it is expected that defaunation of large mammalian herbivores will trigger the population of small rodents (Galetti et al., in press), that in turn will affect plant recruitment (Dirzo et al., 2007; Mendoza and Dirzo, 2007; Wright, 2003).

Here we compare the seed predation of a keystone palm in defaunated and non-defaunated Atlantic rainforests of Brazil. We were particularly interested in testing if the functional extinction of a dominant ungulate seed predator, the white-lipped peccary (*Tayassu pecari*) will translate into shifts in seed predation and seed predators of palms.

2. Material and methods

2.1. Studied species—the palmito *Euterpe edulis*

We tested our hypothesis comparing the seed predation rate and the seed predator assemblage of a keystone palm species (*Euterpe edulis*). *Euterpe edulis* produces medium-size fruits (ranging from 6.7 to 16.62 mm wide) and has recalcitrant seeds (i.e. they are sensitive to desiccation and storage) (Galetti et al., 2013; Panza et al., 2007). Germination experiments have shown that only defleshed seeds germinate and therefore require frugivore consumption (Leite et al., 2012). This palm is widely distributed along the Atlantic forest and several granivorous species, including birds (Galetti and Aleixo, 1998; Galetti et al., 2013), ungulates (Keuroghlian and Eaton, 2009; O’Farrill et al., 2013), and rodents (Galetti et al., 2010; Vieira et al., 2003) prey upon their seeds. There is no evidence that *E. edulis* can be dispersed by scatter hoarding rodents (Galetti et al., 2010).

2.2. Study areas

We sampled three non-defaunated (Ilha do Cardoso, Serra do Mar State Park—Itamambuca, Caetetus Ecologic Station) and four defaunated forests (Carlos Botelho State Park, Serra do Mar State Park—Vargem Grande, São José farm and Mata Santa Genebra) at São Paulo state, southeastern Brazil (Fig. 1). Non-defaunated forests were defined based on the presence of the white-lipped peccaries (*Tayassu pecari*) (Galetti et al., 2009).

2.2.1. Non-defaunated areas

Ilha do Cardoso State Park (hereafter IC) (25 ° 11’S, 47 ° 59’W), with 15,100 ha is a protected area in southernmost SP. About 75% of the whole island is covered with rainforest (11,100 ha), while the rest is divided into mangroves, restinga and

Table 1

Results of the seed predation experiments in defaunated and non-defaunated sites in the Brazilian Atlantic forest.

(Site*)/Name	Camera trap/day	Species of seed predators	Mean (SE) of seeds eaten day ⁻¹	Seeds eaten
<i>Non-defaunated</i>				
(6) E.E. Caetetus	66	7	1.95 (±1.12)	129
(7) P.E. Ilha do Cardoso	18	4	8.05 (±6.08)	145
(2) P.E. Serra do Mar Itamambuca	170	13	3.76 (±0.93)	640
<i>Defaunated</i>				
(3) P.E. Carlos Botelho	91	9	1.31 (±0.30)	119
(1) P.E. Serra do Mar Vargem Grande	60	8	2 (±0.45)	120
(5) São José farm	25	2	9.17 (±1.94)	55
(4) Mata Santa Genebra	12	2	5.17 (±2.22)	62

Site*: Map number of location of study areas in Atlantic Forest Brazil.

dunes (Barros et al., 1992). Game bird and mammal census have shown that white-lipped peccaries are common, yet jaguars and tapirs are extinct since the creation of the Park in 1962 (Galetti et al., 2009).

Itamambuca (ITA) (23 ° 19'S, 45 ° 05'W) covered with rainforest (17,000 ha), this site is located in the north of the Serra do Mar State Park, SP (Ribeiro et al., 2009). Game bird and mammal census have shown that white-lipped peccaries (*Tayassu pecari*), tapir (*Tapirus terrestris*), howler monkeys (*Alouatta guariba*), capuchin monkey (*Sapajus nigritus*), deer (*Mazama americana*) and puma (*Puma concolor*) are present (Galetti et al., 2009; Rocha-Mendes et al., 2015).

Caetetus Ecological Station (Caetetus) (22 ° 24'S, 49 ° 42'W) with 2100 ha is located at Atlantic Forest in Gália and Alvinlândia, São Paulo. It is semi-deciduous forest fragment, which also contains populations of large and medium mammals such as tapirs, white-lipped, and collared peccaries (Cullen et al., 2000; Keuroghlian and Eaton, 2008; Keuroghlian et al., 2004).

2.2.2. Defaunated areas

Carlos Botelho State Park (CB) (24 ° 44'S, 47 ° 44'W;) with 37,644 ha is a protected area in a continuous massif named "Serra de Paranapiacaba" in southeastern São Paulo. The vegetation is characterized as humid montane forest in the upper part to lowland evergreen forest in the lower part (Lima et al., 2011). The area harbors an important population of muriquis and tapirs (Bueno et al., 2013), but lacks white-lipped peccaries (Brocardo et al., 2013).

Vargem Grande (VG) (23 ° 26'S, 45 ° 14'W) with 17,000 ha, protected area in the north of the Serra do Mar State Park. The vegetation is classified as Montane Atlantic Rainforest (Oliveira-Filho and Fontes, 2000). Medium and large mammals as tapir, paca, capuchin monkey and puma are present, but white-lipped peccaries are functionally extinct (Galetti et al., in press).

São José Farm (SJF) (22 ° 22'S, 47 ° 28'W), with 580 ha, is a private and non protected area and it is one of the few remaining semi-deciduous forest within São Paulo state. Census have recorded 16 non-flying mammals, but tapirs, white-lipped and collared peccaries are locally extinct (Bernardo and Galetti, 2004; Briani et al., 2001).

Mata Santa Genebra (MSG) (22 ° 47'S, 49 ° 07'W) with 250 ha in Campinas, São Paulo, is one of the most studied semi-deciduous forests in the Atlantic area (Leitão-Filho and Morellato, 1997). This fragment harbored 15 non-flying mammals of medium to large size, but tapirs, peccaries and agoutis are locally extinct (Galetti and Sazima, 2006; Monteiro-Filho, 1995).

2.3. Seed removal

During the fruiting season of *E. edulis*, we set up from 1 to 5 camera traps (Reconyx®) focused on the understory of fruiting palms in each site (from 4 to 8 palms distant at least 100 m) where fallen fruits and seeds are abundant, and we recorded the behavior of all seed consumers. By timing the camera to take a picture on every second when activity was detected we were able to estimate the number of seeds eaten by each animal (Fig. 2). For the purpose of analyzing all species of small rodents, including squirrels, were pooled into a single category because no reliable identification at species level was possible from the pictures taken by the cameras. Visits to seeds and fruits of *E. edulis* were defined by the time when an animal was pictured when approaching the patch and when leaving the scene.

For gregarious species (white-lipped peccaries) we estimated the number of animals in the foraging herd (by the sequence of the photos) and multiplied the number of seeds visually eaten by the group size. We sampled each area from 12 to 170 consecutive days (Table 1). For seed manipulation events caught in the camera traps we counted the number of seeds eaten by each distinguishable category of seed predators per day in each of the seven sites.

The seed predation events (i.e. only when we could be sure that the animal was eating the seed) were analyzed with a repeated measurements mixed effects model. The fixed component of the model was the factor site status with two levels (non-defaunated and defaunated) and in the random component of the model we defined the repeated measurements nature of the observations given the identity of the camera at each site. Additionally, to meet model assumptions we allowed compound symmetry correlation structure and modeled the variance following a mixed approach: constant variance across the repeated measurement effects and an exponential variance function across site status levels. Statistical analyses were performed in the R environment (R Development Core Team, 2012).

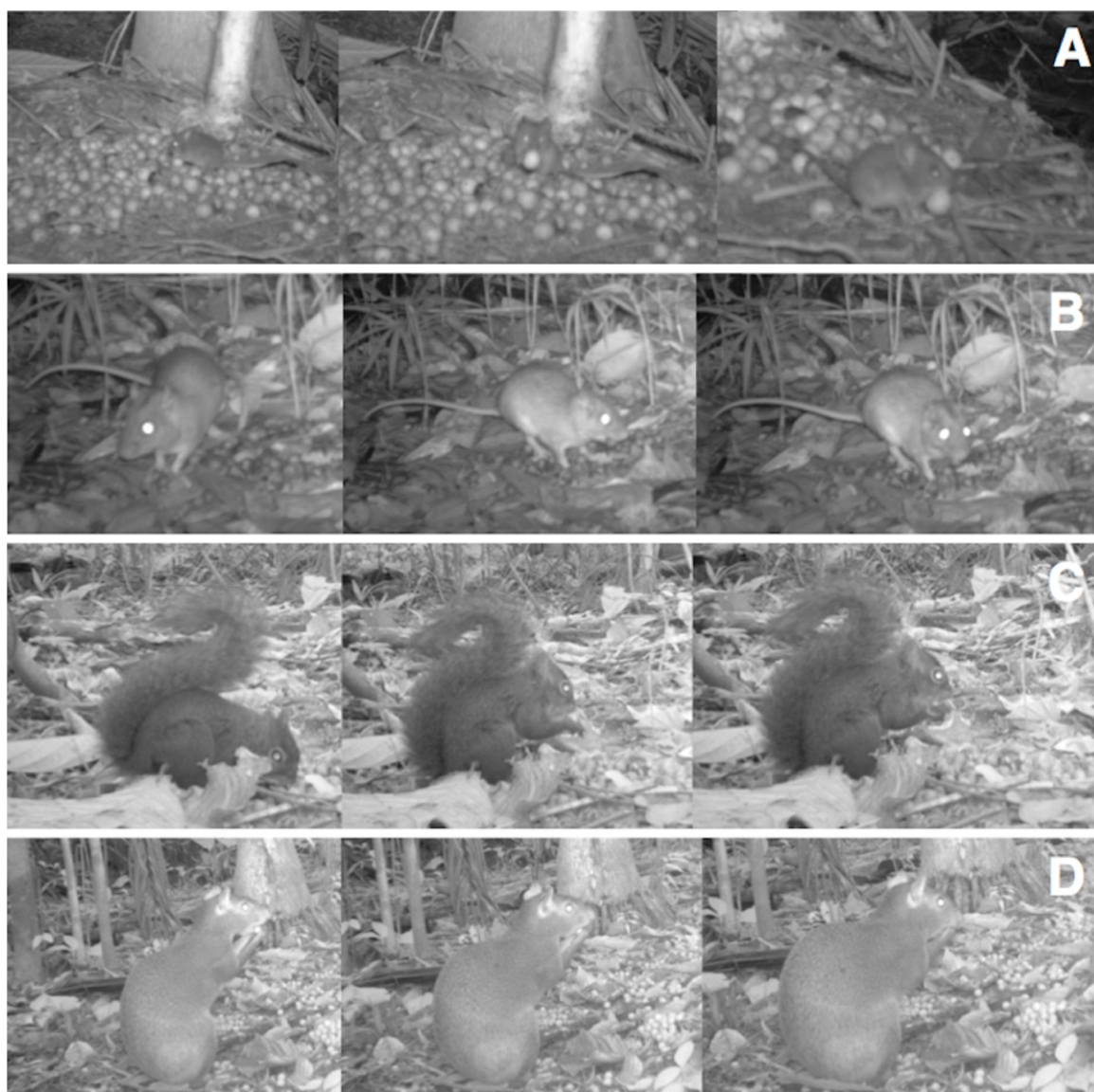


Fig. 2. Example of seed predators feeding on *Euterpe edulis* seeds in the Brazilian Atlantic forest. (A) Small rodent, (B) large rodent, *Trinomys iheringii*, (C) squirrel, *Sciurus aestuans*, and (D) agoutis *Dasyprocta leporina*.

3. Results

3.1. Seed removal

We recorded 1228 events of animals visiting *Euterpe edulis* fruits during 442 camera-days, being 188 from defaunated and 254 camera/day from non-defaunated forests (Table 1). In 732 of these events the animals preyed upon seeds. The number of seed predator species caught in the cameras was similar in both type of sites: 14 species in non-defaunated (*Euryoryzomys russatus*, *Trinomys iheringi*, *Nectomys squamipes*, Muridae spp.1, Muridae spp.2, *Sciurus aestuans*, *Cuniculus paca*, *Dasyprocta leporina*, *Tayassu pecari*, *Mazama* spp., *Geotrygon montana*, *Crypturellus tataupa*, *Odontophorus capoeira*, *Tinamus solitarius*) and 12 species (*Euryoryzomys russatus*, *Trinomys iheringi*, *Nectomys squamipes*, *Oligoryzomys* spp., *Akodon* spp., *Holochilus brasiliensis*, Muridae spp.3, *Sciurus aestuans*, *Mazama* spp., *Geotrygon montana*, *Odontophorus capoeira*, *Tinamus solitarius*) in the defaunated sites. In defaunated sites we recorded an increment of events by small rodents and loss of large rodents (agoutis and pacas), ungulates and granivorous birds (Fig. 3). Granivorous birds (tinamids, quails and doves) were particularly rare in all areas (3 events in each defaunation status).

Of all seeds predated in defaunated sites 98.32% were due to small rodents while in non-defaunated sites they were responsible for the predation of 63.5% of the seeds. The mixed effects models showed that predation was 4.9 time higher

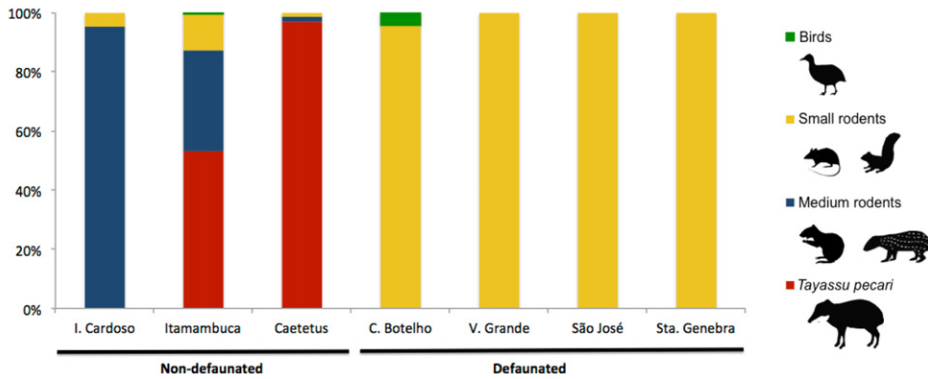


Fig. 3. Proportion of seed predation of the palm *Euterpe edulis* by each predator group in defaunated and non-defaunated Brazilian Atlantic forests.

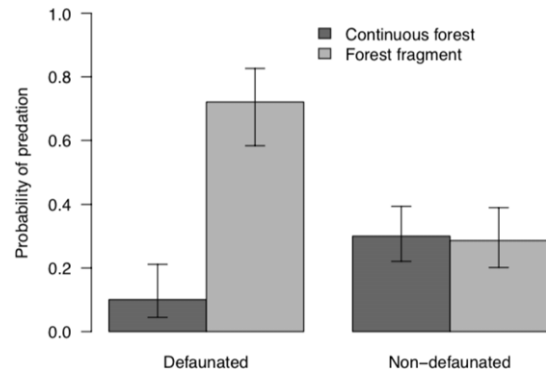


Fig. 4. Probability of predation events on seeds of *Euterpe edulis* in the Brazilian Atlantic forest.

in defaunated forest fragments compared to defaunated continuous forest ($Z = 2.3$, $P = 0.009$) while in non-defaunated sites predation was 2.5 times lower than in defaunated forest fragments ($Z = 2.5$, $P = 0.006$), and there was no effect of landscape status on predation in non-defaunated sites ($Z = 1.3$, $P = 0.08$, Fig. 4).

We did not record seed predation by white-lipped peccaries in one non-defaunated site (Ilha do Cardoso), although they are common in the area (Galetti et al., 2009). However, in this site, agoutis preyed upon most of the palm seeds. We did not record collared peccaries (*Pecari tajacu*) eating *E. edulis* seeds in none of our study areas.

4. Discussion

Our study provides new evidence that demonstrates that defaunation affects positively the seed predation by small resilient rodents in tropical rainforests. Although white-lipped peccaries make up most of the mammalian biomass in Neotropical pristine ecosystem (Peres, 1996), we expected that their extinction would lead to lower seed predation (Dirzo et al., 2007). However, our experiments have showed that rodents overcompensate peccaries' impact on seed predation by almost 5-fold increase. Our methods cannot tease apart if this increase in the predation of seeds by rodents is due to a population increase of small rodents due to reduce competition with large mammals or an increase in rodent activity, but the net predation rate increases substantially in defaunated forests and was particularly high in defaunated forest fragments.

Some authors have argued that small rodents can play a role as secondary seed dispersers (Vander Wall et al., 2005). A study of seed fate of *E. edulis* found that 98.3% of the marked seeds (with spool and line) were indeed preyed upon rodents and only 1.7% of the 456 seeds in his experiment were found cached by rodents (Voltolini, 2004). Therefore, in this study we assume that for the manipulations events where the rodents moved the seeds away, the seeds were preyed upon. Granivorous birds can be important seed predators in fragmented forests (Pizo and Vieira, 2004), but were not important seed predators of *E. edulis*, probably because of their seed size.

We lack information on the pressure of rodents on other plant species, particularly on large-seeded species (Keuroghlian and Eaton, 2009), but we would expect that at least for species that share peccaries and rodents are the main seed predator, defaunated forests will suffer higher predation than non-defaunated forests. In fact, the patterns that we detected in this study may be widespread in Neotropical forests. White lipped peccaries used to occur in several ecosystems from south Mexico to north Argentina, but habitat fragmentation and poaching have eliminated them from most of their former distribution (Altrichter et al., 2011) and they are locally extinct in 99.5% of the fragments in the Brazilian Atlantic forests

(Jorge et al., 2013). Therefore, most of the remaining forests may be suffering intense seed predation by small rodents with potential consequences for plant–animal interactions and plant recruitment.

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