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## Seed dispersal and predation in the endemic Atlantic rainforest palm *Astrocaryum aculeatissimum* across a gradient of seed disperser abundance

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**Abstract** Tropical forests have been subject to intense hunting of medium and large frugivores that are important in dispersing large-seeded species. It has been hypothesized that in areas with extinction or low abundance of medium and large-bodied animals the density of small rodents may increase. Therefore, this increment in the density of small rodents may compensate for the absence or low abundance of medium and large frugivores on seed removal and seed dispersal. Here, we fill up this gap in the literature by determining if seed removal, seed dispersal, and seed predation by small rodents (spiny rats, *Trinomys inheringi* and squirrels, *Sciurus ingrami*) are maintained in defaunated areas. We assessed seed removal, seed dispersal, seed predation, and seedling recruitment of an endemic Atlantic rainforest palm, *Astrocaryum aculeatissimum*, in a gradient of abundance of agoutis. We found that seed removal, scatter hoarding, and seed predation increase with the abundance of agoutis. In contrast, the proportion of dispersed but non-cached seeds decreased with the abundance of agoutis. We did not find any effect of the abundance of agoutis on seed dispersal distance, but we did find a positive trend on the density of seedlings. We concluded that small rodents do not

compensate the low abundance of agoutis on seed removal, scatter hoarding, and seed predation of this palm tree. Moreover, areas in which agoutis are already extinct did not present any seed removal or scatter hoarding, not even by small rodents. This study emphasizes both the importance of agoutis in dispersing seeds of *A. aculeatissimum* and the collapse in seed dispersal of this palm in areas where agoutis are already extinct.

**Keywords** Compensation · *Dasyprocta* · Defaunation · *Trinomys* · *Sciurus*

### Introduction

Fruit and seed size are key traits in animal-dispersed plants because they limit the number of frugivore species that can handle and disperse seeds (Wheelwright 1985; Peres and Van Roosmalen 2002). In the Neotropics, large-seeded fruits are dispersed by a few large and medium-bodied mammals, such as large Ateline monkeys (Peres and Van Roosmalen 2002), tapirs (Fragoso and Huffman 2000; Galetti et al. 2001) and scatter hoarding rodents (Hallwachs 1986; Guimarães et al. 2006). Seed dispersal by scatter hoarding is ubiquitous in forest-dwelling rodents, such as squirrels (*Sciurus*), spiny rats (*Trinomys*, *Proechymis*, *Heteromys*), acouchies (*Myoprocta*), and agoutis (*Dasyprocta*) (VanderWall 1990). However, dasyproctid rodents, such as agoutis and acouchies, are the most important seed dispersers of large-seeded plants because they often scatter hoard seeds in the soil, a favorable microsite for recruitment (Asquith et al. 1999), whereas small rodent species cache seeds in less favorable microsites, such as under the mother tree or under the leaf litter (Forget 1991; Forget et al. 2001; Jansen et al. 2004, but see also Brewer and Rejmanek 1999).

Agoutis (*Dasyprocta* spp.) are the main seed dispersers of at least 45% of all palm species in the Atlantic rainforest of Brazil (Galetti et al. 2006). However, agoutis,

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together with other medium and large-bodied frugivores, are becoming extirpated from many areas due to illegal hunting and predation by feral dogs, especially in small forest fragments (Cullen et al. 2000). Therefore, it has been suggested that the extinction of agoutis can lead to negative consequences on the recruitment of plant species that they disperse (Galetti et al. 2006). On the other hand, small rodents could compensate the absence or the low abundance of medium and large frugivores, either because they may be found in high abundances in these defaunated areas (Wright 2003; Dirzo et al. 2007), although this relationship was only supported by a specific study in the Amazon (Peres 2000), or simply because they could increase their roles as seed dispersers and predators since more seeds could be available in defaunated areas. Given the current high levels of defaunation in the majority of tropical forests, it is important to address if small scatter hoarding rodents are functionally redundant in terms of seed dispersal services in defaunated areas.

Here we compare seed removal, seed dispersal, seed predation, and seedling recruitment of the large-seeded palm *Astrocaryum aculeatissimum* across a gradient of abundance of agoutis. Our prediction is that if there is compensation in seed removal, seed dispersal and seed predation services by small scatter hoarding rodents (spiny rats, *Trinomys inhereingi* and squirrels, *Sciurus ingrami*) in areas where agoutis (*Dasyprocta* spp.) are either extinct or occur in low abundances: (1) seed removal, scatter hoarding, seed predation, and seed dispersal distance will not increase as a function of the abundance of agoutis and, as a result of functional redundancy between small rodents and agoutis, (2) the recruitment of *A. aculeatissimum* will not change with the abundance of agoutis.

## Methods

### Studied species

*A. aculeatissimum* (Schott Burret; Arecaceae) is an arborecent palm endemic to the Atlantic rainforest of Brazil (Henderson et al. 1995; Lorenzi et al. 1996). Flowering in January, the fruits of *A. aculeatissimum* reach maturity from May to October (Galetti et al. 1999). The species fruits every year (Galetti et al. 1999) and each infructescence has  $22.2 \pm 22.9$  ovoid fruits ( $n = 76$ ) (length = 47.9 mm, diameter = 32.2 mm, and weight = 28.7 g,  $n = 30$ ) with a thin mesocarp (about 4 mm of thickness), and one pyrene with a hard endocarp each (length = 42.7 mm, diameter = 28.8 mm, and weight = 17.36 g,  $n = 30$ ). Hereafter, we refer to the pyrenes of the fruits as “seeds.” Agoutis, spiny rats, and squirrels are the only vertebrates that can disperse seeds of *A. aculeatissimum* (Galetti et al. 2006). Agoutis have an average weight of 3.5 kg, spiny rats of 0.6 kg, and squirrels of 0.25 kg (Emmons and Feer 1997). White-lipped peccaries (*Tajacu pecari*) prey on seeds, but tapirs

ignore them, which is probably due to the small amount of fleshy part found in the fruit, unlike in other *Astrocaryum* species that rely on tapirs to disperse their seeds (Fragoso and Huffman 2000).

### Study sites

Our study was focused on 19 trails spread throughout five areas in the Atlantic rainforest of São Paulo State in southeastern Brazil (Anchieta Island State Park, Xivová Japuí State Park, Cardoso Island State Park, Serra do Mar State Park-Picinguaba, and Juréia Ecological Station). All areas are protected parks ranging from 828 to 79,230 ha with the most northerly and southerly separated by 450 km (Fig. 1). All areas are classified as lowland Atlantic rainforest due to their similar floristic composition, rainfall, and soil (Oliveira-Filho and Fontes 2000). Within those five areas, we selected three or four trails that were located at least 3 km far from each other. All trails were censused for medium and large mammals concomitantly with this study (Galetti et al. 2009, see Table 1).

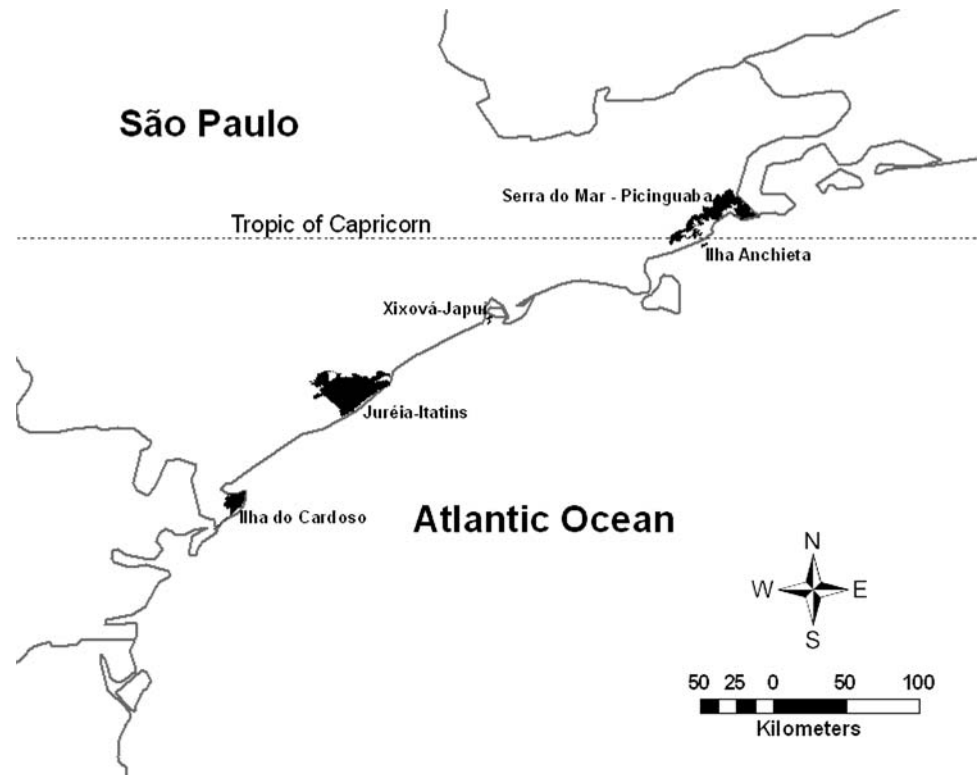
### Seed removal and seed fate experiment

We placed seeds in four trails in each area, with the exception of Cardoso, where we placed seeds in only three trails. In each trail, we had from three to 13 experimental stations, depending on the availability of adult palms, and five marked seeds in each station. We used trails as replicates because we believe one agouti is not able to visit more than one trail, since trails are located at least 3 km from any other within the same study site and agoutis have a relatively small home range that varies from 1.6 to 8.5 ha (for *D. leporina*, Silvius and Fragoso 2003).

Fruits from *A. aculeatissimum* were collected from seven individuals in each of the five areas, the pulp removed manually, and the seeds visually inspected for insect infestations. Only interactions between rodents and seeds were investigated to measure seed removal, seed dispersal, and seed predation of *A. aculeatissimum*. The adult palms used in the experiment were at least 50 m from one another and 10 m away from other conspecific adult palm, which was not used in the experiment. Seeds were placed beneath the palm just after the period of fruit fall (December to February).

We assessed the fate of seeds by drilling them, attaching threads to the seeds, and following their fate through a modification of the spool and line method (see Forget and Wenny 2005). Each seed was threaded with a line spool that was placed inside a small box, allowing the line to easily unroll when the seed was removed. Five of these boxes (each with one seed attached) were fixed in one palm stipe representing one experimental station. All seeds that were in a 2-m radius

**Fig. 1** Study sites in the Atlantic rainforest of São Paulo State, Brazil



**Table 1** Study site, trail number, the total number of *Astrocaryum aculeatissimum* seeds placed in the experiment, and the abundance of agoutis in number of sightings/10 km walked and, from trails with absence of agoutis to trails with high abundance of agoutis, based on Galetti et al. (2009)

Study site	Trail no.	Seeds placed in the experiment	Abundance of agoutis
Cardoso	2	40	0
Picinguaba	3	20	0
Xixová	1	40	0
Xixová	2	40	0
Xixová	3	40	0
Xixová	4	40	0
Juréia	1	40	0.10
Juréia	2	40	0.10
Juréia	3	40	0.10
Juréia	4	40	0.10
Picinguaba	1	35	0.12
Picinguaba	4	50	0.12
Picinguaba	2	35	0.25
Cardoso	3	40	0.41
Cardoso	1	40	1.70
Anchieta	4	65	2.44
Anchieta	1	15	6.54
Anchieta	3	15	7.47
Anchieta	2	35	10.71

from these experimental stations where removed before setting up this experiment.

We used a spool line of 35 m because previous studies have shown that rodents do not usually carry the seeds for longer distances (Forget 1990; Peres et al. 1997; Pimentel and Tabarelli 2004; but see

Hallwacks 1986). Due to rapid removal of seeds during the pilot study, we followed the threads to locate the seeds after 5 days. To avoid the effects of the availability of other fruit species in the seed removal of *A. aculeatissimum*, we searched for fruits found in the floor in 4 m around each experimental station. We did not find, however, a correlation between the seed removal rate of *A. aculeatissimum* in our experimental stations and the number of vertebrate-dispersed fruits around stations.

Seeds were counted as intact if they were not removed from the experimental stations. Seeds were considered removed if they were found in a place other than where we originally placed them (i.e., found at least 1 m away from the palm stipe). Removed seeds were further separated as preyed on or dispersed. Damaged seeds were considered preyed on by rodents. Dispersed seeds were then separated into non-cached seeds (seeds dispersed on the forest floor) or scatter hoarded seeds (cached in the soil or beneath the leaf litter). Seeds attached to a jammed thread or those with broken threads were considered only in the estimation of seed removal, but not in the estimation of seed fate, seed dispersal distance, or in the inference of the seed disperser.

The rodent species that removed or preyed on seeds were identified by the previously recorded patterns of teeth marks in the seeds (see Beck-King et al. 1999). The paths used by seed dispersers and the places where the rodents placed the seeds (i.e., holes below the mother plant) were also considered in the inference of the rodent species.

## Density of seedlings, juveniles, and adults

We randomly demarcated ten plots of  $50 \times 4$  m in each of the same trails used in the seed removal and seed fate experiment, totaling 0.2 ha in each trail. All seedlings, juveniles, and adults of *A. aculeatissimum* were counted; individuals less than 0.5 m high were considered seedlings (Losos 1995; Vormisto 2002), those with current or past flowering and/or fruiting signals were considered adults, while those higher than 0.5 m and without flowering and/or fruiting signals were considered juveniles.

## Analyses

We first summed up the number of removed seeds, scatter hoarded seeds, preyed on seeds and non-cached seeds per experimental station in each trail. Then, we analyzed the proportions of: (1) the number of removed seeds/total number of seeds placed in the experiment, (2) scatter-hoarded seeds/total number of seeds placed in the experiment, (3) preyed on seeds/total number of seeds placed in the experiment, and (4) non-cached seeds/total number of seeds placed in the experiment in each of the 19 trails as a function of both the abundance of agoutis and study sites, and as a function of the abundance of agoutis only, using Generalized Linear Models with binomial function. To assess the effect of agoutis and small rodents separately, we also analyzed seed removal, scatter hoarding, seed predation and seed dispersal without caching by agoutis and by small rodents separately as a function of both the abundance of agoutis and study sites, and as a function of the abundance of agoutis only.

All seed dispersal distances in each experimental station were averaged per trail and analyzed as a function of both the abundance of agoutis and study sites, and as a function of the abundance of agoutis only, using a Generalized Linear Model assuming a gamma error and link function log. Distances of dispersed seeds by agoutis and by small rodents were also compared using a *t* test. The proportion of seedlings/(adults + 1) and the proportion of juveniles/(adults + 1) recorded in each trail were also analyzed as a function of both the abundance of agoutis and study sites, and as a function of the abundance of agoutis only, using Generalized Linear Models with binomial function. In this variable, we added one in the total number of adults in each trail, given that we did not find any adult in some of these trails. The abundance of agoutis was log transformed in all analyses to improve normality. We analyzed our data using only the abundance of agoutis (besides using both the abundance of agoutis and study sites) in all our models to be able to address if small scatter hoarding rodents are functionally redundant in terms of seed dispersal services in defaunated areas.

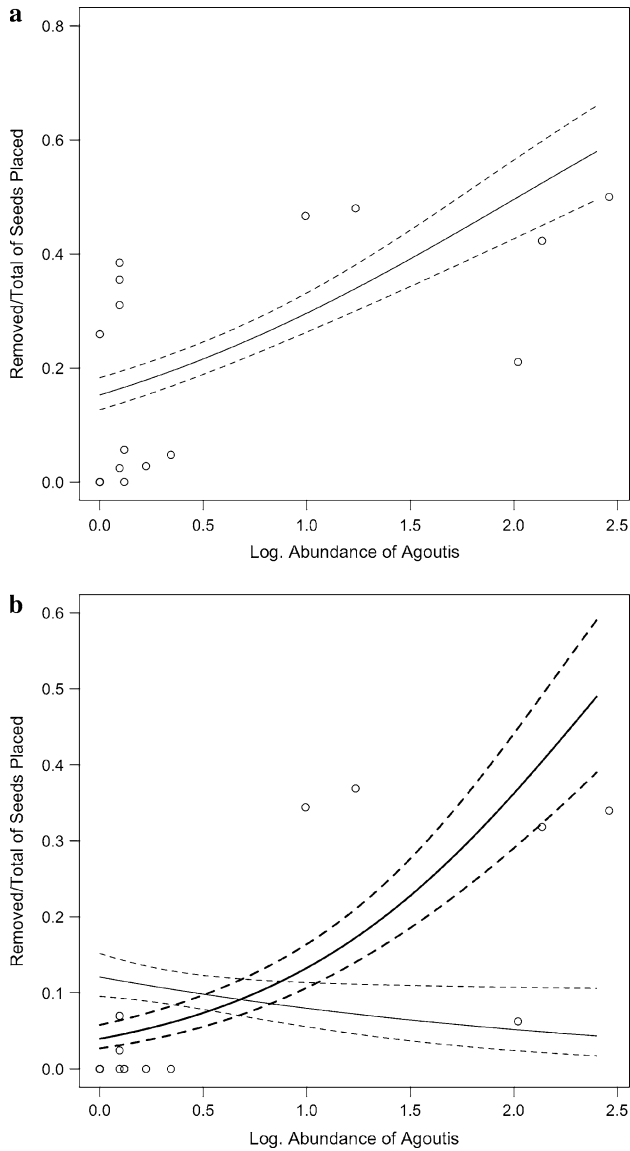
## Results

### Seed removal and seed fate experiment

When both the abundance of agoutis and study site were included in the model, study site was the main factor that explained the variation in all seed fates except scatter hoarding by small rodents, seeds preyed on by small rodents and seeds dispersed in the soil, that were also explained by the abundance of agoutis. Either study site or abundance of agoutis did not explain scatter hoarding by small rodents and agoutis combined, as well as the average distance of seed dispersal. When only the abundance of agoutis was included in the models, the effect of this factor was significant for all seed fates, except for scatter hoarding by small rodents and for seeds preyed on by small rodents, and for the average distance of seed dispersal.

There was a positive effect of the abundance of agoutis on seed removal, when all removed seeds were included in the analyses ( $\chi^2 = 176.37$ ,  $P < 0.01$ ,  $df = 17$  explains 32.5% of the variance,  $n = 231$ , Fig. 2a). Agoutis removed more seeds than small rodents (respectively,  $n = 92$  and  $n = 83$ ) and our model showed that seed removal increased from 16% in areas with low abundance of agoutis to 57% in areas with high abundance of agoutis. When removed seeds by agoutis and by small rodents were analyzed separately, there was a positive and significant effect of the abundance of agoutis on seed removal by agoutis ( $\chi^2 = 95.43$ ,  $P < 0.01$ ,  $df = 17$ , explains 52.6% of the variance,  $n = 92$ ). Seed removal by agoutis increased from four percent in areas with low abundance of agoutis to 48% in areas with high abundance of agoutis. In contrast we found a negative effect of the abundance of agoutis on seed removal by small rodents ( $\chi^2 = 116.98$ ,  $P = 0.03$ ,  $df = 17$ , explains four percent of the variance,  $n = 83$ , Fig. 2b). Seed removal by small rodents decreased from 11% in areas with low abundance of agoutis to four percent in areas with high abundance of agoutis.

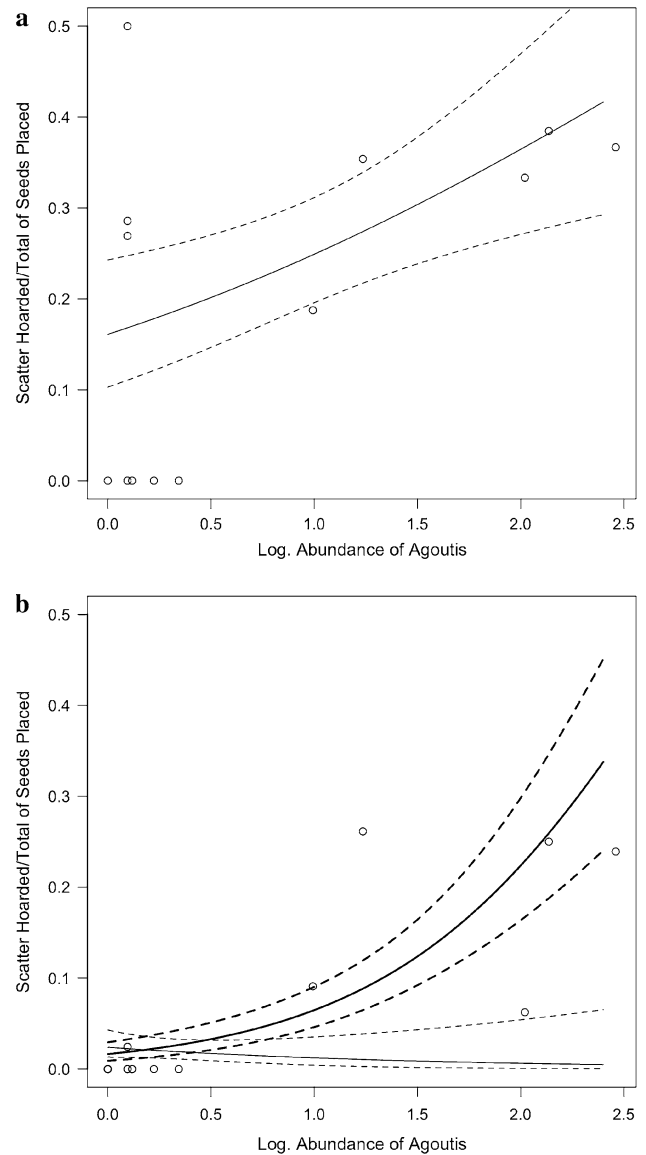
We also found a positive effect of the abundance of agoutis on scatter hoarding, when seeds scatter hoarded by both agoutis and small rodents were included in the analysis ( $\chi^2 = 68.23$ ,  $P < 0.001$ ,  $df = 17$  explains 42.9% of the variance,  $n = 60$ ). Again, agoutis scatter hoarded more seeds than small rodents did (respectively,  $n = 46$  and  $n = 14$ ) and our model showed that scatter hoarding increased from 4% in areas with low abundance of agoutis to 32% in areas with high abundance of agoutis (Fig. 3a). When scatter-hoarded seeds by agoutis and by small mammals were analyzed separately, there was a positive and significant effect of the abundance of agoutis on the number of scatter-hoarded seeds by agoutis ( $\chi^2 = 46.71$ ,  $P < 0.001$ ,  $df = 17$ , explain 60.8% of the variance,  $n = 46$ ). Scatter hoarding by agoutis increased from 2% in areas with low abundance of agoutis to 32% of seeds in areas with high abundance



**Fig. 2 a** Proportion of removed seeds/total of seeds of *A. aculeatissimum* placed in the experiment as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil. **b** Proportion of removed seeds by agoutis/total of seeds of *A. aculeatissimum* placed in the experiment (*thicker line*) and by small rodents (*thinner line*) as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil

of agoutis. In contrast, there was no significant effect of the abundance of agoutis on the number of scatter hoarded seeds by small rodents ( $\chi^2 = 43.95$ ,  $P = 0.261$ ,  $df = 17$ ,  $n = 14$ , Fig. 3b).

There was also a positive effect of the abundance of agoutis on seed predation ( $\chi^2 = 80.444$ ,  $P < 0.001$ ,  $df = 17$ , explains 33.1% of the variance  $n = 56$ , Fig. 4a). Again, agoutis preyed on more seeds than small rodents (respectively,  $n = 46$  and  $n = 10$ ) and seed predation increased from 4% in areas with low abundance of agoutis to 26% in areas with a high abundance of agoutis. When the number of seeds preyed on by

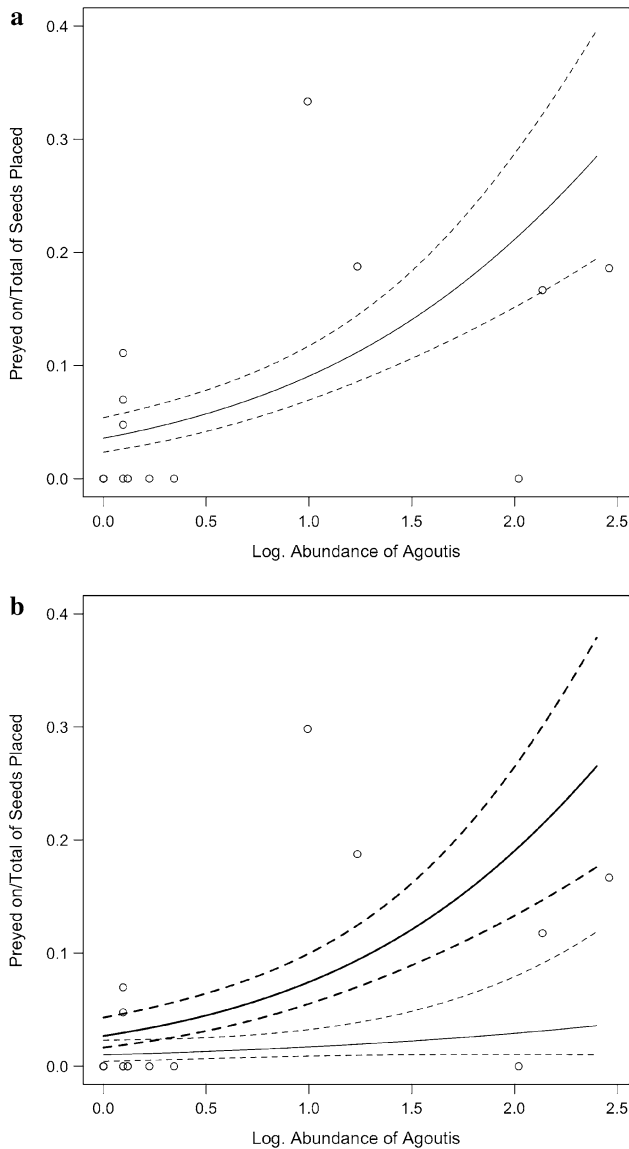


**Fig. 3 a** Proportion of scatter-hoarded seeds/total of seeds of *A. aculeatissimum* placed in the experiment as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil. **b** Proportion of scatter-hoarded seeds by agoutis/total of seeds of *A. aculeatissimum* placed in the experiment (*thicker line*) and by small rodents (*thinner line*) as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil

agoutis and by small rodents were analyzed separately, there was a positive and significant effect of the abundance of agoutis on the number of seeds preyed on by agoutis ( $\chi^2 = 71.897$ ,  $P < 0.001$ ,  $df = 17$ , explains 35.8% of the variance,  $n = 46$ ), but there was no effect of the abundance of agoutis on the number of seeds preyed on by small rodents ( $\chi^2 = 23.350$ ,  $P = 0.120$ ,  $df = 17$ ,  $n = 10$ , Fig. 4b). Seed predation by agoutis increased from 3% in areas with low abundance of agoutis to 25% in areas with high abundance of agoutis.

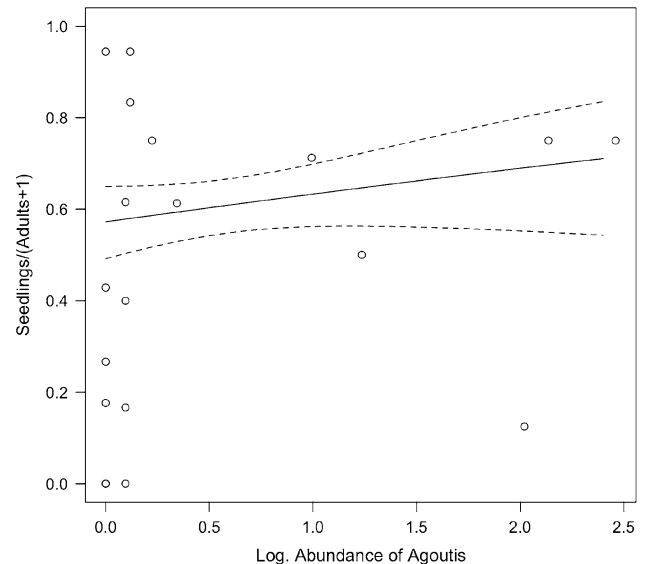
Among the removed seeds that were dispersed without caching, there was a negative and significant effect of





**Fig. 4** **a** Proportion of seeds preyed on/total of seeds of *A. aculeatissimum* placed in the experiment as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil. **b** Proportion of seeds preyed on by agoutis/total of seeds of *A. aculeatissimum* placed in the experiment (*thicker line*) and by small rodents (*thinner line*) as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil

the abundance of agoutis ( $\chi^2 = 15.47$ ,  $P < 0.01$ ,  $df = 11$ , explains 73.8% of the variance,  $n = 59$ ). Dispersed seeds without caching decreased from 11% percent in areas with low abundance of agoutis to less than 1% in areas with a high abundance of agoutis. In this seed fate, we could not identify the seed dispersal agent, given that seeds were left on the forest floor without any sign that could be used to identify the seed disperser. Therefore, we were not able to analyze this data separately by dispersal agent. However, our data suggests that small rodents are driving this pattern, especially because we found a decrease in the number of non-cached seeds with the abundance of agoutis.



**Fig. 5** Proportion of seedlings of *A. aculeatissimum*/(adults + 1) as a function of the abundance of agoutis in the Atlantic rainforest of São Paulo State, Brazil

Our generalized linear model showed no effect of the abundance of agoutis on seed dispersal distance ( $P = 0.599$ ,  $df = 11$ ). However, agoutis dispersed seeds a further distances from the mother plant than small rodents did (mean seed dispersal distance = 5.2 m and mean seed dispersal distance = 3.6 m, respectively,  $t$ -test = 2.972,  $df = 356$ ,  $P = 0.0031$ ).

#### Density of seedlings, juveniles, and adults

There was no significant effect of study site or of the abundance of agoutis on the number of juveniles/(adults + 1) recorded in each trail ( $\chi^2 = 68.855$ ,  $P = 0.518$ ,  $df = 17$ ), neither on the number of seedling/(adults + 1) ( $\chi^2 = 86.611$ ,  $P = 0.173$ ,  $df = 17$ ), although there was a trend for a positive effect of the abundance of agoutis in the later variable (see Fig. 5).

## Discussion

### Seed removal and seed fate experiment

Study site was the main factor that explained the variation in the majority of seed fates analyzed here, given the similarity of the abundances of agoutis across trails within study sites for some of these sites. However, when only the abundance of agoutis was included in the model, we found a positive effect of this factor on seed removal, scatter hoarding and seed predation and a negative effect on seed dispersal without caching. Our analysis, separating the role of agoutis and small rodents in all these variables except non-cached seeds, confirms that agoutis are indeed responsible for such patterns.

Even though it is not clear whether the abundance of small rodents increases in areas with low abundance of medium- and large-bodied animals (but see Peres 2000; Wright 2003; Dirzo et al. 2007), or if small rodents can interact with more seeds simply because seeds are more available, we did not find either one to be true in our study system.

Scatter hoarding increased with the abundance of agoutis and, therefore, small rodents did not compensate the rate of scatter hoarding in areas with low abundance of agoutis. Moreover, the behavior of the two small rodents species differ from agoutis: both spiny rats and squirrels usually cache seeds under the leaf litter, a microsite with low probability for seed survival, whereas agoutis cache seeds in the soil where they present high germination rates (Asquith et al. 1999) and are presumably more protected from pathogens and seed predators.

Seed predation has been shown to increase in forest fragments or defaunated areas due to the high abundance of small rodents (Sanchez-Cordero and Martinez-Gallardo 1998; Guariguata et al. 2002; Asquith and Mejia-Chang 2005), but this pattern was not found in this study. We found that seed predation by small rodents in areas with a low abundance of agoutis was not as high as in areas with a high abundance of agoutis, a similar result found by Roldán and Simonetti (2001) that observed a low seed predation of *Astrocaryum murumuru*, a large-seeded species, in a heavily hunted area in Bolivia. A possible explanation for these results is that an increment in seed predation in areas with a high density of small mammals is likely only for small-seeded species, given the preference of small mammals in preying on small seeds (Blate et al. 1998; Dirzo et al. 2007).

Even though seed predation increased with the abundance of agoutis, the rate of increment in scatter hoarding from areas with low abundance of agoutis to areas with high abundance of agoutis was higher than the rate of seed predation in the same gradient. Seed predation increased 6.5 times from areas with low abundance of agoutis to areas with high abundance of agoutis, whereas scatter hoarding increased eight times from areas with low abundance of agoutis to areas with high abundance of agoutis. This data shows that agoutis, even though being the main seed predators of *A. aculeatissimum* seeds, scatter hoarded more seeds than they preyed on, emphasizing their role as important seed dispersers of this palm tree.

Although small rodents did not increase seed predation in areas with low abundance of agoutis, they did contribute in increasing dispersal of seeds that were not cached. Those seeds that are left on the forest floor, despite being dispersed from the mother plant, can suffer high mortality because they are not as protected against other seed predators and pathogens as scatter hoarded seeds are.

Even though we found no significant and positive effect of the abundance of agoutis on seed dispersal

distance, we did find that agoutis, besides increasing the rates of seed removal and scatter hoarding, also disperse seeds at farther distances from the mother plant when compared to small rodents as was also shown by other studies (Almeida and Galetti 2007). Seed dispersal at farther distances from the mother plant could have some potential advantages to seeds. One of them is a decrease in the level of predation by beetles, especially because the timing of beetle attack was shown to vary along the distance gradient. Thus, seeds dispersed far from the mother plant could germinate and produce seedling before the attack by these seed predators (Hammond et al. 1999).

#### Density of seedlings, juveniles, and adults

We found no significant effect of the abundance of agoutis on seedling and juvenile densities of *A. aculeatissimum*, although our results showed that the density of seedlings presents a positive trend as a function of the abundance of agoutis. This non-significant effect can occur due to heavy seedling herbivory by agoutis or other vertebrates that were not accessed in this study.

Another important and more meaningful variable that is not analyzed here could be the spatial distribution of seedlings around adult palms. In this study, the density of seedlings did not present a strong relation with the abundance of agoutis, but the effect of the abundance of agoutis could be strong on the distribution of seedlings around adults, given that we have shown that the distance of seed dispersal by agoutis is higher than by small rodents. The reason for the absence of a relation between the density of juveniles and the abundance of agoutis could be that we have not yet seen the effects of low abundances of agoutis in this plant stage.

#### The overall role of small rodents in compensating the low abundance of agoutis

We have shown here that small rodents did not compensate for the low abundance of agoutis in defaunated areas in terms of seed removal and scatter hoarding. Therefore, seed removal and scatter hoarding in defaunated areas were not maintained as high as in areas with a high abundance of agoutis. Seed predation also increased from areas with low abundances of agoutis to areas with high abundances of agoutis, but the increment in the rate of scatter hoarding was indeed higher than in the rate of seed predation.

The non-compensation by small rodents for the low abundance of agoutis on seed removal and on scatter hoarding indicates that seed dispersal of this species is very low in areas with low abundance of agoutis. Moreover, areas in which agoutis are absent did not present any seed removal or scatter hoarding by small rodents, highlighting that these areas are already compromised in terms of seed dispersal of this and possibly

other large-seeded plants. It is also valuable to mention that this study was done in a short period of time and more definitive conclusions should be made when looking at the same hypotheses addressed here in different seasons and years.

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