

Can forest fragmentation disrupt a conditional mutualism? A case from central Amazon

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Abstract This is the first study to investigate whether scatter-hoarding behavior, a conditional mutualism, can be disrupted by forest fragmentation. We examined whether acouchies (*Myoprocta acouchy*, Rodentia) and agoutis (*Dasyprocta leporina*, Rodentia) changed scatter-hoarding behavior toward seeds of *Astrocaryum aculeatum* (Arecaceae) as a consequence of a decrease in forest-patch area. Our study was conducted at the 30-year-old Biological Dynamics of Forest Fragments Project, in central Amazon, Brazil. We tested whether forest size affected the number of *Astrocaryum* seeds removed and scatter-hoarded (and likely dispersed) by acouchies and agoutis, as well as the distance that the seeds were hoarded. The study extended over three seasons: the peak of the rainy season (March–April), the transition between the rainy and the dry season (May–June), and the peak of the dry season (August–

September). Our results revealed that the number of seeds removed was larger in smaller fragments, but that the percentage of seeds hoarded was much lower, and seeds eaten much higher, in 1-ha fragments. Moreover, fewer seeds were taken longer distances in fragments than in the continuous forest. Site affected the number of seeds removed and season affected the percentage of seeds hoarded: more seeds were removed from stations in one site than in two others, and hoarding was more important in April and September than in June. Our study reveals that scatter-hoarding behavior is affected by forest fragmentation, with the most important disruption in very small fragments. Fragmentation converts a largely mutualistic relationship between the rodents and this palm in large forest patches into seed predation in small fragments.

Keywords Brazil · Caviomorph rodents · Seed caching · Seed dispersal · Seasonal mutualism

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Introduction

Large seeds abound in the tropics, and trees bearing them contribute to the astonishing diversity of tropical forests (Moles et al. 2007). Seeds larger than 1 g produce seedlings that establish, grow, and often out-compete smaller seedlings from smaller seeds on the shaded forest floor (Leishman and Westoby 1994; Westoby et al. 1996). On the other hand, large seeds may be less mobile and more nutritionally valuable than smaller seeds, leading to high rates of density-dependent mortality from insect and mammalian seed predation (Janzen 1969; Howe and Vande Kerckhove 1980; Pringle et al. 2007). The prevalence of large seeds and the animals that disperse and kill them in tropical forests makes the ecology of dispersal and

recruitment of large-seeded trees a priority in tropical forest conservation.

In Neotropical forests, two genera of scatter-hoarding rodents (agoutis, *Dasyprocta* sp., and acouchies, *Myoprocta* sp.) play important roles in dispersal and predation of seeds larger than 1 g (see Jorge 2007, p. 37). Scatter-hoarded seeds escape from negative density-dependent effects of high seed fall directly under parent trees, while burial by rodents presents better physical conditions for germination (e.g., higher humidity, more stable microclimate) than exposure on the forest floor (Vander Wall 1990). However, scatter-hoarding is a conditional mutualism (Bronstein 1994). The potential food of the animal is the seed itself, not pulp or an aril; benefits of discovery by acouchies or agoutis to the plant depend on the animal's decision to hoard the seed instead of immediately eat it. The decision to hoard or not to hoard may be influenced by several factors, including the quantity and quality of the focal seed species and the overall abundance of other foods. Once hoarded, seeds may be eaten later, or may escape death by the hoarder if they are not retrieved. Hoarding constitutes initial seed dispersal rather than immediate mortality.

Deforestation is rapidly removing large tracts of tropical forest around the world (Achard et al. 2002; Hansen and DeFries 2004). Forest fragmentation, a byproduct of deforestation, reduces and partitions the forest available to animals and plants, with well-known negative direct effects on many species (Laurance and Bierregaard 1997). Because tropical forests harbor countless biotic interactions (Gilbert 1980), it is plausible to expect a cascade of negative indirect effects if fragmentation alters the opportunity for or strength of interactions among species. A variety of recent studies document disruption of seed dispersal by forest fragmentation (Asquith et al. 1999; Cordeiro and Howe 2003; Cramer et al. 2007; Galetti et al. 2006; Wright and Duber 2001). This disruption may be due to two factors: fewer seeds are dispersed because fragments hold fewer dispersal agents (quantity sensu Schupp 1993), dispersers that are still present do not carry seeds as far in fragments as in larger forest patches (dispersal quality sensu Schupp 1993; see Howe and Smallwood 1982). Either or both factors alter the spatial distribution of recruitment to the seedling stage, and therefore the understory template that influences spatial distribution of adults.

The present study uniquely addresses disruption of seed dispersal quality due to changes in behavior of primary dispersal agents as a consequence of forest fragmentation, rather than changes in disperser abundance. Because scatter-hoarding is a conditional mutualism, changes in the spatial and temporal distribution of resources available to rodents could transform a mutualistic interaction of seed

dispersal into an antagonistic interaction of seed predation, with scatter-hoarders in small habitat patches eating most of the seeds that they would normally bury (Theimer 2005). To test this hypothesis, we ask whether agoutis and acouchies scatter-hoard less, and therefore disperse less, in forest fragments where we know, a priori, that individuals of either species are still present (Jorge 2008). Forest fragments, by virtue of a much reduced area, lack many fruiting species of trees that might provide food resources to rodents. In the smallest fragments (1 ha), patch size is substantially smaller than the home range of resident rodents, and likely holds far fewer tree species (and therefore fruit crops) than a home range in continuous forest. We ask whether seeds in small fragments are eaten more frequently, and dispersed shorter distances, than seeds in larger fragments or continuous forest. This is the first study to investigate whether forest fragmentation disrupts a mutualism by affecting animal behavior rather than animal population abundance.

Materials and methods

Study site

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) located 80 km north of Manaus, in central Amazon, Brazil. The forest of the region is upland mature forest, not subjected to flooding (Floresta de Terra Firme) with annual precipitation of approximately 2,600 mm (Bierregaard et al. 2001). Fragments were 20–25 years old during data collection (2004). They are surrounded by matrices composed of pasture and secondary vegetation, spread among three cattle ranches (Colosso, Porto Alegre and Dimona). The ranches are 5–10 km apart, each surrounded by large tracts of primary forest (hereafter “continuous forest”) where control sites were established (Km 41, Cabo Frio and Dimona). See Bierregaard et al. (2001) for additional description of the area and its history of fragmentation. In the present study, six square fragments (three of 1 ha and three of 10 ha) and three sites within the continuous forest are used, one triplet (1-ha fragment, 10-ha fragment and control site) per ranch. Except for Dimona (where the continuous forest is within the ranch, and therefore is given the same name), the other sites of continuous forest are given names which are different from those of the nearest ranch (Km 41 is near Colosso, and Cabo Frio is near Porto Alegre). For simplicity, in this article we will refer to the triplet that includes fragments from the Colosso ranch and the continuous forest site of Km 41 only as “Colosso”, and to the triplet that includes fragments from the Porto Alegre ranch and

the continuous forest site of Cabo Frio only as “Porto Alegre”.

Study species

Agoutis (*Dasyprocta* spp.) and acouchies (*Myoprocta* spp.) are two genera in the family Dasyproctidae. The genus *Dasyprocta* ranges from southern Mexico to northern Argentina east of the Andes. The species near Manaus is the red-rumped agouti, *Dasyprocta leporina* (Voss and Emmons 1996), which occurs from central Amazon to southeast Brazil. The genus *Myoprocta* is restricted to the core area of the Amazon. The species present in our study area is the red acouchy, *Myoprocta acouchy* (Voss and Emmons 1996).

Both genera are strictly terrestrial. They eat mainly fruits and seeds that fall on the forest floor (Dubost and Henry 2006) and scatter-hoard seeds for future use (Morris 1962; Smythe 1978). They are similar morphologically, but acouchies are, on average, one-third to half of the size of agoutis (0.5–1 vs. 3–6 kg). Ecologically, they exhibit few differences. South American agoutis have larger home ranges: 5–10 ha (Jorge and Peres 2005; Silvius and Fragooso 2003) versus 1–2 ha for acouchies (Dubost 1988). During periods of fruit scarcity, agoutis switch diet to eat mostly seeds (76%) whereas acouchies still include a large amount fruit pulp (60%) in their diet (Dubost and Henry 2006). Agoutis appear to be more generalist in habitat selection than acouchies, which are restricted to mature forest (Dubost 1988; Voss and Emmons 1996). Differences in habitat selection and use mean that the genera may respond differently to changes in habitat and resource conditions despite similar morphology (Jorge 2008).

The plant species used in our seed-fate experiments was *Astrocaryum aculeatum* (Arecaceae). *A. aculeatum* is monoecious palm of moderate height (10–25 m; Uhl and Dransfield 1987) restricted to the Amazonian region (Kawn and Granville 1992). It is widespread in Amazonian forests, where it occasionally dominates secondary forests (Henderson et al. 1995), but this species as well as congeners are also common in mature forests (M. L. S. P. Jorge, personal observation; Forget 1991; Terborgh et al. 1993). The yellowish-green fruit of *A. aculeatum* consists of farinaceous mesocarp that envelops a black, hard woody shell. The single kernel is white, oily, hard, and covered with an adherent brown testa (Pesce 1985). The diaspore, including seed with its shell, is approximately 3.7 cm in diameter (M. L. S. P. Jorge, unpublished data). The pulp is sought by a variety of vertebrates, especially medium to large mammals, and the seeds are predated by insect larvae, rodents (spiny rats, acouchies and agoutis) and peccaries.

We chose to use *A. aculeatum* seeds for three reasons: *Astrocaryum* seeds are known to be scatter-hoarded by

agoutis (Smythe 1989) and acouchies (Forget 1991), *A. aculeatum* naturally occurs in the study site, and peeled seeds are easily acquired in the local market of Manaus throughout the year. Peeled seeds were used to eliminate the possibility of other animals visiting the seed stations and removing the fruits for the pulp rather than for the seeds themselves.

Experimental design and data collection

We placed ten seeds on the forest floor at random places in the fragments and continuous forest (hereafter called “seed stations”). We attached a 15-cm-long nylon thread to each seed with a screw. The nylon thread had a pink plastic flag at its other end, with an individual code for further identification.

Because of differences in forest size, we placed two seed stations in each 1-ha fragment, six in each 10-ha fragment, and six to eight in the control sites (the continuous forest of *Dimona* had six stations because there were fewer trails to assess the forest in that site, and that of Porto Alegre had one seed station removed from the analysis due to problems with data collection in one of the months; Table 1). Stations were placed at regular intervals within a site (~50-m intervals in 1-ha fragments and ~100-m intervals 10-ha and continuous forest). That arrangement led to a slightly higher station density in 1-ha fragments (2 vs. 0.6 stations per hectare), which could affect removal and hoarding numbers. Nevertheless, this effect would be in the

Table 1 Number of seed stations of *Astrocaryum aculeatum* (Arecaceae) placed on the forest floor of nine sites of the Biological Dynamics of Forest Fragments Project, Manaus, Brazil

Ranch	Fragment size	Month			Total
		April	June	September	
Colosso	1 ha	2	2	2	6
	10 ha	6	6	6	18
	Continuous forest ^a	8	8	8	24
Porto Alegre	1 ha	2	2	2	6
	10 ha	6	6	6	18
	Continuous forest ^b	7	7	7	21
Dimona	1 ha	2	2	2	6
	10 ha	6	6	6	18
	Continuous forest	6	6	6	18
Total		45	45	45	135

Ten seeds were placed in each seed station

^a The site of the continuous forest of Colosso was at the Km 41 Research Station

^b The site of the continuous forest of Porto Alegre was at the Cabo Frio Research Station

opposite direction to that which we expected (fewer seeds removed and more seeds hoarded in 1-ha fragments). Experiments were set up in March, May and August 2004, and checked in April, June and September 2004, respectively. These months correspond to the peak of the rainy season (March and April), the transition between rainy and dry seasons (May and June), and the peak of dry season (August and September; Bierregaard et al. 2001). The peak of the rainy season corresponds to the period of fruit abundance for 67 large-seeded tree species, and the dry season corresponds to the period of fruit scarcity (Jorge 2007).

All stations were first set up in all fragments and control sites of all three ranches. Then they were all checked in the same order in which they were set up to minimize temporal variation between sites. Each station was checked 20–30 days later. At each check, the number of seeds removed was counted and the area searched for removed seeds within a radius of approximately 30 m with the help of three assistants. Removed seeds were either: (1) not found; (2) hoarded: (if the seed was buried in the soil); (3) predated by a rodent (if the seed shell was gnawed, with no embryo left inside); (4) displaced (if the seed was removed from the station, but neither hoarded nor eaten); and (5) predated by another animal (if the seed shell without the embryo was found, but there were no signs of gnawing). Hoarded seeds were assumed to be initially dispersed. In addition to the final fate of the seed, the distance between the seed station and the seed's final fate (whenever the seed was found) was measured.

Statistical analyses

We used three-way ANOVA with repeated measures to evaluate the effects of forest size, ranch and month (and interaction between them) on the number of seeds removed in each station. We used two-way ANOVA with repeated measures to evaluate the effects of forest size, ranch and month on the: (1) percentage of seeds found among the ones removed, (2) percentage of seeds hoarded among the ones found, (3) percentage of seeds predated by a rodent among the ones found, and (4) percentage of seeds displaced or predated by another animal among the ones found (seeds displaced or predated by another animal were lumped together due to very low numbers for each of them). The interaction between forest size and ranch could not be evaluated due to the lack of replicates in a few sites when both factors were considered together. To achieve assumptions of normality and homoscedasticity (Zar 1999), we used square-root transformations of the number of seeds removed and arcsine-square-root transformations of the percentage of seeds found, hoarded, predated by a rodent and other fates (“other”). We

tested for the assumption of sphericity with Mauchly's test of sphericity. Only “other” violated the assumption, for which we report *P*-values corrected by Greenhouse–Geisser.

A total of 45 seed stations was set up in each fragment and continuous forest of each ranch, and the experiments were replicated in each seed station over the course of 3 months. Therefore, there was a total of 135 seed station × month for the analyses (Table 1). For the analysis of the percentage of seeds found, 81 cases were considered (27 per month) due to the lack of complete temporal replication for the 3 months in 54 cases (18 per month). For the analysis of the percentage of seeds hoarded, gnawed and other, 66 cases were considered (22 per month) due to the lack of temporal replication in 69 cases (23 per month).

To test for the effects of forest size, ranch and month on the distance of seeds hoarded, we used a log linear model because of the natural skewed distribution of the data (Agresti 1996), using dispersal distance in two categories: closer and greater than 7 m. Seven meters approximated mean dispersal distance for all forest sizes (6.4 m). The most parsimonious model employed all two-way interactions. For analysis of dispersal distance differences, data from all seed stations were pooled, excluding those in 1-ha fragments, where very few seeds were hoarded (9 vs. 134 in 10-ha fragments and 76 in continuous forest).

Results

Acouchies and agoutis visited seed stations regularly. Out of 135 seed stations × month that were in place, 104 (77%) had at least one seed removed, and 96 (71%) had at least one seed found by investigators. Of 1,350 seeds, 875 (65%) were removed, 437 (32%) were found, 220 (16%) were hoarded, 203 (15%) were predated by one of the two rodent species, and 14 (1%) were either displaced or predated by another animal. Ninety-nine percent of the seeds predated by a rodent had teeth marks compatible with agoutis' or acouchies' teeth marks (smaller than marks from pacas and larger than marks from spiny rats), therefore we assumed rodent predation as predation from agoutis or acouchies.

On average, 6.5 ± 0.4 (\pm SE) seeds were removed per station, 4.2 ± 0.2 (or $50 \pm 3\%$ of the removed seeds) were found, 2.3 ± 0.2 (or $50 \pm 4\%$ of the seeds found) were hoarded, and 2.1 ± 0.2 (or $50 \pm 4\%$ of the seeds found) were predated by rodents. The maximum hoarding distance was 40 m, but more than half of the seeds were found hoarded within 5 m ($n = 115$), with a mean dispersal distance of 6.4 ± 0.3 m.

Effects of forest size, site and month on the number of seeds removed, found, hoarded, predated by a rodent and other fates

Forest size and site affected the number of seeds removed (Fig. 1a, b). On average, 9.4 ± 0.5 seeds (mean \pm SE; $n = 18$ stations) were removed from 1-ha fragments, 7.0 ± 0.6 ($n = 54$ stations) were removed from 10-ha fragments, and 5.2 ± 0.6 ($n = 63$ stations) were removed from the continuous forest. More seeds were removed from Colosso (8.8 ± 0.4 ; $n = 48$ stations) than the other two ranches (Porto Alegre, 5.4 ± 0.7 , $n = 45$ stations; and Dimona, 5.0 ± 0.8 , $n = 42$ stations), indicating an interaction between forest size and site (Table 2). The number of seeds removed did not differ significantly among the 3 months. Interaction between forest size and site was the result of Colosso having high removal numbers at all three treatments, whereas in the other two ranches, there was a decline with an increase in forest size.

The most interesting contrast was between percentage of seeds found and percentage hoarded. The percentage of seeds found did not differ significantly by forest size, site or month (1-ha fragments, $38 \pm 7\%$, $n = 18$; 10-ha fragments, $55 \pm 4\%$, $n = 35$; continuous forest, $52 \pm 4\%$, $n = 31$; Colosso, $54 \pm 3\%$, $n = 42$; Porto Alegre, $54 \pm 7\%$, $n = 24$; Dimona, $38 \pm 8\%$, $n = 15$; April,

$51 \pm 6\%$, $n = 27$; June, $52 \pm 5\%$, $n = 27$; September, $50 \pm 6\%$, $n = 27$; Table 2). In contrast, the percentage of seeds hoarded (and likely dispersed) and predated by a rodent differed significantly by forest size (Fig. 1c) and month (Fig. 1d); only $16 \pm 7\%$ of the seeds found in 1-ha fragments were hoarded, whereas $76 \pm 10\%$ were predated by a rodent. In 10-ha fragments, $63 \pm 6\%$ of the seeds found were hoarded, whereas $34 \pm 6\%$ were predated by a rodent. In the continuous forest, $50 \pm 8\%$ of seeds found were hoarded, whereas $49 \pm 8\%$ were predated by a rodent ($n_{1\text{-ha}} = 12$ stations; $n_{10\text{-ha}} = 27$ stations; $n_{\text{continuous}} = 27$ stations; Fig. 1c). More seeds were hoarded in April ($69 \pm 8\%$; $n = 22$ stations) than in June ($48 \pm 7\%$; $n = 22$ stations) and more in the latter than in September ($31 \pm 8\%$; $n = 22$ stations), and the opposite was true for seeds predated by rodents ($24 \pm 8\%$ in April, $51 \pm 7\%$ in June, and $67 \pm 8\%$ in September; Fig. 1d). The percentages of seeds hoarded, predated by a rodent and with another fate were similar between the three sites (Table 2).

Forest size and month interacted with respect to the percentage of seeds hoarded. In the continuous forest, there was a linear decrease in the percentage of seeds hoarded from April to September (April, $78 \pm 11\%$; $n = 9$ stations; June, $57 \pm 11\%$; $n = 9$ stations; September, $17 \pm 11\%$; $n = 9$ stations). In 10-ha fragments, a high percentage of seeds were hoarded in April ($90 \pm 4\%$; $n = 9$ stations),

Fig. 1 Effects of **a** forest size and **b** site on the number of seeds removed (mean \pm SE); and effects of **c** forest size and **d** month on the percentage of seeds scatter-hoarded by a rodent (and likely dispersed), predated by scatter-hoarding rodents and with a fate other than hoarded or predated (mean \pm SE). *F*-statistics are summarized in Table 2

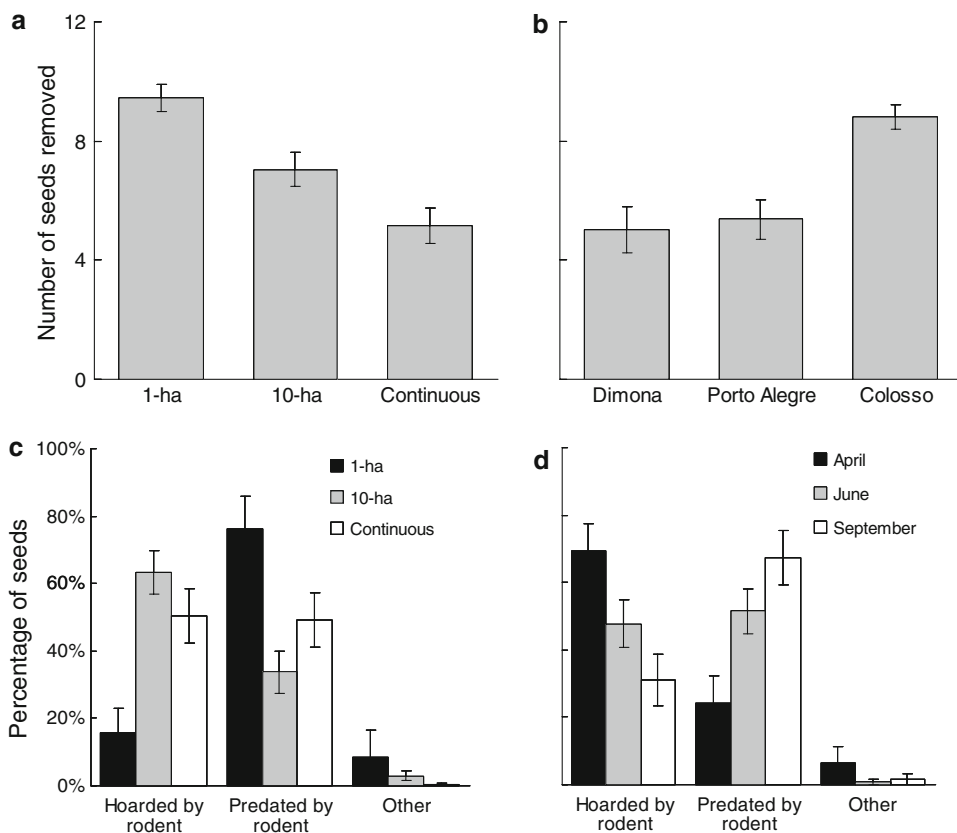


Table 2 Statistical results of the ANOVA with repeated measures

Factor	Variable	<i>n</i>	<i>df</i>	<i>F</i>	<i>P</i>
Forest size	Removed	45	2,36	9.707	0.000
Ranch	Removed	45	2,36	4.916	0.013
Forest size × ranch	Removed	45	4,36	3.865	0.010
Month	Removed	105	2,72	2.864	0.064
Forest size × month	Removed	105	4,72	1.744	0.150
Ranch × month	Removed	105	4,72	0.907	0.465
Forest size × ranch × month	Removed	105	8,72	0.818	0.589
Forest size	Found	27	2,24	2.139	0.204
Month	Found	81	2,48	0.031	0.981
Forest size × month	Found	81	4,48	0.118	0.939
Ranch	Found	27	2,24	1.523	0.333
Ranch × month	Found	81	4,48	2.449	0.069
Forest size	Hoarded	22	2,19	11.92	0.000
Month	Hoarded	66	2,38	4.236	0.045
Forest size × month	Hoarded	66	4,38	3.409	0.041
Ranch	Hoarded	22	2,19	1.748	0.092
Ranch × month	Hoarded	66	4,38	0.571	0.863
Forest size	Gnawed	22	2,19	9.266	0.002
Month	Gnawed	66	2,38	6.505	0.008
Forest size × month	Gnawed	66	4,38	1.947	0.205
Ranch	Gnawed	22	2,19	1.041	0.331
Ranch × month	Gnawed	66	4,38	0.33	0.964
Forest size	Other	22	2,19	1.222	0.294
Month	Other	66	2,38	3.271	0.063 ^a
Forest size × month	Other	66	4,38	1.487	0.221 ^a
Ranch	Other	22	2,19	0.504	0.529
Month	Other	66	2,38	2.084	0.159 ^a
Ranch × month	Other	66	4,38	1.203	0.286 ^a

Significant results are *in bold*

^a *P*-values corrected by the Greenhouse–Geisser test because the data for “other” violated the assumption of sphericity (Mauchly’s test of sphericity: $W = 0.489$, $P = 0.002$)

with a decrease in June ($44 \pm 10\%$; $n = 9$ stations), and no further change in September ($56 \pm 11\%$; $n = 9$ stations; Table 2). Finally, in 1-ha fragments, a low percentage of seeds was hoarded in all 3 months (April, $3 \pm 3\%$; $n = 4$ stations; June, $38 \pm 18\%$; $n = 4$ stations; September, $6 \pm 6\%$; $n = 4$ stations; Fig. 2).

Assuming that most seeds not found were removed by scatter-hoarding rodents and that a positive correlation exists between seeds not found and distance, we used distance of seeds found to rule out the possibility that most of the seeds not found in the 1-ha fragments were hoarded, or most seeds not found in 10-ha fragments were predated by the rodents. In 1-ha fragments, seeds hoarded were about as far away from stations as seeds eaten by the rodents (mean \pm SE_{hoarded} = 8.8 ± 2.0 m, $n = 9$; mean \pm SE_{predated by rodent} = 8.1 ± 1.5 m, $n = 51$; *t*-test,

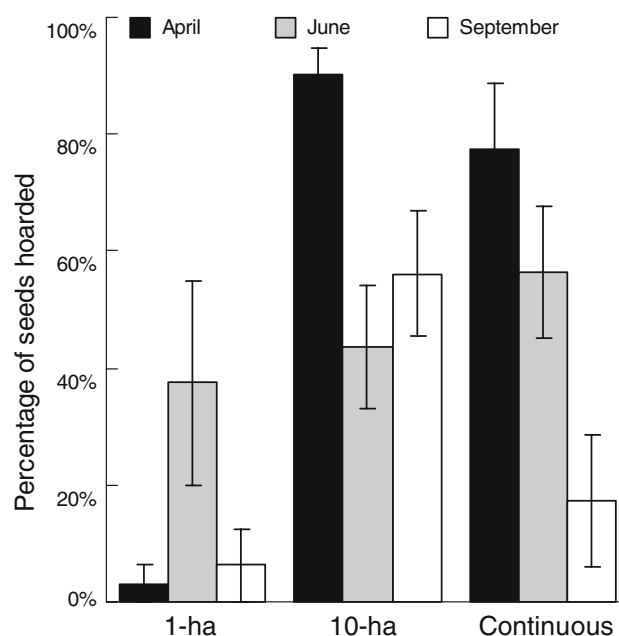


Fig. 2 Monthly variation of the percentage of seeds hoarded (and likely dispersed) at the three forest sizes. *F*-statistics are summarized in Table 2

$P = 0.763$). In 10-ha fragments, hoarded seeds were found at shorter distances than seeds eaten by the rodents (mean \pm SE_{hoarded} = 5.7 ± 0.5 m, $n = 134$; mean \pm SE_{predated by rodent} = 7.5 ± 0.6 m, $n = 102$; *t*-test, $P = 0.032$). The significantly greater distance of seeds found predated by a rodent in 10-ha fragments may suggest that more seed predation by the rodents occurred in 10-ha fragments than our direct results (gnawed seed coats) revealed.

Effects of forest size, site and month on dispersal distance

More seeds were hoarded (and likely dispersed) at longer distances in the continuous forest than in 10-ha fragments, and the same was true for September when compared to June and April. In the continuous forest, 45% of the seeds were hoarded more than 7 m away from stations ($n = 76$ seeds), whereas in 10-ha fragments only 29% were hoarded more than 7 m away ($n = 134$ seeds; log linear model—forest size \times distance interaction, $\chi^2_{df=1} = 7.62$; $P = 0.006$; Fig. 3a). As indicated previously, too few records of hoarded seeds existed in 1-ha fragments to include in the analysis ($n = 9$). The model also depicted a suggestive interaction between month and dispersal distance ($\chi^2_{df=2} = 5.00$; $P = 0.08$; Fig. 3b), with more seeds apparently hoarded at distances greater than 7 m in September (43%, $n = 53$ seeds) than in June (35%, $n = 49$ seeds) which exceeded the percentage hoarded in April (31%, $n = 108$ seeds).

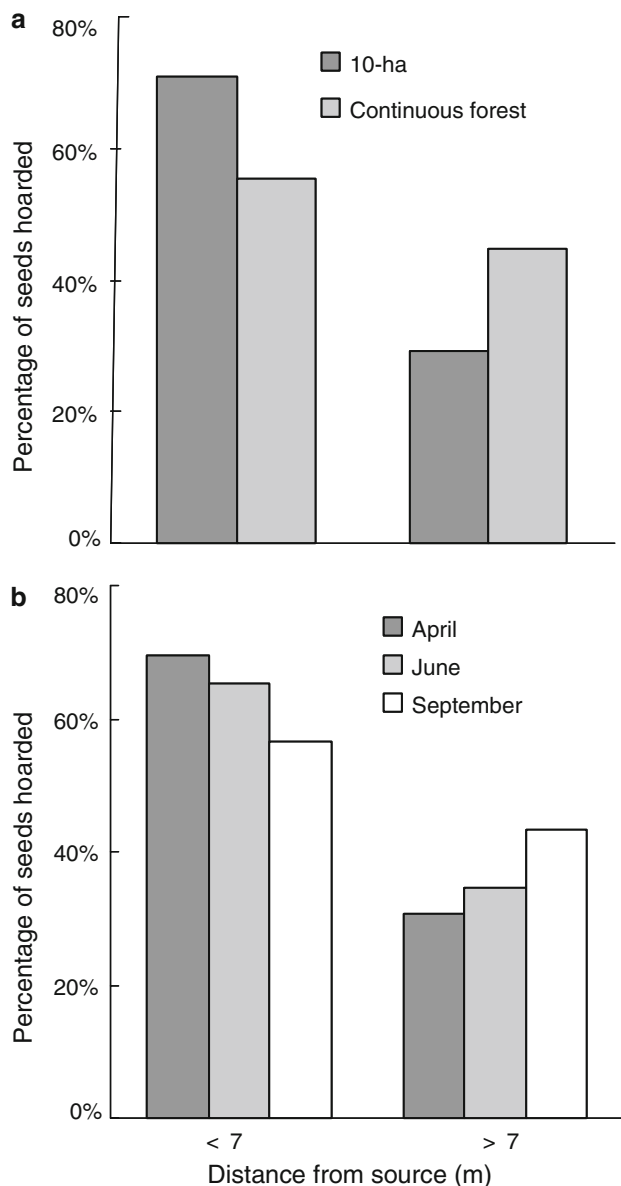


Fig. 3 Effects of **a** forest size and **b** month on the distance that seeds were hoarded. **a** In the continuous forest, 45% of the seeds were hoarded at distances greater than 7 m ($n = 76$); in 10-ha fragments, 29% of the seeds were hoarded at distances greater than 7 m ($n = 134$) (log linear model: forest size \times distance interaction, $\chi^2_{df=1} = 7.62$; $P = 0.006$). **b** In September, 43% of the seeds were hoarded at distances greater than 7 m ($n = 53$), whereas in June, only 35% ($n = 49$), and in April, only 31% ($n = 108$) were hoarded that far away from the seed station (log linear model: month \times distance interaction: $\chi^2_{df=2} = 5.00$; $P = 0.08$). One-hectare fragments were not considered for this analysis due to the small number of seeds hoarded ($n = 9$)

Discussion

Interactions among species are often contingent on conditions that vary in space and time (Lawton 1999). The present study is the first to show that forest fragmentation

disrupts seed dispersal quality (*sensu* Schupp 1993) by changing the behavior of dispersal agents. Scatter-hoarding behavior of agoutis and acouchies is a conditional mutualism (Bronstein 1994) in which the animals make a choice of eating seeds, which kills them, or hoarding seeds, leaving open the possibility of effective seed dispersal that results in seedling and juvenile recruitment. We ask whether rodent behavior that usually benefits the plant's reproduction to a greater or lesser degree shifts to a predatory interaction because of changes in landscape conditions that influence resource availability, as suggested by Theimer (2005). We find that forest fragmentation disrupts scatter-hoarding dynamics in a complex manner: the quantity of dispersal (number of seeds removed by scatter-hoarding rodents) is higher in smaller fragments whereas the quality (proportion of seeds hoarded and hoarding distance) is lower in smaller fragments. From the plant perspective, acouchies and agoutis that are often dispersal agents in continuous forest, disperse the seeds at shorter distances in medium-size fragments, and become potent seed predators in small fragments.

Spatial and temporal effects on removal, hoarding and predation of *A. aculeatum*

Dynamics of variation in seed removal and hoarding differed in space and time. Significant spatial variation occurred in the number of *A. aculeatum* seeds removed at BDFFP ranches (distance between ranches is approximately 10 km), driven mainly by the much higher removal from the continuous forest at Colosso than at the two other ranches. Spatial variation in seed removal is expected because it is likely to be influenced by the other plant species that are present in the surrounding area, which varies greatly in Neotropical forests (Foster 1982; Wright et al. 1999). Other studies have found similar patterns. For instance, toucans and other birds are satiated by dense stands of trees at the height of the fruiting season in Panama, taking a smaller proportion of fruits of *Virola nobilis* (Myristicaceae) than from more isolated trees or at other times of the season (Manasse and Howe 1983). In the same forest, agoutis remove fewer seeds of *V. nobilis*, *Gustavia superba* (Lecythidaceae) and *Dipteryx panamensis* (Fabaceae), where conspecifics of the tree species are more abundant (Forget 1992; Forget 1993; Forget and Milleron 1991). At BDFFP, there is a significant spatial variation of resource availability on the basis of 67 large-seeded tree species ($\chi^2 = 0.002$; Jorge 2007) that partially correlates with variation in removal numbers between sites (Colosso, higher removal, low food availability; Porto Alegre, low removal, high food availability; Dimona, low removal, low food availability). But the correlation must be considered with caution due to the small sample size ($n = 3$). The

community context of resources may alter the use of any particular one in several ways.

The spatial variation in removal at BDFFP was not reflected in hoarding or predation levels, which were not significantly different in the three sites. Resource availability in the surrounding area and the relative quality of seeds available for hoarding may influence the rodent's decision of how many seeds to *remove* from a certain seed patch, but not the decision of how many seeds to hoard or eat, which is consistent across patches.

Seasonality did not affect removal, but affected scatter-hoarding and predation levels, a pattern expected from observation of other hoarding studies (Vander Wall 1990) as well as from theoretical models (Jorge 2007). Animals are expected to hoard food in periods of surplus and predate more during periods of scarcity. Surplus may reflect peak fruiting periods of a focal tree species (e.g., Vander Wall 2002), or may reflect the overall fruit abundance in the forest, as suggested Forget et al. (2002) in a compilation of results from different seed species, from Barro Colorado Island, Panama. In our study, hoarding of *Astrocaryum* seeds reached a maximum in the peak of the fruiting season for 67 large-seeded tree species monitored at the same areas in the same period (Jorge 2007) and decreased monotonically into the months of greatest fruit scarcity. Our results provide stronger support for the idea of a response to community-wide resources (Forget et al. 2002) because the same seed species (*Astrocaryum*) is tested throughout different seasons.

Effects of forest size on the removal, scatter-hoarding, predation and dispersal distance of *A. aculeatum*

Seed removal varied with forest size. More seeds were removed from stations in 1-ha fragments, intermediate levels from 10-ha hectare fragments, and fewer from the continuous forest. Other studies on the effects of forest fragmentation on seed dispersal systems show an opposite trend (Asquith et al. 1999; Cordeiro and Howe 2003; Cramer et al. 2007; Galetti et al. 2006; Wright and Duber 2001), which result from fewer species or numbers of dispersal agents in fragments than in larger forests. An exception is a study by Guariguata et al. (2002), who report a similar pattern to the one revealed in this study, but suggest that their results are related to increases in the abundance of smaller, strictly predatory rodents. This explanation is not relevant to the present study, in which camera surveys of some seed stations (M. L. S. P. Jorge, unpublished data) and evidence from the seeds removed and found (hoarding patterns or teeth marks) revealed that almost all (99%) removal is by agoutis and acouchies (M. L. S. P. Jorge, personal observation). *Astrocaryum* seeds are clearly more valuable for agoutis and acouchies

in smaller than in larger forest patches. The question is: are seeds more valuable for immediate consumption (and negative for the plant) or for future use (potentially positive for the plant) in forest patches of different size?

The answer is not straightforward. *Astrocaryum* seeds are as valuable for future consumption in 10-ha fragments as they are in the continuous forest, but are more valuable for immediate consumption in 1-ha fragments, where a higher proportion of seeds are predated. Acouchies are more abundant in the continuous forest and 10-ha fragments, whereas agoutis are practically the only scatter-hoarders present in 1-ha fragments (Jorge 2008). The species shift from acouchies to agoutis from 10-ha to 1-ha fragments may explain the differences in scatter-hoarding proportions for two reasons. Scatter-hoarding levels should be lower with lower seed:hoarder ratios (Theimer 2005). A home range that includes a 1-ha forest fragment is likely to have fewer tree species than a home range in a 10-ha forest fragment or in the continuous forest, especially considering that the hoarders present in 1-ha fragments (agoutis) have larger home ranges than the hoarders that are more abundant in 10-ha fragments and continuous forest (acouchies). Moreover, in times of food scarcity, acouchies still include a large amount of fruit pulp in their diet (60% fruit pulp vs. 20% seeds), whereas agoutis switch mainly to seeds (76% seeds vs. 12% fruit pulp; Dubost and Henry 2006). Such distinct dietary patterns may reflect more seeds predated where agoutis are more prevalent. Differences in scatter-hoarding and predation proportions between 1-ha and 10-ha fragments revealed by our study may reflect distinct spatial and dietary needs of the two rodent species, and the absence of acouchies from small fragments.

The final aspect considered within the context of forest fragmentation was dispersal distance. We restricted our comparisons to 10-ha fragments and the continuous forest because there were too few seeds hoarded in 1-ha fragments to include them in the analysis. There was a significant negative effect of forest size on dispersal distance. In 10-ha fragments, only 30% of the seeds was cached at distances longer than 7 m, whereas in the continuous forest, 45% of the cached seeds was taken to distances greater than 7 m. Seeds that are taken longer distances have a better chance of survival because they escape density-dependent mortality from insects, pathogens, vertebrates, or competition within seedling cohorts (Howe and Smallwood 1982). Shorter dispersal distances in previous studies (Cordeiro and Howe 2003; Wright and Duber 2001), reflect disperser absence, which results in accumulations of seeds under parent trees. In our study, a change in the behavior of the animals results in hoarding of seeds closer to stations in 10-ha fragments, which may also ultimately affect density-dependent mortality from the plant's perspective.

Conclusion

The present study addresses three aspects of scatterhoarding dynamics: removal, hoarding versus predation, and hoarding distance. Removal varies at the spatial level, whereas hoarding versus predation varies at the seasonal level. Our results suggest that each step is affected by different contexts. The decision to take a seed or not seems to depend on where the animal is and what other alternative resources are available, but not how resources vary over time. The decision to immediately eat the seed or hoard it seems to depend more on how resources vary over time.

Forest fragmentation positively affects removal (there is more removal in smaller forest patches), but negatively affects potential seed dispersal (less hoarding, more predation). Because a higher proportion of seeds is eaten rather than hoarded in small fragments, the relationship in small fragments is primarily one of seed predation rather than potential dispersal in those fragments. In 10-ha fragments, animals remain eager to scatter-hoard palm seeds, but scatter-hoard them at closer distances. In 1-ha fragments, the mutualism is completely disrupted and animals eat the seeds that they remove. Agents of seed dispersal thus become agents of seed predation.

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