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Original article

Effects of microhabitat on palm seed predation in two forest fragments in southeast Brazil

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Abstract

The establishment of plants depends crucially on where seeds are deposited in the environment. Some authors suggest that in forest understory seed predation is lower than in gaps, and higher than at the forest edge. However, most studies have been carried out in large forest patches and very little is known about the effects of microhabitat conditions on seed predation in forest fragments. We evaluated the effects of three microhabitats (gaps, forest edge, and understory) on seed predation of two palm species (*Euterpe edulis* and *Syagrus romanzoffiana*) in two semi-deciduous forest fragments (230 and 2100 ha) in southeast Brazil. Our objective was to test two hypotheses: (1) Low rodent abundance in small fragments as a result of meso-predator action levels leads to lower seed predation in small fragments. (2) Most mammal species in small fragments are generalists with respect to diet and habitat, so that seed predation is similar in different microhabitats (gaps, forest edge and understory) in the small fragment, but not in the larger one. The study community of small fragments is usually composed of generalist species (in diet and habitat aspects), so we expected the same rate of seed predation among microhabitats (gaps, forest edge and understory) in the tested smaller fragment. The experiment was carried out in the dry season (for *E. edulis*) and in the wet season (for *S. romanzoffiana*) in 1999. We conclude that post-dispersal seed predation in forest fragments can be directly connected with mammal communities, reflecting their historical and ecological aspects.

Keywords: Atlantic forest; Forest fragmentation; Seed predation; Microhabitat; Palm; *Euterpe edulis*; *Syagrus romanzoffiana*

1. Introduction

Habitat fragmentation results in reduced area and increased isolation of the remaining habitat patches (Saunders et al., 1991). Forest fragmentation leads to gradual loss of diversity as a consequence of changes in microclimate, affecting factors such as solar radiation, humidity, and wind pattern (Laurance, 1991, 1994; Young and Mitchell, 1994), and of biotic alterations, such as the immediate local extinction of large mammals and top predators (Lovejoy et al., 1986; Cullen et al., 2000). These changes likely alter forest structure, causing large and in long term alterations in ecological processes such as species feeding habits, territorial behaviour, pollination and predation (Lovejoy et al., 1986; Laurance, 1991, 1994). In addition, fragmentation increases the proportion of edge zones in the landscapes. Obviously, the proportion of edge is inversely related to the size of the forest fragment (Ranta et al., 1998). Small forest fragments usually fail to support species assemblages found in original ecosystems because of their reduced area and edge effects (Lovejoy et al., 1986; Redford, 1992; Burkey, 1993; Chiarello, 1999; Cosson et al., 1999; Lynam and Billick, 1999; Sizer and Tanner, 1999). The edge is physically different from forest interior habitat, and these two microhabitats may differ in quality for seed establishment.

The establishment of plants depends crucially on where seeds are deposited; microhabitat characteristics associated with deposition site will ultimately define the probability of seed and seedling survival (Schupp, 1989; Burkey, 1993;

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Schupp, 1993; Laurance, 1994; Schupp and Fuentes, 1995; Cintra, 1998; Russell and Schupp, 1998; Benítez-Malvido et al., 1999). Laurance (1994) and Malcolm (1994) suggest that seed predation at the forest edge should be higher than in the forest understory because of the high diversity of small mammals in this microhabitat. However, Burkey (1993), observed that seed predation was reduced closer to the forest edge due to the lower density of rodents in this microhabitat, caused by an increase in the density of meso-predators (coatis and opossums).

Most studies carried out on seed predation do not consider the size of the forest patch and/or the effects of defaunation (Janzen and Martin, 1982; Smythe, 1986, 1989; Schupp, 1988a, b; Schupp and Frost, 1989, 1990; Forget and Milleron, 1991; Burkey, 1993; Forget, 1997; Russell and Schupp, 1998; Sánchez-Cordero and Martínez-Gallardo, 1998). The current rates of defaunation and habitat fragmentation are affecting drastically the interactions between animals and plants in the tropical forests (Wright et al., 2000; Silva and Tabarelli, 2000; Galetti, 2001; Galetti et al., 2003). For instance, the Brazilian Atlantic forest (Mata Atlântica) is considered as one of the most threatened ecosystems in the world (SOS Mata Atlântica and INPE, 1992; Viana and Tabanez, 1996; Viana et al., 1997; Conservation-International, 2000; Myers et al., 2000). Before European settlement in the 16th century, the Brazilian Atlantic coastal forest covered 1.0–1.5 million km^2, representing 12% of Brazilian territory. After 500 years of colonisation 95% of these forests have been logged and fragmented, and are now reduced to about 5% of their original size (SOS Mata Atlântica and INPE, 1992, 1993).

The objective of our study was to experimentally test two main hypotheses concerning seed predation and forest fragmentation. (1) If the abundance of rodents is lower in small forest fragments because of the action of meso-predators, such as opossums (Fonseca and Robinson, 1990), we expect lower seed predation in the small patch than in the larger one. (2) If small fragments are usually occupied by species that are diet and habitat generalists (Fonseca and Robinson, 1990; Stevens and Husband, 1998), we expect similar seed predation among the different microhabitats (gaps, understory and forest edge) in the small forest fragment but not in the large fragment.

2. Material and methods

For the experiments, we used two semi-deciduous forest fragments in São Paulo State, southeast Brazil. The smaller fragment, Mata São José (47°28′W, 22°25′S), is 230 ha in area and has dense vegetation with a canopy varying between 10 and 25 m in different places, with extensive vine tangles and treefall gaps in some parts (Pagano, 1987). The frugivore community is drastically reduced due to human pressure. Mammals such as collared (*Tayassu tajacu*) and white-lipped peccaries (*Pecari tajacu*), tapirs (*Tapirus terrestis*), and agoutis (*Dasyprocta azarae*) are extinct in the area. The major frugivores in this fragment are brown capuchin monkeys (*Cebus apella*), marmosets (*Callithrix aurita*), titi monkeys (*Callicebus personatus*), and squirrels (*Sciurus ingrami*) (São Bernardo and Galetti, unpublished).

The larger fragment, Estação Ecológica dos Catetus (49°40′–49°43′W and 22°22′–22°27′S) is a 2200 ha fragment, is situated in a deforested area with small forest patches (1–5 ha), surrounded by rubber, coffee and pasture fields (Viana and Tabanez, 1996). The E.E. dos Caetetus represents one of the most largest native forest fragments of the area, being a significant refuge for many animal species (Cullen, 1997; Cullen et al., 2000).

Except for the disturbed edge, where the forest has a broken canopy and an undergowth rich in lianas and *Merostachys* bamboos, the LF-EEC is composed of young mature forest and older undisturbed forest averaging 30–40 m in height (Cullen, 1997). The LF-EEC still contains most of its original mammalian fauna, including tapirs (*Tapirus terrestris*), collared (*P. tajacu*) and white-lipped peccaries (*T. tajacu*), and capuchin monkeys (*C. apella*) (Cullen et al., 2000). Large predators such as jaguar (*Panthera onca*) are lacking, however. Agoutis (*D. azarae*) are surprisingly rare, probably due to a local disease that exterminated most of the population (Cullen, 1997).

Experiments were conducted with the two most common palm species in semi-deciduous forests: the “jerivá”, *Syagrus romanzoffiana* (seed mass 1.62 ± 0.3 g, $n = 50$) and the “palmito”, *Euterpe edulis* (seed mass 0.54 ± 0.1 g, $n = 50$). These species are consumed and dispersed by a large assemblage of vertebrates, including guans, toucans, monkeys, foxes, and tapirs (Galetti et al., 1992; Paschoal and Galetti, 1995; Galetti et al., 1999), and are considered keystone species by some authors (Terborgh, 1986; Peres, 1994; Passos, 1998; but see Galetti and Aleixo, 1998).

Endocarps (one seed each) were removed from ripe fruits collected from infructesences, cleaned of pulp, and placed on the forest floor, mimicking seeds dispersed by animals. Experiments were carried out during the peak fruiting season of each palm species. Seeds of *E. edulis* were set out in the dry season (May–July 1999), whereas *S. romanzoffiana* were set out in the wet season (August–November 1999). This procedure avoided possible temporal differences as for each species the experiments were conducted at the same time in the two fragments (Hurlbert, 1984). In each fragment, we sampled three microhabitats: gaps, forest edge and understory.

As the effect of seed density can vary with habitat, microhabitat, co-occuring types of seeds, season, species and type of predator (Willson and Whelan, 1990), the numbers of seeds used were based on the numbers normally found dispersed together in the environment. Six seeds from *E. edulis* (M.A. Pizo, pers. comm.) and 15 from *S. romanzoffiana*, the number of seeds of this species typically found in tapir faeces (Galetti et al., 2001) were placed in 10 plots per microhabitat in the smaller fragment and 20 in the large one. The propor-

Table 1
Nominal logistic tests showing the effects of site, microhabitat (gap, forest edge and understory) and the interaction between them on seed predation for each palm species

Species	Source	Nparm	DF	Wald χ^2	$P > \chi^2$
E. edulis	Site	1	1	0.6087	0.4352
	Microhabitat	2	2	18.9385	0.0001
	Site × microhabitat	2	1.779	3.6279	0.1630
S. romanzoffiana	Site	1	1	151.0662	<0.0001
	Microhabitat	2	2	47.78471	<0.0001
	Site × microhabitat	2	2	81.19687	<0.0001

tion of seeds removed was checked after 40 days, minimising the effects of moonlight on activity of small mammals (Longland and Price, 1991; Bowers and Dooley, 1993).

In both fragments, edge effects can reach up to 50 m, but we concentrated our “edge” plots less than 10 m from the dirt road that surrounds each reserve. Both forest fragments had edges much more than 50 years old, time enough for the effects of fragmentation to have become pronounced and stable (Kammesheidt et al., 2001). The two forest remnants have a similar Shape Index (*sensu* Patton, 1975; modified by Laurance, 1991; Laurance and Yensen, 1991), the large fragment SI = 2.1 and the small fragment SI = 2.4 (Fleury and Galetti, unpublished data). A SIs value ranges from 1, for a circular area to 8 for very irregular area, and is obtained from perimeter (P) and total area (TA):

$$SI = P/200[(\pi\ \ TA)^{0.5}]$$

Understory plots were located at least 100 m from the edge, and >50 m from any gaps. In both forest fragments, we found a low density of large gaps, and our “gap” plots were set up in gaps bigger than 20 m^2.

To evaluate seed fate, we glued to each seed of *E. edulis* a thin nylon thread 25 cm with a pink flag attached to the end (see Forget, 1990; Forget and Milleron, 1991). We did not follow this procedure with *S. romanzoffiana* because we found no secondary seed dispersal as a consequence of the low abundance of agoutis (*D. azarae*) on large fragment (Cullen et al., 2000) and their absence on the small forest fragment (C. São Bernardo and M. Galetti, unpublished). Agoutis were identified as seed dispersers/predators by some authors (Silva and Tabarelli, 2001; Melo and Tabarelli, 2003; Silvius and Fragoso, 2003). Along with seeds found destroyed by vertebrates (as peccaries and rodents), we considered seeds that we were unable to locate as having suffered predation (Schupp and Frost, 1989; Cintra, 1998; Hulme, 1998).

The proportions of seeds removed were analysed by likelihood χ^2 (G)-tests with the main effects of microhabitat, forest fragment, and species. A nominal logistic test was used to detect differences among microhabitats and between sites for each species (Zar, 1996).

3. Results and discussion

Our results did not support the hypothesis that seed predation is lower in small fragments. Seed predation on *E. edulis* did not differ between fragments (Table 1, nominal logistic test, $\chi^2 = 0.6087$, $P = 0.4352$), and although predation of *S. romanzoffiana* did differ between forest fragments ($\chi^2 = 151.0662$; $P < 0.0001$), it was the larger fragment that had lower predation (Fig. 1). The difference between the forest fragments was mainly due to contradictory effects of forest edges on seed predation of *S. romanzoffiana* ($\chi^2 = 227.959$; $P < 0.0001$) (Fig. 1, Table 2).

When we compared microhabitats, regardless of site, the forest edge had the lowest rate of *E. edulis* seed predation (2.38%; $\chi^2 = 1623$; $P < 0.0001$), differing from understory (8.73%) and from gap (9.52%) microhabitats. In the large fragment, the rate of seed predation was different between understory and forest edge for both species (*E. edulis,* $P < 0.0001$ and *S. romanzoffiana,* $P < 0.0001$), where fewer seeds were removed from the anthropogenic edge than from the forest microhabitats (gaps and understory).

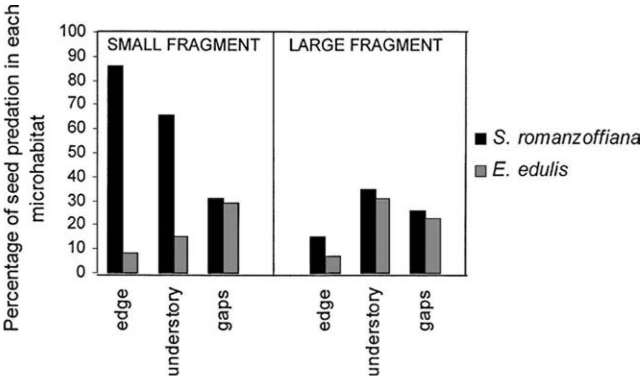

Fig. 1. Percentage of seed predation for two palm species (*S. romanzoffiana* and *E. edulis*) in three microhabitats, forest edge, understory and gap, in the two forest fragments.

Table 2
Seed predation on *E. edulis* and *S. romanzoffiana* in three microhabitats in two forest fragments of different sizes

	Small fragment (230 ha)			Large fragment (2200 ha)		
	Gap (%)	Understory (%)	Edge (%)	Gap (%)	Understory (%)	Edge (%)
E. edulis	29	15	8	23	31	7
S. romanzoffiana	31	66	86	26	35	15

In the large fragment, we found the same pattern of seed predation for both species, but in the small fragment microhabitat effects differed between species (Fig. 1). Seed predation rate in the small fragment, regardless of species, was lower in gaps (10.27%), than in forest edge (22.39%, $P = 0.001$) and understory (17.85%, $P = 0.032$). We found no differences among microhabitats for *E. edulis* in the smaller forest fragment ($\chi^2 = 7.566$, $P = 0.30$).

Palm nuts, such as those of *E. edulis* and *S. romanzoffiana*, suffer from intense seed predation in tropical forests, especially by rodents and peccaries (Forget, 1996). In the large fragment, high seed predation rates in gaps and understory for both palms may be related to the high abundance of peccaries in the area (Cullen et al., 2000). This forest fragment still sustains around 15 herds of collared peccaries and one herd of white-lipped peccaries, and their foraging activity is not restricted to a single microhabitat (A. Keroughlian, pers. comm.). In areas highly used by peccaries (close to swampy areas), 91.7% of the seeds were evidently destroyed, regardless of the microhabitat where they were exposed (gap or understory).

We also found no support for our second hypothesis according to which seed predation should be similar among microhabitats in small forest fragment. In the small fragment while *E. edulis* lowest seed predation were observed at the edge and higher seed predation in gaps, *S. romanzoffiana* showed the opposite pattern, with lowest seed predation rates found in gaps and higher seed predation at the edge. A possible reason for higher *S. romanzoffiana* seed predation in edge and understory in the small fragment is the high abundance of squirrels (*S. ingrami*). Squirrels are the main seed predator of *S. romanzoffiana* in semi-deciduous forest and they rarely forage in large gaps (Galetti et al., 1992; Paschoal and Galetti, 1995; Bordignon et al., 1996; Olmos et al., 1999). In the small fragment the abundance of squirrels was remarkably high (3.47 squirrels per 10 km transect, São Bernardo and Galetti, unpublished) while in the large fragment their abundance reached only 0.7 squirrels per 10 km transect (Cullen et al., 2000). In the small fragment we found no statistically significant difference in seed predation of *E. edulis* among microhabitats, probably because the edge effect somehow affected the entire fragment.

In the large fragment the patterns of seed predation between the palm species were similar among microhabitats, with lowest seed predation rates at the edge and similar seed predation rates between forest microhabitats (gaps and understory), but the same did not occur in the small fragment. Our results show that the edge effect on seed predation may be distinct in each area and will depend on the plant species analysed and their response to consequences of forest fragmentation (see also Burkey, 1993; Restrepo and Vargas, 1999; Kammesheidt et al., 2001; Terborgh et al., 2001).

4. Conclusion

Although this study is limited by the absence of replication; we do not know any study that tested gaps, undestory and forest edges at Atlantic Forest. Certainly experiments on seed predation in forest fragments should use more replicates (fragments), but we point out that it is likely that seed predation in each fragment will behave differently depending on the species, the mammal communities, and thereby in turn on the matrix surrounding each fragment.

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