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Forest fragment size and microhabitat effects on palm seed predation

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ABSTRACT

The establishment of plant species depends crucially on where the seeds are deposited. However, since most studies have been conducted in continuous forests, not much is known about the effects of forest fragmentation on the maintenance of abiotic and biotic characteristics in microhabitats and their effects on seed survival. In this study, we evaluated the effects of forest fragmentation on the predation upon the seeds of the palm *Syagrus romanzoffiana* in three microhabitats (interior forest, forest edge and gaps) in eight fragments of semi-deciduous Atlantic forest ranging in size from 9.5 ha to 33,845 ha in southeastern Brazil. Specifically, we examined the influence of the microhabitat structure, fauna and fragment size on the pattern of seed predation. Fragments <100 ha showed similar abiotic and biotic characteristics to those of the forest edge, with no seed predation in these areas. Forest fragments 230–380 ha in size did not present “safe sites” for *S. romanzoffiana* seed survival and showed high seed predation intensity in all microhabitats evaluated. In fragments larger than 1000 ha, the seed predation was lower, with abiotic and biotic differences among gaps, interior forests and forest edges. In these fragments, the survival of *S. romanzoffiana* seeds was related to squirrel abundance and interior forest maintenance. Based on these results, we concluded that there are no safe sites for *S. romanzoffiana* seed establishment in medium- and small-sized fragments as result of the biotic and abiotic pressure, respectively. We suggest that on these forest fragments, management plans are needed for the establishment of *S. romanzoffiana*, such as interior forest improvement and development in small-sized sites in order to minimize the edge effects, and on medium-sized fragments, we suggest post-dispersal seed protection in order to avoid seed predation by vertebrates. Our findings also stress the importance of assessing the influence of forest fragmentation on angiosperm reproductive biology as part of the effective planning for the management of fragmented areas.

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1. Introduction

Most fragmented systems do not support the same species diversity as the original ecosystems due to the edge effects

(Lovejoy et al., 1986; Burkey, 1993; Carvalho and Vasconcelos, 1999; Chiarello, 1999; Lynam and Billick, 1999; Mesquita et al., 1999; Sizer and Tanner, 1999; Tabarelli et al., 1999). The transition between forest fragments and the adjacent ecosystem

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is frequently very abrupt and creates an edge that exposes the forest to atypical conditions and converts this area into an ecotone zone that suffers microclimatic changes (Williams-Linera, 1990; Young and Mitchell, 1994; Jose et al., 1996; Turton and Freidburger, 1997; Baldi, 1999). These changes include alterations in the vegetation composition and structure (Laurance and Yensen, 1991; Laurance, 1994, 1997; Brand and George, 2000; Laurance et al., 2000; King and DeGraaf, 2002; Laurance et al., 2002; Moruzzi et al., 2002). Changes in the forest structure may drastically affect phenomena such as pollination, seed predation, and the territorial behavior and feeding habits of various animal species (Lovejoy et al., 1986; Janzen, 1988; Laurance and Yensen, 1991; Myster and Pickett, 1993; Aizen and Feinsinger, 1994a,b; Laurance, 1994; McCollin, 1998; Cadenasso and Pickett, 2000; Laurance et al., 2002), in addition to causing a loss of plant and animal diversity and, in extreme cases, total defaunation (Terborgh, 1988; Brown and Heske, 1990; Redford, 1992).

The size of a forest fragment has a strong influence on ecological processes, mainly through the changes caused by the edge formation (Collinge, 1996). The intensity of the edge effect is inversely proportional to the size of the fragment (Ranta et al., 1998) since fragmentation increases the forest perimeter/surface area ratio and the permeability to conditions imposed by peripheral ecosystems (Laurance, 1991; Laurance and Yensen, 1991; Hill and Curran, 2001; Estrada and Coates-Estrada, 2002). Hence, in small fragments in which a larger proportion of the environment is modified, plants and animals that depend exclusively on the interior forest lose their habitats as the edge expands into the interior of the remnant (Yahner, 1988; Fonseca and Robinson, 1990; Laurance, 1994; Stevens and Husband, 1998; Terborgh et al., 2001).

Microhabitats present abiotic and biotic conditions that ensure the survival of animals, seeds and seedlings (Schupp, 1988a,b; Schupp and Frost, 1989; Burkey, 1993; Schupp, 1993; Laurance, 1994; Malcolm, 1994; Schupp and Fuentes, 1995; Cintra, 1997; Cintra and Horna, 1997; Russell and Schupp, 1998; Benítez-Malvido and García-Guzmán, 1999). Laurance (1994) and Malcolm (1994) suggested that seed predation at the forest edge could be intense due to the high density of small rodents in this microhabitat. However, Burkey (1993) reported a decrease on seed predation by rodents towards the forest edge. Gaps in continuous forest were pointed out as an unsafe site for seed survival, with high seed predation by terrestrial small- and medium-sized seed predators, such as pacas and mice, that use gaps as a shelter against their natural predators (Auspurger, 1983, 1984; Schupp, 1988a; Schupp and Frost, 1989; Schupp et al., 1989; Cintra, 1997; Cintra and Horna, 1997).

Some authors showed that the edge formation increases the frequency of gaps formed by trees that have been felled by high intensity winds, being greater on forest fragments than in continuous forest (Malcolm, 1994; Ferreira and Laurance, 1997; Laurance et al., 2000; Laurance, 2002). The higher frequency of gaps on fragmented habitats changes the structure of microhabitats, impacting mammal communities with consequences on seed predation. Most studies that have examined the effect of microhabitat on seed predation have not considered the influence of forest area and/or defaunation on this process (Smythe, 1986; Schupp, 1988a,b; Smythe,

1989; Forget and Milleron, 1991; Tellería et al., 1991; Schupp and Fuentes, 1995; Cintra and Horna, 1997; Sanchez-Cordero and Martínez-Gallardo, 1998 but see Tellería et al., 1991; Santos and Tellería, 1994; Santos et al., 1999; Wright et al., 2000; Wright and Duber, 2001). In view of this, we examined the effect of forest fragmentation on the seed predation of palm tree (*Syagrus romanzoffiana*) in eight fragments of semi-deciduous Atlantic forest. Specifically, we assessed the influence of interior forest, gaps, forest edge and fauna on seed survival. This is the first study to establish a relationship between post-dispersal seed predation and attributes such as fragmentation, microhabitat type, defaunation and structural characteristics in tropical rainforests.

2. Materials and methods

2.1. Study areas

In this study, we evaluated the post-dispersal seed predation of “queen palm”, *S. romanzoffiana* (Cham.) Glassman (Arecaceae), in eight fairly well studied fragments of semi-deciduous Atlantic forest on the inland Atlantic Plateau in the State of São Paulo, southeastern Brazil (Fig. 1 and Table 1). The forest fragments ranged in size from 9.5 ha to 33,845 ha and presented a humid and temperate climate characterized by a pronounced dry season (Koeppen, 1948) with the mean annual precipitation ranging from 1200 to 1600 mm (Table 2). The large-sized fragments, larger than 1000 ha in area, still support high mammal diversity, as large herbivores and top predators, once these animals are extinct in medium (200–400 ha) and small-sized sites (<20 ha) (Table 3). All forest fragments presented edges much older than 50 years, time enough for the effects of fragmentation to have become pronounced and stable (Kammesheidt et al., 2002).

2.2. Seed predation

The experiments were conducted with *S. romanzoffiana*, a shade-tolerant palm tree species, with large and recalcitrant seeds (seed mass 1.62 ± 0.3 g, $n = 50$), because this species (i) is the most common palm species in the semi-deciduous Atlantic forests, (ii) produces large quantities of sugar-rich fruits, (iii) produce fruits throughout most of the year and (iv) their fruits are consumed and dispersed by a large variety of vertebrates (Galetti et al., 1992; Paschoal and Galetti, 1995; Galetti et al., 2001; Fleury and Galetti, 2004) and play a key role for ungulates in semi-deciduous forests (Keuroghlian et al., 2004; Passos, 1999).

Endocarps (one seed each) were removed from ripe fruits collected from infructescences, cleaned of pulp and placed gathered on the forest ground in order to mimic seeds dispersed by animals. To facilitate subsequent location of the site and to measure the microhabitat target variables described below, we marked the center of each plot with a 20 cm long stake to which a pink ribbon was fastened (Fleury and Galetti, 2004). To evaluate seed fate, we marked one seed per plot with a plastic reel with 10 m of high resistance cotton thread that was glued to the seed by a wire ring 1 mm thick. Additionally, we analyzed marks on predated seeds or sign on site that could indicate us the presence of *S. romanzoffiana*

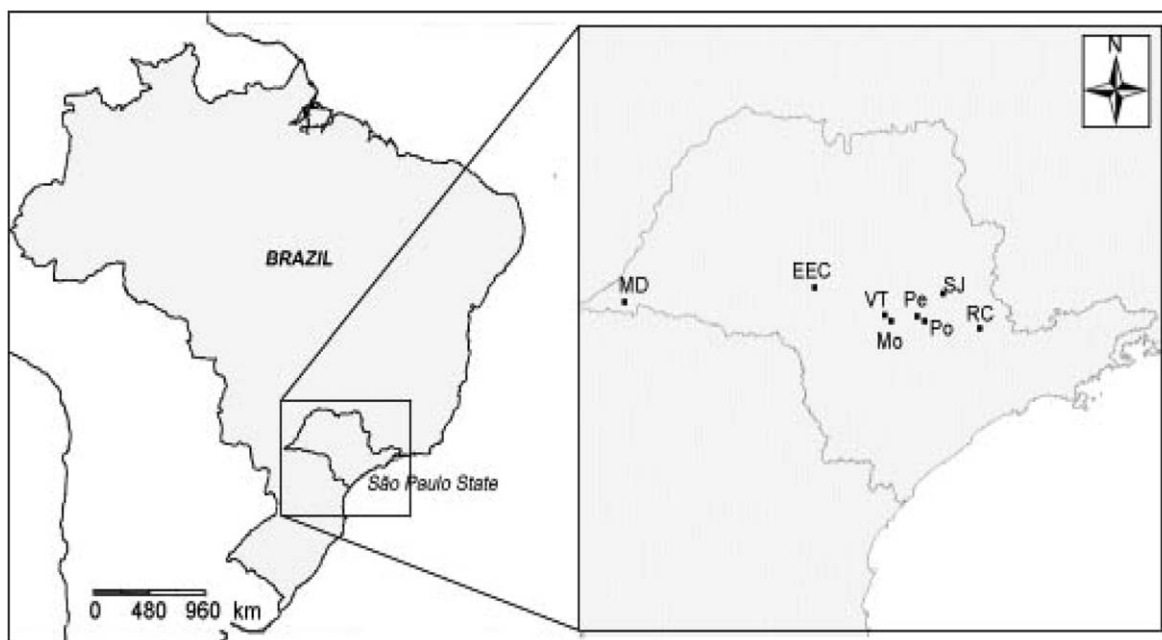


Fig. 1 – Location of the eight fragments of semi-deciduous Atlantic forest studied in southeastern Brazil. See Table 1 and corresponding legend for fragment areas and definition of abbreviations.

Table 1 – Shape index (SI), surrounding habitats and the references of the semi-deciduous Atlantic forest fragments: MD – Parque Estadual do Morro do Diabo, EEC – Estação Ecológica dos Caetetus, VT – Mata do Viveiro Tabatingüera, Mo – Mata do Monal, SJ – Mata São José, RC – Mata do Ribeirão Cacheira, Pe – Mata da Pedreira and Po – Mata do Pomar				
Site	Area (ha)	Shape index (SI)	Surrounding habitats	Authors
MD	33,845	2.529	Pasture for cattle	Valladares-Pádua (1987), Schlitter et al. (1995), Cullen Jr. (1997) and Cullen Jr. et al. (2001)
EEC	2178	2.12	Coffee and rubber plantations and pasture for cattle	Willis and Oniki (1991), Cullen Jr. (1997) and Olmos et al. (1999)
VT	1471	2.896	Pasture for cattle and sugarcane fields	Cullen Jr. (1997)
Mo	374	2.384	Pasture for cattle and sugarcane fields	Assumpção et al. (1982), Cesar and Leitão Filho (1990), Magalhães (1999) and Martins (2003)
SJ	230	2.403	Sugarcane fields and rubber plantation	Pagano (1987), Manzatto (2001), Bernardo (2001) and Bernardo and Galetti (2004)
RC	208	1.409	Urban area, crop fields, reforestation and natural fragments	Gaspar (1997, 2005)
Pe	13	2.63	Urban area, <i>Pinus</i> spp. and <i>Eucalyptus</i> spp. plantation and pasture for cattle	Nascimento (1998) and Gheler-Costa (2002)
Po	9.5	1.48	Orchard and urban area	Catharino (1989), Tabanez et al. (1997), Nascimento (1998) and Gheler-Costa (2002)

seed predator. Surgical gloves were worn during handling of the fruit and seeds in order to avoid contamination of the seeds with human scent (Duncan et al., 2002). Experiments were carried out during dry season (June–September 2001), peak fruiting of *S. romanzoffiana* that corresponds to the period of limited food resources in semi-deciduous Atlantic forest, in all eight forest fragments in order to avoid possible temporal differences (Hurlbert, 1984). We associated trampling of seedlings, overturned leaf-litter and exposed roots with teeth marks with peccaries (*Pecari tajacu* and/or *Tayassu pecari*, Kerouglhian, A., personal communication) seed predation, and

bitted seeds in a triangular format with squirrels seed predation (Bordignon et al., 1996). Since the experiments were carried out during the dry season, and since the only resource available was endosperm, destroyed and unallocated seeds were both scored as having suffered predation (Schupp and Frost, 1989; Cintra, 1998; Hulme, 1998).

In each fragment, three microhabitats were sampled: gaps, forest edges and the interior forest. As the effect of seed density may vary with habitat, microhabitat, concurrent seed types, season, species and type of predator (Willson and Whelan, 1990), we used 10 seeds per plot (15 cm × 15 cm), a

Table 2 – General characteristics of the studied semi-deciduous Atlantic forest fragments

MD (33,845 ha) 52°17'W and 22°27'S Dense vegetation with canopy varying between 20 m and 40 m Mean annual precipitation – 1200 mm Is the largest and best protected remnant semideciduous Atlantic forest of São Paulo State
EEC (2178 ha) 49°42'W and 22°24'S Mean annual precipitation – 1260 mm Except for the disturbed edge, the forest fragment is composed of mature forest, averaging 20–30 m in canopy height, and old undisturbed forest, averaging 30–40 m in canopy height
VT (1471 ha) 48°08'W and 22°41'S Mean annual precipitation – 1240 mm Dense vegetation with canopy varying between 10 m and 35 m Three distinct sites (floristic and fitossociology aspects), established by edaphically conditions Large extension of the forest fragment shows disturbs signs, as scarce emerging big trees and opened areas
Mo (374 ha) 48°11'W and 22°40'S Mean annual precipitation – 1240 mm Canopy varying between 10 m and 20 m Hardly logged, extensive vine tangles and low abundance of large trees in some parts
SJ (230 ha) 47°28'W and 22°25'S Mean annual precipitation – 1600 mm Dense vegetation with a canopy varying between 10 and 30 m Extensive vine tangles and tree fall gaps in some parts
RC (208 ha) 46°55'W and 22°50'S Mean annual precipitation – 1409 mm Dense vegetation, averaging 15–25 m in canopy height
Pe (13 ha) 47°49'W and 22°47'S Mean annual precipitation – 1430 mm Presents broken and sparse canopy in most extension of forest fragment. Largest part of forest fragment is composed by great tree fall gaps, with few individuals reaching 20 m
Po (9.5 ha) 47°37'W and 22°42'S Mean annual precipitation – 1430 mm Logged and burned fragment, being the last fire registered 20 years ago with 20–30% of the total forest area burned. Broken canopy, reaching 20 m

number based on the quantity normally found dispersed together in the environment by carnivores and ungulates in the wild (Galetti et al., 2001). Due to differences in the total areas of the forest fragments and to avoid pseudo-replication (Hurlbert, 1984), we used the experimental design with different number of repetitions per treatment for each area studied. We placed 30 plots per microhabitat in the largest fragment (MD – 33,845 ha), 15 plots per microhabitat in the fragments with areas from 200 to 3000 ha (EEC – 2178 ha, VT – 1471 ha, Mo – 374 ha, SJ – 230 ha and RC – 208 ha) and five plots per microhabitat in fragments Po (9.5 ha) and Pe (13 ha).

Although the edge effects may reach up to 60 m into Atlantic forest fragments (Stevens and Husband, 1998), we concentrated our “edge” plots less than 5 m from the dirt road that surrounds each reserve. Forest interior and gap plots were located at least 100 m from the edge. The gaps and interior forest plots were arranged 50 m from each other, being established gap plots when openings in the can-

opy are observed, whereas interior forest plots were set up when the canopy was closed. Since the density of large gaps was low in most fragments studied, we considered “gap” as sites or clearings that presented a canopy opening greater than 20 m². The proportion of seeds removed was checked after 30 days and it was verified that this period was sufficient to allow *S. romanzoffiana* seed predation in semi-deciduous Atlantic forest (Fleury and Galetti, 2004) and to minimize the effect of moonlight on the activity of small mammals (Longland and Price, 1991; Bowers and Dooley Jr., 1993).

2.3. Site characteristics

In order to determine the effect of fragment size and microhabitat structure on seed predation, we surveyed a range of attributes at each site that could potentially influence the access of predators to the experimental sites and that would

Table 3 – Mammals that use the fruits *Syagrus romanzoffiana* and their predators in the studied forest fragments in south-east Brazil

Species/site	MD (33,845 ha)	EEC (2178 ha)	VT (1471 ha)	Mo (374 ha)	SJ (230 ha)	RC (208 ha)	Pe (13 ha)	Po (9.5 ha)
Didelphimorphia								
<i>Didelphis albiventris</i>	x	x	x	x	x	x	x	x
Primates								
<i>Callithrix jacchus</i> ^a						x	x	x
<i>Cebus nigritus</i>	x	x	x		x	x		
<i>Alouatta guariba</i>	x	x	x	x				
<i>Leontopithecus chrysopygus</i>	x	x						
Carnivora								
<i>Cerdocyon thous</i>	x	x	x	x	x	x		
<i>Procyon cancrivorus</i>	x	x						
<i>Nasua nasua</i>	x	x	x		x		x	x
<i>Eira barbara</i>	x	x	x					
<i>Panthera onca</i>	x							
<i>Puma concolor</i>	x	x	x			x		
<i>Herpailurus yagouondi</i>	x	x	x		x	x		
<i>Leopardus pardalis</i>	x	x						
<i>Leopardus weidi</i>	x	x						
<i>Leopardus tigrinus</i>	x	x	x					
Perissodactyla								
<i>Tapirus terrestris</i>	x	x						
Artiodactyla								
<i>Pecari tajacu</i>	x	x	x					
<i>Tayassu pecari</i>	x	x						
<i>Mazama americana</i>	x	x	x	x	x			
Rodentia								
<i>Sciurus ingrami</i>	x	x	x	x	x	x		
<i>Coendou prehensilis</i>	x	x	x	x	x		x	x
<i>Agouti paca</i>	x	x	x					
<i>Dasyprocta azarae</i>	x							

a Introduced species.

qualify the environment as suitable for small- and medium-sized rodents, which are the main predators of *S. romanzoffiana* seeds (Galetti et al., 1992; Paschoal and Galetti, 1995; Fleury and Galetti, 2004). All experimental plots in each fragment were scored for 12 target variables adapted from Jordano and Schupp (2000) (Table 4), and were measured by the same observer in order to minimize errors at the end of seed predation experiment (30th day).

For further site characterization, for each evaluated forest fragment we assessed mammal richness, considering all mammals that interact directly and indirectly with *S. romanzoffiana* based on the available literature or unpublished data (Table 1), and then ranked squirrel abundance on a scale from 0 to 3 in., where 0 corresponds to total absence, 1 to low, 2 to medium and 3 to high abundance of squirrel. Additionally we measured small- and medium-sized rodent predators. These variables were assessed once squirrels are described as an important predators of *S. romanzoffiana* seeds (Galetti et al., 1992), whereas mammal richness were included because they feed directly on fruits or seeds, e.g. peccaries (*Pecari tajacu* and *Tayassu pecari*, Forget, 1996), or influence the communities of small- and medium-sized rodents, e.g. carnivores (Fonseca and Robinson, 1990).

To assess the influence of forest fragment shape on seed predation, we determined the perimeter-length and total area of the fragments using images provided by the satellite Landsat 7 (for the 33,845 ha, 2178 ha, 1471 ha, 374 ha and 230 ha fragments) and aerial photographs (for the 208 ha, 13 ha and 9.5 ha fragments; Idrisi for Windows, version 2.0) and then calculated the SI (Shape Index sensu Patton, 1975, modified by Laurance, 1991; Laurance and Yensen, 1991). The SI is obtained dividing the perimeter-length fragment by that of an equal-sized circle, varying from 1.0 for a perfect circular area to 8 or higher for very irregular shape fragments. The SI is calculated as $SI = P/200[(\pi TA)^{0.5}]$, where P is the perimeter-length and TA is the fragment total area.

2.4. Data analysis

Before performing the analysis of data, we coded the binomial absence and the presence of target variables as 0 (zero) and 1 (one), respectively (Table 4), and we converted the distances between the flag of each plot and the nearest woody vegetation into six class intervals (1 = 0–0.1 m, 2 = 0.1–0.2 m, 3 = 0.2–0.3 m, 4 = 0.3–0.4 m, 5 = 0.4–0.5 m, 6 = >0.5 m) for the three height intervals (0–0.5 m, 0.5–1 m and >1 m), once we

Table 4 – List of structural variables surveyed on the eight fragments of semi-deciduous Atlantic forest studied in southeastern Brazil

Target variable and units	Methodology	Quadrat radius (m)
<i>Syagrus romanzoffiana</i> (binomial, 0–1)	Absence/presence of the studied palm species	5
Fruits (binomial, 0–1)	Absence/presence of flesh fruits that could attract animals to the plots	5
Woody debris (binomial, 0–1)	Absence/presence of dead wood >30 cm diameter. Open microhabitats and treefall logs are normally related with seed loss to rodents, presumably because seed predators forage where they cannot find their natural predators (Herrera, 1984; Schupp, 1988a)	5
Woody lianas (binomial, 0–1)	Absence/presence of woody lianas, described as an important connection between soil and canopies for arboricoles animals (Lurz et al., 1997)	5
Herbaceous liana (binomial, 0–1)	Absence/presence of herbaceous lianas, associated with perturbed environment (Schnitzer and Bongers, 2002) and connection between soil and canopies for arboricoles animals (Lurz et al., 1997)	5
Vegetation cover (%)	Visual estimation of projective cover of vegetation, assessed in three height classes (0–0.5 m, 0.5–1 m and >1 m)	0.5
Distance between plant and the experimental plot (index, 0–5)	Distance between the central plot and nearest plant = B3 1 cm diameter, that could represent a connection between canopy and soil, or woody debris as a shelter for small rodents. Assessed in three height classes (0–0.5 m, 0.5–1 m and >1 m)	0.5

considered as very opened areas with distances longer than 0.5, as previously established.

The proportions of seed predation were analyzed by likelihood χ^2 (G)-tests with the main effects of microhabitat and forest fragment. A nominal logistic test was used in order to detect differences on seed predation among microhabitats and sites (Zar, 1998), and G-test to identify which target variables were significant to proceed the multivariate analysis (SAS Institute, 2002).

To evaluate the structure of the microhabitats, we used the mode for binomial and categorical variables and the arithmetic mean for continuous data, being obtained for each microhabitat in each forest fragment. In order to avoid bias, we only used the structural variables and did not insert data with regard to seed predation, total area, SIs and animal presence/absence or abundance on non-metric multidimensional scaling (MDS) analysis. On the R Package (Casgrain and Legendre, 2001), the data was converted into χ^2 similarity coefficient (R-mode) and was transformed into distances (Q-mode) by $D_{ij} = (1 - S_{ij})^{0.5}$, where D_{ij} is the distance matrix and S_{ij} is the similarity matrix, and then we proceed the MDS (Legendre and Legendre, 1998).

The Shepard diagram validated the MDS (stress = 0.08), which evaluates the regression coefficient with the objective of establishing correspondence between distances and the proximities to measure the distortion (stress) between matrices (Legendre and Legendre, 1998). The coordinates (eigenvectors) calculated by the MDS were used to plot the

objects – microhabitat per forest fragment – in a dispersion diagram, and vectors of structural attributes associated with patterns in ordinations were displayed using a principal axis correlation (PCC) procedure (Fig. 2). For further interpretation, the Spearman rank correlation with MDS eigenvalues compared to site variables, *S. romanzoffiana* seed predation, mammal richness, rank of squirrel abundance and predators for each fragment, as well as the total areas and SIs values, permuted 10,000. Multivariate analyses were run on R-package (Casgrain and Legendre, 2001).

3. Results

3.1. Seed predation

The *S. romanzoffiana* seed predation was different among forest fragments (Nominal logistic model, $\chi^2 = 1129.58$, $p < 0.0001$) and between fragments and microhabitats ($\chi^2 = 194.78$, $p < 0.0001$). The highest seed predation was observed in medium-sized fragments (374 ha and 230 ha), and very low and absent seed predation was observed in large (33,845 ha) and small-sized forest fragments, respectively (13 ha and 9.5 ha), following an inverse U shape in relation to forest fragment size (Fig. 3 and Table 5). Considering the overall seed predation in the eight forest fragments, 96% of the predation was attributable to squirrels (*Sciurus ingrami*), 3% to peccaries (*Pecari tajacu* and/or *Tayassu pecari*) and 1% to small rodents. On the largest-sized forest fragments,

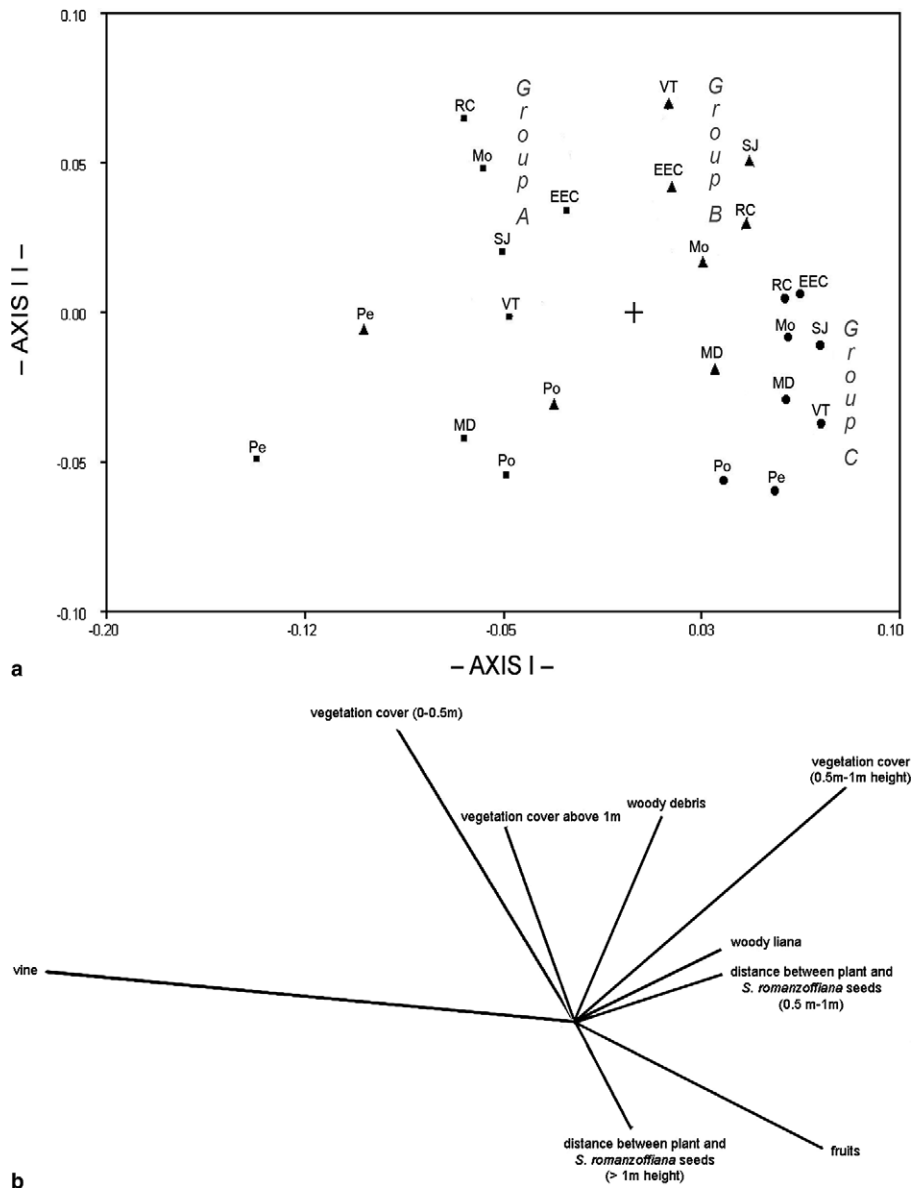


Fig. 2 – Multivariate analysis of microhabitats (■ – gaps, ▲ – forest edge and ● – forest interior) in the eight fragments of semi-deciduous Atlantic forest studied in southeastern Brazil. (a) Ordination of sites by 10 structural attributes and (b) PCC showing vectors of structural attributes significantly associated ($P < 0.05$) with patterns in each ordination. See Table 1 and corresponding legend for fragment areas and definition of abbreviations.

the main seed predators were peccaries (*Pecari tajacu* and *Tayassu pecari*). On this forest fragment, in some interior forest plots, the seeds and their marks were destroyed and expelled after mastication by peccaries. The predation of *S. romanzoffiana* seeds by small rodents was observed only at one plot of the forest edge in the 33,845 ha fragment. At medium-sized forest fragments, all removed seeds that were located showed characteristic marks of predation by squirrels.

3.2. Site characteristics

The target variables explained the seed predation pattern on microhabitats and forest fragment (Nominal logistic model, $\chi^2 = 1266.16$, $p < 0.0001$). None of the MDS inserted variables

presented correlation with MDS eigenvalues, being positively correlated with forest fragment area (Spearman's correlation; $r^2 = 0.8364$; $p = 0.0001$) and with the mammal richness in the area ($r^2 = 0.9157$; $p < 0.0001$). The scattergram of the MDS eigenvectors resulted in three groups that corresponded to the three microhabitats evaluated, namely, gaps (A), edges (B) and the interior forest (C), all of them were characteristic of fragments with an area >200 ha (Fig. 2). The 9.5 ha and 13 ha forest fragments microhabitats were not grouped and were distinguished from the other remnants by their discontinuous canopies, high frequencies of fallen trunks, herbaceous and woody lianas, and a low percentage of seedling cover (0–0.5 m of height). The forest edge of the 13 ha fragment differed considerably from the other microhabitats because it was essentially composed of vine and grass.

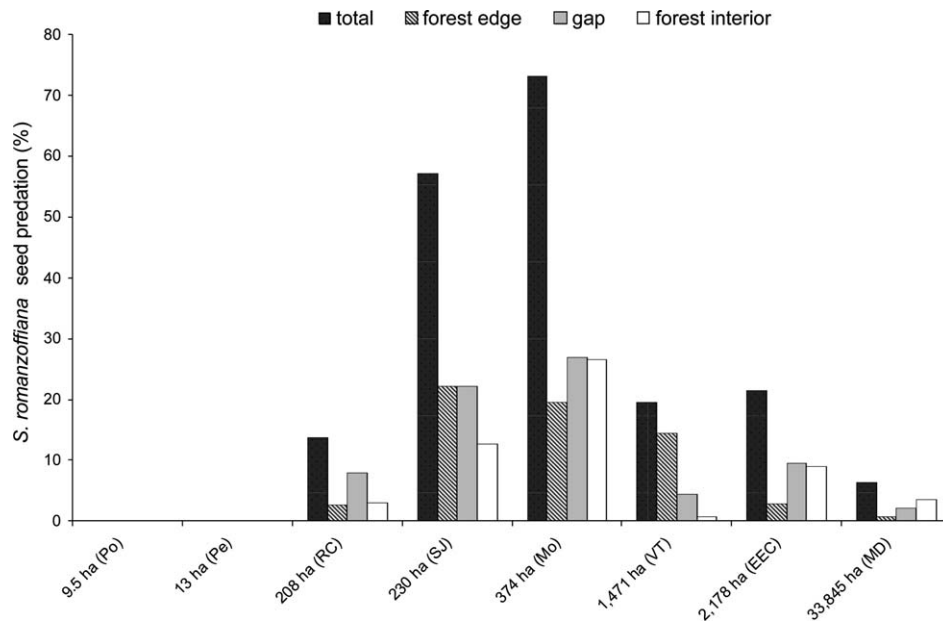


Fig. 3 – Total (black) and relative *S. romanzoffiana* seed predation in three microhabitats (forest edge – dark grey, gaps – light grey and forest interior – white) in the eight semi-deciduous Atlantic forest fragments, Brazil.

Table 5 – Total and relative seed predation on eight fragments of semi-deciduous Atlantic forest and in each microhabitat, respectively

Forest fragment	Seed predation (%)	Microhabitat	Relative seed predation	χ^2	P
MD (33,845 ha)	6.30	Forest edge	10.53	20.73	<0.0001
		Gaps	33.33		
		Forest interior	56.14		
EEC (2178 ha)	21.60	Forest edge	13.40	24.97	<0.0001
		Gaps	44.33		
		Forest interior	42.27		
VT (1471 ha)	19.56	Forest edge	73.86	92.28	<0.0001
		Gaps	22.73		
		Forest interior	3.41		
Mo (374 ha)	73.11	Forest edge	58.67	23.09	<0.0001
		Gaps	80.67		
		Forest interior	80.00		
SJ (230 ha)	57.11	Forest edge	38.91	33.57	<0.0001
		Gaps	38.91		
		Forest interior	22.18		
RC (208 ha)	13.78	Forest edge	19.35	18.81	<0.0001
		Gaps	58.06		
		Forest interior	22.58		
Pe (13 ha)	0.00	Forest edge	0.00	–	–
		Gaps	0.00		
		Forest interior	0.00		
Po (9.5 ha)	0.00	Forest edge	0.00	–	–
		Gaps	0.00		
		Forest interior	0.00		

Woody debris were frequent at sites where a high percentage of vegetation cover up to 0.5 m above the ground level was observed ($r^2 = 0.4263$; $p = 0.0167$), where there was a low percentage of vegetation cover >1 m above the ground ($r^2 = -0.4262$; $p = 0.0168$) and low densities of elements with

perimeter ≥ 1 cm above 0.5 m of height (in the interval of 0.5–1 m $r^2 = 0.4417$; $p = 0.0159$; above 1 m $r^2 = 0.6763$; $p = 0.0001$). These microhabitat characteristics defined the group A that corresponded to gaps (Fig. 2), locations of low squirrel abundance ($r^2 = -0.3883$; $p = 0.0424$) and conse-

quently low seed predation. Squirrel abundance was strongly related to the predation of *S. romanzoffiana* seeds ($r^2 = 0.7109$; $p = 0.0004$).

Group B (forest edges; Fig. 3) consisted of locations with high abundance of woody lianas resulting in shorter distances between plots and the plants for the interval of 0–0.5 m ($r^2 = -0.4684$; $p = 0.05$). Group B sites presented a low percentage of seedlings cover ($r^2 = -0.647$; $p = 0.0073$). The *S. romanzoffiana* seed predation was particularly high at locations of groups B and C and the forest interior grouping, determined by the presence of woody lianas ($r^2 = 0.27$; $p = 0.0351$) accomplished a connection between trees and soil. However, the group C was distinguished on dense vegetation cover between 0.5 m and 1 m above the ground level ($r^2 = 0.52$; $p = 0.006$; Fig. 3).

There was a positive correlation between the SIs values and the mammal richness ($r^2 = 0.7785$; $p = 0.023$), and between the SIs values and the fragment size ($r^2 = 0.8333$; $p = 0.0102$). Fragment size was also positively correlated with mammal richness ($r^2 = 0.9222$; $p = 0.0011$), but not with the rank of squirrel abundance ($r^2 = 0.2646$; $p = 0.5266$). However, the rank of squirrel abundance was related with mammal richness ($r^2 = -0.4598$; $p = 0.05$), but not with rodent predators ($r^2 = 0.2678$; $p = 0.5214$).

4. Discussion

4.1. Seed predation

No secondary dispersal was recorded at any of the sites studied and all located removed seeds were apparently destroyed, as also observed by Schupp and Frost (1989) with *Welfia georgii* in Costa Rica. In agreement with other studies (Galetti et al., 1992; Paschoal and Galetti, 1995; Bordignon et al., 1996; Olmos et al., 1999; Bordignon and Monteiro-Filho, 2000), squirrels (*Sciurus ingrami*) were the main *S. romanzoffiana* seed predators (96%) when compared to small rodents and peccaries (4%), indicating that this species could markedly influence the post-dispersal survival of *S. romanzoffiana* seeds in semi-deciduous Atlantic forest fragments. Small, non-squirrel rodents are also considered as important seed predators (Laurance, 1994; Malcolm, 1994), but their activity as *S. romanzoffiana* seed predator was only seen at the edge of the largest fragment. This finding may reflect the fact that the hard endocarp of *S. romanzoffiana* seeds is difficult to be open by small rodents and would require a very high-energy investment.

S. romanzoffiana seed survival was intimately related with squirrels distribution and abundance (Emmons and Gentry, 1983), which in turn was related to the fragment size and habitat structure. The presence of interior forest characteristics was the main factor influencing the abundance of squirrels and high mammal richness. Fragments with larger SI values supported a larger diversity of mammals, but the more irregular fragments corresponded to the larger areas. Thus, higher mammal richness is probably associated with large areas and not with more irregular fragment shapes, and this correlation could be a spurious one. The other possibility is that the elevated environmental diversity in fragments with more irregular forms leads to higher diversity levels, in agreement with the hypothesis of Leopold (1933).

In areas >1000 ha, the predation of *S. romanzoffiana* seeds varied among microhabitats, mainly because these larger fragments present greater heterogeneity, with different stages of succession throughout the forest. Since the animal community responds differently between these environments, seed predation also varied and reflected the heterogeneity of the microhabitats (Peña-Claros and deBoo, 2002). Forest fragments >1000 ha presented other *S. romanzoffiana* seed predators in addition to squirrels, including peccaries, pointed as important palm nut predators (Forget, 1996), and their foraging activity is not restricted to a specific microhabitat. Indeed, these animals hardly consume *S. romanzoffiana* seeds in the interior forest and in gaps when compared to forest edge (Forget, 1996; Fleury and Galetti, 2004). An unusual finding was the higher seed predation by squirrel at the 1471 ha forest edge, since seed predation was low in this microhabitat on forest fragments >1000 ha. In an assessment of spatial and temporal effects on the habitat quality of *Sciurus vulgaris*, Lurz et al. (1997) noted that in stable environments, such as fragments with large areas, squirrels are loyal to the habitat due to the seasonal lack of food. However, in the 1471 ha fragment, palm trees produce fruits only in the forest edge, and this could have attracted the squirrels to this environment (Otani, 2001).

The medium-sized forest fragments suffered high intensity of *S. romanzoffiana* seed predation by squirrels. Large- and medium-sized fragments presented a large number of small gaps, except for the largest fragment (33,845 ha), where gaps were formed by large trees fall that created great openings in the canopy. Bayne and Hobson (2000) reported that the essentially arboreal nature of squirrels meant that only large canopy openings were not suitable for these predators. At medium-sized fragments, sites with low seedling coverage, and high understorey and canopy coverage, generally characterized interior forest, although woody lianas were frequent in this microhabitat. In contrast, seed predation was more intense at locations where the access to seeds was easier, e.g., by lianas stretching from the tree canopies to the ground with seeds.

The 208 ha forest fragment suffered only a small amount of seed predation when compared with the other medium-sized fragments (230 ha and 374 ha). Structurally, the 208 ha fragment is similar to the other medium-sized fragments, but the fragment is inserted into a matrix with reforested and natural fragments, which is probably minimizing the fragmentation effects acting as source for the local fauna. Further, Danielson et al. (1997) found that urban remnants suffer lower seed removal than rural forest fragments and the 208 ha is located in a suburb of a big city, and the 230 ha and 374 ha are both surrounded by pastures and sugarcane fields.

No seed predation was recorded on small-sized (13 ha and 9.5 ha) fragments, as result of defaunation at these sites. Small forest fragments present larger perimeter and surface area ratio than continuous forest and are therefore more exposed to the edge effect (Turner, 1996; Turner et al., 1996; Hill and Curran, 2001; Estrada and Coates-Estrada, 2002). There were no clearly identifiable microhabitats in small-sized fragments due to the edge effect that extended throughout the fragments. This finding is in agreement with Pimm (1998),

who noted that fragments of the Amazonian forest with an area <36 ha were predominantly edge environment. At 9.5 ha and 13 ha fragments, a low seedling and juveniles establishment was observed, resulting in a low amount of vegetation coverage (Sizer and Tanner, 1999). Bruna (1999) reported that the germination in continuous forests was 3–7 times greater than in forest fragments, mainly because microclimatic alterations resulted in low recruitment in the fragments, and also due to the increased seed predation and litter accumulation under the edge effect. Bayne and Hobson (2000) compared 0.2–82 ha fragments with continuous forest (382,500 ha) and noted that squirrel density and vegetation cover were positively correlated, and that the 82 ha forest fragment presented a higher density of squirrels when compared with the extended area. The small size of the forest fragment made it unsuitable for most animals, including generalists as squirrels that are largely arboreal that require dense vegetation, which means a nuclear area (Carey et al., 1999). Another factor that could account for the lack of seed predation by squirrels in small forest fragments is that these animals mostly feed on nuts and fungi (Carey et al., 1999; Paschoal and Galetti, 1995).

As described here, as the area increased, the *S. romanzoffiana* seed predation also increased. However, in larger areas (e.g., 1471 ha fragment) the opposite was observed, with an accentuated decrease in the total seed predation. This situation may reflect the existence of a threshold size area between 374 ha and 1471 ha for optimal squirrel density and seed predation, caused by the absence of their natural predators (such as margays and ocelots), habitat and resource availability, resulting in a more abundant squirrel population, whereas in greater fragments (>1471 ha) the higher number of large carnivorous would keep the squirrel population low and result in small and heterogeneous seed predation. Moreover, at larger forest fragments *S. romanzoffiana* distribution are less aggregated, and there is a greater variety and quantity of food sources than in smaller forest fragments.

4.2. Forest fragmentation and seed predation

Extinctions caused by direct habitat loss as result of forest fragmentation may reduce the richness of species and modify the organization of trophic communities (Terborgh et al., 2001). These alterations may also lead to ecological distortions, such as the increase on the number of mammalian seed predators after the extinction of large carnivores (Terborgh et al., 2001). An increase in the number of seed predators could present harmful effects on plants or trees that produce big seeds, including *S. romanzoffiana*, due to the lack of safe sites for new individuals to become established (Sork, 1987; Asquith et al., 1997). Our results for forest fragments <1000 ha in size corroborate with those of Manzatto (2001), who reported a strong decline in the population of *Syagrus* species over 20 years in the 230 ha fragment studied here. However, our findings were opposite from those of Terborgh et al. (2001), who suggest increased seed and seedling predation in small forest fragments.

We identified two main factors that adversely affected the post-dispersal survival of *S. romanzoffiana* seeds: (1) abi-

otic factors present in very small fragments (13 ha and 9.5 ha) that are entirely influenced by the edge effects, and (2) biotic factors, such as a high density of seed predators in all extension of medium-sized fragments. These findings suggested that the long-term populations of *S. romanzoffiana* could only be maintained by forest fragments >1000 ha.

Our results reinforces that on small forest fragments (<100 ha), it would be necessary the enrichment of understorey species to promote the successional process, apparently disrupted by the edge effect. An increase on the interior forest environments should increase the likelihood of introducing arboreal animals into these habitats. Such an approach would attenuate the abiotic effects. In medium-sized fragments (>100 ha and <1000 ha), post-dispersal seeds protection by cages is needed in order to prevent their predator access and to ensure the establishment of *S. romanzoffiana* on fragmented areas. Our findings also stress the importance of assessing the influence of forest fragmentation on angiosperm reproductive biology as part of the effective planning for the preservation, restoration and management of forest areas, as, certainly, fragmentation might not only affect seed predation of the studied species, but also all steps on the recruitment process, such as pollination, reproductive phenology, seed dispersal, germination, herbivory and seedling survival.

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