The Palms
Guest edited by William J. Baker and Scott Zona

Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation

MAURO GALETTI[1,2]*, CAMILA I. DONATTI[1,2,3], ALEXANDRA S. PIRES[1],
PAULO R. GUIMARÃES JR[4,5] and PEDRO JORDANO[5]

[1]*Laboratório de Biologia da Conservação, Grupo de Fenologia e Dispersão de Sementes, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), CP 199, 13506-900 Rio Claro, SP, Brazil*
[2]*Instituto de Biologia da Conservação (IBC), Av. P-13, 294, Vila Paulista, Rio Claro, SP, Brazil*
[3]*Escola Superior de Agricultura Luiz de Queiroz (ESALQ/USP), Av. Pádua Dias 11, Caixa Postal 9, 13418-900, Piracicaba, SP, Brazil*
[4]*Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109, 13083-970, Campinas, SP, Brazil*
[5]*Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Pabellón del Perú, Avda. M. Luisa S/N, E-41013, Seville, Spain*

About 45 palm species occur in the Atlantic forest of Brazil, and most of them are affected by loss of seed dispersers resulting from forest fragmentation and hunting. Here we report the effects of habitat loss and defaunation on the seed dispersal system of an endemic palm, *Astrocaryum aculeatissimum*. We evaluated seed removal, insect and rodent seed predation, and scatter-hoarding in nine sites, ranging from 19 ha to 79 000 ha. We report the seedling, juvenile and adult palm densities in this range of sites. Endocarps remaining beneath the parent palm had a higher probability of being preyed upon by insects in small, mostly fragmented and more defaunated sites. The frequency of successful seed removal, scatter-hoarding and consumption by rodents increased in the larger, less defaunated sites. Successful removal and dispersal collapsed in small (< 1000 ha), highly defaunated sites and frequently resulted in low densities of both seedlings and juveniles. Our results indicate that a large fraction of Atlantic forest palms that rely on scatter-hoarding rodents may become regionally extinct due to forest fragmentation and defaunation. Current management practices including palm extraction and hunting pressure have a lasting effect on Atlantic forest palm regeneration by severely limiting successful recruitment of prereproductive individuals. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, **151**, 141–149.

ADDITIONAL KEYWORDS: *Astrocaryum* – caching – *Dasyprocta* – *Proechymis* – scatter-hoarding – *Sciurus* – seed predation.

INTRODUCTION

The high importance of palms for vertebrates has led to the concept that this family is 'keystone' in the Neo-

tropics, acting as the main staple food source for most animals in periods of fruit scarcity (Terborgh, 1986; Galetti & Aleixo, 1998). Although some species are dispersed by a large coterie of frugivores (e.g. *Euterpe edulis*; Galetti, Ziparro & Morellato, 1999), several palm species, particularly the large-seeded ones, rely on few animals for dispersal (Smythe, 1989; Silva &

*Corresponding author. E-mail: mgaletti@rc.unesp.br

Tabarelli, 2001; Fragoso, Silvius & Correa, 2003). Besides this lack of seed dispersers, palm populations can also be highly affected by deforestation.

One of the tropical ecosystems facing a fast-paced destruction is the Atlantic forest of Brazil. This ecosystem, which once stretched about 4000 km along the coast of Brazil from the state of Rio Grande do Norte (6°N) up to Rio Grande do Sul (30°S), covers more than 1 million km² and has one of the highest recorded levels of endemism (Myers *et al*., 2000). For instance, 10 genera and about 45 species of palms occur in the Atlantic forest, most of them endemic to this ecosystem (Henderson, Galeano & Bernal, 1995; plus additions of Lorenzi *et al*., 2004). Today, less than 8% of the Atlantic forest remains. The remaining forest occurs as many small fragments and a few large blocks of forest (SOS Mata Atlântica & INPE, 1998). Among the main threats to the palms are habitat loss, forest fragmentation (Scariot, 1999; Tabarelli, Silva & Gascon, 2004), palm harvesting (especially for edible species such as the *Euterpe edulis*; Galetti & Fernandez, 1998) and the pervasive effects of isolation (edge effects) (Laurance *et al*., 2002; Fleury & Galetti, 2004).

A serious threat to local persistence of plant species is the disruption of ecological interactions, both mutualistic (such as pollination or seed dispersal) and antagonistic (such as herbivory) (Wright, 2003). Seed dispersal is particularly important, because this process links the reproductive cycle of adult plants with the establishment of their offspring, and has a profound effect on vegetation structure and species distribution (Herrera *et al*., 1994; Wang & Smith, 2002). A wide range of frugivore species has been recorded feeding on the fruits and dispersing the seeds of Atlantic forest palm species (Galetti, Paschoal & Pedroni, 1992; Galetti *et al*., 1999; Silva & Tabarelli, 2001; Pimentel & Tabarelli, 2004; Guimarães *et al*., 2005). Large-seeded palm species rely extensively on medium- and large-sized birds and mammals for dispersal and recruitment (Zona & Henderson, 1989; Fragoso & Huffman, 2000), yet this fauna is being seriously threatened by increased hunting pressure and habitat loss (Chiarello, 1999; Cullen, Bodmer & Valladares-Pádua, 2000; Peres, 2001; Fa, Peres & Meeuwig, 2002; Wright, 2003).

Recent studies have shown that the loss of seed dispersers negatively influences recruitment by impairing seed removal, increasing seed loss to pathogens and vertebrate predators, and reducing seedling establishment (Chapman & Chapman, 1995; Chapman & Onderdonk, 1998; Cordeiro & Howe, 2001, 2003). Therefore, we can predict that palms that rely on large-bodied bird or mammal species for seed dispersal would be more vulnerable to local extinction than species dispersed by small frugivores, which are not severely affected by poaching or fragmentation.

Palm species that rely on scatter-hoarding rodents are particularly prone to extinction in defaunated sites, because very few frugivores can act as efficient seed dispersers of these palms (Smythe, 1989; Forget, 1991; Brewer & Rejmanek, 1999; Wright *et al*., 2000; Wright & Duber, 2001). Moreover, several scatter-hoarding rodents, such as agoutis, are among the most hunted mammals in neotropical forests (Cullen *et al*., 2000).

This paper examines the effects of forest fragmentation and defaunation pressure on the seed dispersal and predation of the endemic palm *Astrocaryum aculeatissimum* (Schott) Burret in the Brazilian Atlantic Forest. Specifically, we studied patterns of seed predation by both insects and rodents at the individual level and how they correlated with habitat preservation. In addition, we assessed dispersal efficiency across forest tracts that vary in size and defaunation level, and examined how the density of seedlings, juveniles and adults varied with forest size and defaunation level.

MATERIAL AND METHODS

STUDIED SPECIES

Astrocaryum aculetassimum (Arecaceae) is endemic to the Atlantic Forest of Brazil, occurring from Bahia to Santa Catarina (Henderson *et al*., 1995; Lorenzi *et al*., 2004). The fruits mature from May to December (Galetti *et al*., 1999; A. S. Pires, unpubl. data). Infructescences may have from 10 to 116 ($N = 86$) ovoid fruits with a thin mesocarp and a hard endocarp. Maximum fruit length and diameter are 4.8 ± 0.4 and 3.2 ± 0.2 mm, respectively ($N = 30$). Throughout the paper, we use the terms 'seeds' or 'endocarps' interchangeably to refer to the whole structures surrounded by the mesocarp, which are the propagules consumed or dispersed by the animals.

The large fruit dimensions limit the range of frugivorous vertebrates that can handle and consume *Astrocaryum* fruits. Only peccaries and rodents have been reported as consumers of the fruits of this genus, and rodents are the main seed dispersers (Kiltie, 1981; Smythe, 1989; Forget, 1991; Brewer & Rejmanek, 1999; Brewer, 2001). Agoutis either consume the seeds *in situ* or scatter-hoard them for later consumption; some of these seeds are not retrieved and survive to the seedling stage. Small rodents (chiefly spiny rats, *Trinomys* spp. and *Proechymis* spp.) may also disperse seeds away from the parent palm (Brewer & Rejmanek, 1999; Brewer, 2001).

STUDY REGIONS

The effects of forest fragmentation and defaunation were investigated in nine Atlantic Forest sites in Rio de Janeiro and São Paulo states. These areas support

Table 1. Characteristics of the study sites in the Atlantic forest of south-east Brazil

Site	Region	Area (ha)	Defaunation level[1]
Afetiva (Af)	Rio de Janeiro	19	3
Vendaval (Ve)	Rio de Janeiro	26	3
Santa Helena (SH)	Rio de Janeiro	57	3
Xixová-Japuí State Park (XJ)	São Paulo	901	3
União Biological Reserve (Un)	Rio de Janeiro	3 100	2
Poço das Antas Biological Reserve (PA)	Rio de Janeiro	3 500	2
Ilha do Cardoso State Park (Ca)	São Paulo	15 100	1
Picinguaba State Park (Pi)	São Paulo	47 500	2
Juréia-Itatins Ecological Station (JI)	São Paulo	79 230	1

[1]The ranking of defaunation intensity varies from level 1 (areas with high densities of agoutis and other frugivores) to level 3 (areas with low densities or absence of agoutis). See Material and methods: Study regions.

lowland Atlantic forest in different sucessional stages (Oliveira-Filho & Fontes, 2000). Average annual rainfall ranges from 2100 mm (Poço das Antas) to 3500 mm (Juréia). Taken together, these two regions combine different levels of fragmentation and defaunation, and represent a wide sample of localities where *A. aculeatissimum* is present. The study sites include protected parks and reserves, and small forest remnants located in private properties (Table 1), encompassing a gradient of defaunation levels that roughly corresponds with protection status and poaching intensity. Details on the vegetation structure of the fragments can be found in Carvalho (2005) for Rio de Janeiro state and in Donatti (2004) for the areas in São Paulo.

For all forest sites, we compiled ranked data on the level of defaunation (three classes), based on line transect censuses, camera trap data, footprints and other observations (M. Galetti *et al.*, unpubl. data). These categories were based on the abundance of agoutis, the main natural seed dispersal agent (Smythe, 1989). Areas with the highest density of agoutis (2–5 individuals/km^2) were assigned the lowest category of defaunation (level 1), while areas with no recent records of agoutis were assigned the highest defaunation rating (level 3); the intermediate category (level 2) was assigned to sites with moderate defaunation, where sizeable agouti densities can be found despite sustained hunting (São Bernardo & Galetti, 2004). Within each site we demarcated a variable number of plots for seed removal experiments and several locations of adult palms for monitoring of seed fate (see below).

SEED PREDATION BENEATH THE PARENT PALM

In each site we collected all endocarps found within a 2 m radius around adult *A. aculeatissimum* individuals, each adult sampled was spaced at least 50 m between each other and at least 5 m away from any other conspecific adult that was not used in the sample. Adults sampled were located at least 5 m from pre-existing trails and in a flat topography.

The collected endocarps were categorized as intact, preyed upon by rodents, or preyed upon by insects. Distinctive tooth marks of the rodents or exit holes of insects were used as diagnostic criteria. However, we also opened all intact endocarps that had no external sign of insect damage and found that ~30% had insect remains in them. Thus, predation estimates were based on both external signs and dissection of endocarps. Previous studies considering only external evidence of seed viability (see Wright & Duber, 2001), may have underestimated predation rates. Old endocarps were not sampled (see, e.g., Wright *et al.*, 2000; Wright & Duber, 2001).

SEED REMOVAL EXPERIMENTS

Groups of five threaded endocarps (modified spool and line method; Forget & Milleron, 1991; Donatti, 2004), were placed in experimental stations spaced every 50 m along pre-existing trails within each site. We set up 32 experimental stations (160 seeds) in each site in the São Paulo region except Picinguaba (28 stations and 140 seeds). In the Rio de Janeiro region, we set up 20 experimental stations (100 seeds) in each site.

All experiments were carried out in 2002 and 2003 (November to December), just after the beginning of the period when ripe fruits naturally fall. Experiments were run for 5 consecutive days in the São Paulo sites, while a monitoring period of 30 d was required in the Rio de Janeiro sites owing to lower removal rates. The fate of every removed endocarp was recorded as intact, preyed upon by rodents, dispersed but not buried, or scatter-hoarded (dispersed and buried). Dispersal was recorded whenever the seed (1) was moved from its initial presentation, (2)

exhibited signs of handling by animals, or (3) was not predated by insects or rodents.

SEEDLING, JUVENILE, AND ADULT PALM ABUNDANCE

At each site, the abundance of *A. aculeatissimum* individuals was estimated in plots situated in flat and noninundated places. In each site we set up 40 plots, 50 m × 4 m (São Paulo region), or 10 plots, 50 m × 10 m (Rio de Janeiro region). In each plot we counted the number of seedlings, juveniles and adults of *A. aculeatissimum*. We defined seedlings as individuals < 50 cm height; juveniles were individuals > 50 cm height but without signs of current or previous reproduction; and adults were plants that either were reproductive at census time or showed evidence of previous reproduction (modified from Scariot, 1999).

STATISTICAL ANALYSES

In order to analyse the fate of endocarps beneath the parent palm, we calculated the proportions of intact, rodent- and insect-consumed endocarps relative to the total sample. These variables were fitted by two different Generalized Linear Models (GLMs), both specifying binomial errors and a logit link function (Venables & Ripley, 2002). In the first model, our aim was to search for differences among sites and we used the site as predictor variable. In the second model our aim was to investigate how variables related to endocarp fate are affected by defaunation level and site area, and we used both as predictor variables. The same procedures and predictor variables were used to analyse the significance of these factors for the endocarp removal experiments.

The census data of seedlings, juveniles and adults were analysed using GLMs (Venables & Ripley, 2002). A model specifying defaunation level and site area (log-transformed) was fitted to the number of individuals in each stage obtained from the censuses in each site, specifying a quasi-Poisson family and log link function. All the analyses were carried out with the R package (Venables & Ripley, 2002; R Development Core Team, 2003).

RESULTS

SEED FATE BENEATH THE PARENT PALM

We collected a total of 4389 endocarps from 185 individuals. The probability of seed survival, defined as the proportion of intact endocarps, varied significantly among sites ($F = 86.2$, d.f. = 7, $P < 0.001$; Fig. 1A). The same is true for the probability of a seed surviving insect damage ($F = 122.0$, d.f. = 7, $P < 0.001$; Fig. 1B) or rodent predation ($F = 98.5$, d.f. = 7, $P < 0.001$; Fig. 1B).
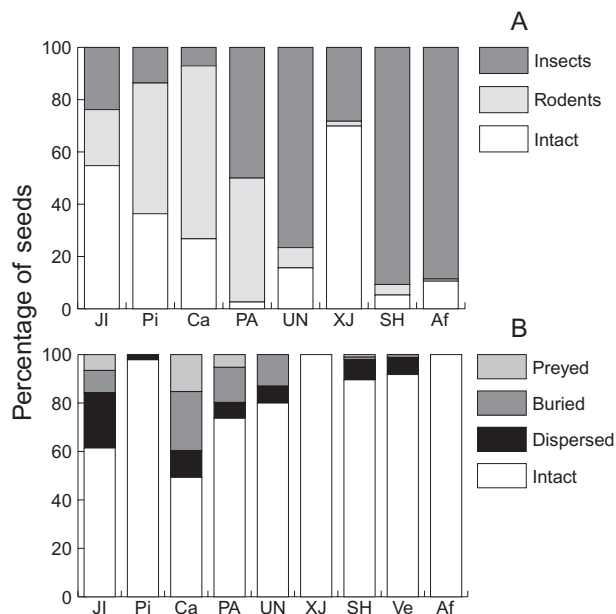

Figure 1. Seed fate of *Astrocaryum aculeatissimum* seeds. A, percentage of seeds intact, preyed upon by rodents or preyed upon by insects beneath the parent tree at Atlantic forests sites in south-east Brazil. B, percentage of intact, preyed-upon by rodents, scatter-hoarded by rodents, and scattered seeds (removed but left on the ground surface by small rodents) in controlled experiments. Each bar corresponds to sites listed in Table 1.

In order to assess patterns of seed survival related to site area and defaunation level, we ranked the sites according to area (Fig. 1) and tested the pair wise differences by means of Tukey HSD tests. Only the most defaunated site (Af) showed a consistently lower probability of seed survival relative to the larger and/or less defaunated sites (JI, Pi and Ca). The probability of seed survival increased with area ($F = 347.5$, d.f. = 1, 119, $P < 0.0001$) and decreased with defaunation level ($F = 11.4$, d.f. = 1, 120, $P < 0.001$).

Seed loss to rodents and insects was extremely variable among sites (Fig. 1A). The larger sites (JI, Pi, and Ca) consistently showed a higher (> 20%) fraction of seeds preyed upon by rodents, differing significantly only with that of the smallest fragment (Af; Tukey HSD test, $P < 0.05$). Both Ca and PA had significantly higher fractions of seeds consumed by rodents relative to smaller, more hunted sites (UN, XJ and SH). Along the size–defaunation gradient, the probability of seed loss to rodent seed predation increased significantly with site area ($F = 23.7$, d.f. = 1, 119, $P < 0.0001$), but decreased significantly in the more defaunated sites ($F = 371.9$, d.f. = 1, 120, $P < 0.0001$).

The small and medium-sized (UN) or highly defaunated sites (XJ, SH and Af) consistently showed high seed loss to insect predators (> 50%) relative to well-

preserved and larger sites (JI, Pi and Ca; Fig. 1A), which usually have < 25% of the seeds preyed upon by insects beneath the parent (Tukey HSD test, $P < 0.05$). Only the smallest, most defaunated site (Af) had significantly higher insect seed predation relative to the larger and/or better-preserved sites (JI, Pi and Ca; Tukey HSD test, $P < 0.05$). The probability of seed loss to invertebrate predation decreased with area ($F = 361.0$, d.f. = 1, 119, $P < 0.0001$) and increased with defaunation level ($F = 279.0$, d.f. = 1, 120, $P < 0.0001$). Overall, the effects of defaunation level, measured as the coefficients in the GLM models, were consistently higher than the area effects on the probability of seed survival, seed loss to rodent predation, and seed loss to invertebrate predation. To sum up, patterns of seed loss beneath the parent palm to insects and rodents were largely complementary along a gradient of decreasing site size and/or increasing defaunation (Fig. 1A). Only sites with > 10 000 ha and light or moderate defaunation level (JI, Pi and Ca) had high rates of seed survival. Otherwise, seed predation by insects or small rodents was too high to compensate for the loss of agoutis, the main seed disperser.

SEED REMOVAL EXPERIMENTS

Among the 224 experimental stations placed in the study sites 110 (49.1%) had at least one seed removed. The number of experimental stations with removed seeds differed among sites ($\chi^2 = 112.41$, d.f. = 9, $P < 0.0001$). Larger and less defaunated sites had more stations showing removal and more defaunated sites than smaller fragments. In order to test the effects of defaunation and area on the probability of a station having at least one seed removed, we fitted a simple logistic regression. The probability of a station showing removal decreased with both defaunation level ($\chi^2 = 46.80$, $P < 0.0001$) and site area ($\chi^2 = 11.8$, $P < 0.0001$). Defaunation explained a larger fraction of variation ($R^2 = 19.7\%$) than site area ($R^2 = 4.1\%$) in the proportion of stations with at least one seed removed.

Experimental seeds in a given station had distinct fates across sites (Fig. 1B). The fraction of intact seeds was > 80% for all the smaller sites (XJ, SH, Ve and Af), although Pi also had a very high proportion of intact seeds for its area as a result of its severe defaunation (Fig. 1B). Predated seeds were relatively infrequent in the experiments (always < 15%), especially in the smaller sites. The proportion of seeds removed (either buried or dispersed) per station differed among sites ($F = 39.4$, d.f. = 8, 215, $P < 0.0001$; Fig. 1B). Smaller and more defaunated sites (XJ, SH, Ve and Af) had a significantly lower probability of seed removal per station relative to the larger and/or less defaunated sites (JI, Ca, Pi and PA) (Tukey HSD test, $P < 0.05$). The proportion of scatter-hoarded seeds differed signifi-

cantly among sites ($F = 3.95$, d.f. = 7, 76, $P = 0.003$; Fig. 1B), although only the Ca site, a relatively large and less defaunated area, differed from the rest of sites (Tukey HSD test, $P < 0.05$). The probability of seeds being removed and/or scatter-hoarded tended to decrease with increasing defaunation and decreasing site area (all $F > 35.8$, d.f. = 1, 82, $P < 0.01$,). The effects of defaunation level on the probability of successful removal and/or scatter-hoarding of the seeds were consistently larger than the effects of site size, as estimated from the GLM model coefficients.

SEEDLING, JUVENILE AND ADULT ABUNDANCES

Differences among sites in seedling, juvenile and adult densities were highly significant ($F > 8.6$, d.f. = 8, 201, $P < 0.0001$ in all cases; Fig. 2). Seedling densities differed among sites, particularly when considering site area (Fig. 2). The smallest sites (XJ, SH, Ve and Af) with severe defaunation had < 50 seedlings/ha, a figure well below the larger, less defaunated sites. The pattern for juveniles was very similar to that for seedlings (Fig. 2), although the SH site had an unexpectedly high density, perhaps as a result of its proximity to the larger and less defaunated PA site. Variation in adult densities deviated from the patterns observed in seedlings and juveniles, with a trend for density increasing in some of the smallest sites, probably a result of past management history.

All the three stages (Fig. 2) showed significant effects of defaunation level and site area, as revealed by the GLM fits incorporating these effects ($F > 3.29$, $P < 0.01$ in all cases). The densities of the three stages decreased with increasing defaunation and decreasing site area, with larger effects of defaunation as estimated from the model effect coefficients. Sites with defaunation levels 1 and 2 had significantly higher seedling densities when contrasted with defaunation level 3 (Tukey-HSD test, $P < 0.05$; Fig. 2), although the contrast for levels 1 vs. 3 was only marginally significant. The variation in adults, juveniles and seedlings among sites was associated with site area and defaunation, but the negative effects of defaunation were larger.

DISCUSSION

We examined how the combined effects of fragment area and defaunation level influence seed removal, dispersal and survival of *Astrocaryum aculeatissimum*. Scatter-hoarding rodents (chiefly agoutis) are key elements for the dispersal of this palm, because they removed and buried up to 22% of the seeds away from the parent plant. *Astrocaryum* seeds have higher seedling recruitment when buried because they escape predation from bruchids and large vertebrates such as
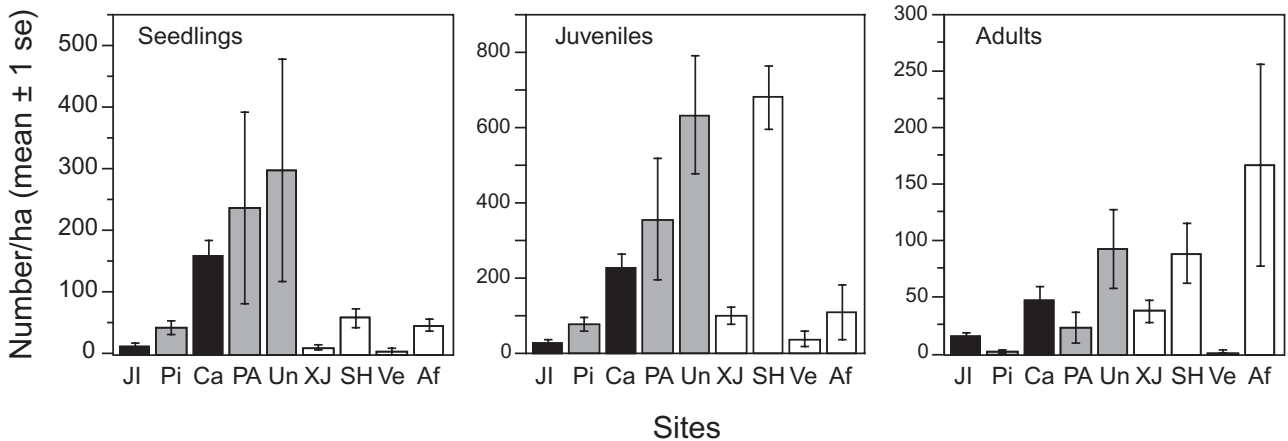
Figure 2. Mean density (number of individuals/ha; ± 1 SE) of different demographic stages of *Astrocaryum aculeatissimum* at nine sites (see Table 1) in the Atlantic Forest of south-east Brazil. Solid bars indicate largely preserved sites (defaunation level 1); greyed bars, sites with moderate hunting pressure (defaunation level 2); and open bars, severely defaunated sites (defaunation level 3).

peccaries (Smythe, 1989). In addition, squirrels and spiny rats do not compensate for the decrease in seed removal in the absence of agoutis, because they exhibit low seed removal rates and short dispersal distances of *A. aculeatissimum* seeds (Donatti, 2004). Therefore, the interactions of seeds and scatter-hoarding rodents can be widely variable across sites that differ in defaunation level and forest size. As a result, variable patterns of seed mortality beneath the parent plants have been previously reported (Wright *et al*., 2000; Wright & Duber, 2001), but the success of scatter-hoarding dispersal and the escape from insect seed predators have scarcely been studied experimentally.

Agoutis are usually absent in areas smaller than 2000 ha, because these fragments do not support sustainable hunting (Peres, 2001). Therefore, a palm species that relies on agoutis for seed dispersal will face local extinction earlier in small forest fragments than in larger fragments. Previous studies have shown that the proportion of successfully dispersed palm seeds was inversely related to poaching intensity, ranging from 85–99% dispersal at protected sites to 4–50% at unprotected sites (Wright *et al*., 2000). In defaunated areas or small forest fragments, variation in the intensity of seed predation beneath adult palms is driven mainly by insects. In the range of sites studied here, excluding the São Paulo state areas where the specialist bruchid *Caryoborus serripes* (subfam. Pachymerinae) was never recorded, the proportion of seeds beneath adult palms lost to insects was consistently > 50% in the smaller sites with higher defaunation levels. Large, lightly hunted sites consistently had < 25% of seeds preyed upon by insects.

Poaching also affects the seed dispersal rates for large palms. For example, in *Attalea butyracea* and

Astrocaryum standleyanum, the proportion of seeds dispersed away from fruiting conspecifics was inversely related to poaching intensity, ranging from 0–10% at protected sites where mammals were abundant to 3–40% at unprotected sites where poachers were most active (Wright *et al*., 2000). Our results concerning the density of individuals are in agreement with the patterns of disruption of *Astrocaryum aculeatissimum* seed dispersal observed in small, defaunated fragments.

Our results indicate that seedling densities increase with reduction of area and increasing defaunation. However, in areas in which size is very small (< 1000 ha) and the level of defaunation is high, the seedling recruitment collapses, and the natural regeneration of the palm population is blocked. For instance, demographic models have shown that *Attalea humilis* populations in small forest fragments will first increase, forming monospecific, high-density stands, and then collapse under the prevalence of secondary vegetation and lack of rodent seed dispersers, which are frequently extinct in such habitats (Souza & Martins, 2004). In fact, forest fragmentation aggravates the effects of defaunation because it: (1) reduces and isolates vertebrate populations adverse to the surrounding habitat matrix; (2) reduces the recolonization of highly defaunated areas from adjacent, nondefaunated areas; (3) increases the accessibility to hunters; and (4) reduces the area of suitable habitat for species adverse to forest edges (see Peres, 2001).

The density of *Astrocaryum* seedlings in large fragments may be a result of intense predation by white-lipped peccaries (*Tayassu pecari*) in some rainforests (Silman, Terborgh & Kiltie, 2003), but peccaries occur in only two of our studied areas (Ilha do Cardoso and

Juréia-Itatins). Harrington *et al*. (1997) did not detect any significant response to fragmentation in terms of the ratio of juveniles to adults for some large-seeded species in Australia, a finding that suggests that long-lived trees respond slowly to land use change. In any case, the low density of seedlings in our large forests may be as low as that of small (< 50 ha) fragments even though the overall population size is much bigger.

The negative effects of forest fragmentation and defaunation on the abundance of seedlings have been reported for several plant species (Chapman & Chapman, 1995; Benitez-Malvido, 1998; Asquith *et al*., 1999; Cordeiro & Howe, 2001; Bruna, 2003), including palms (Scariot, 1999). Our results corroborate the evidence that the loss of effective seed dispersers could be an important cause of such patterns, especially for large-seeded species. The seedling and juvenile densities showed similar responses to the gradient of increasing defaunation and reduced area, with very low densities in highly defaunated sites. In fact, the direct negative effect of defaunation was higher than the reduction in forest area.

The effects of lost seed dispersers can be especially pervasive for plants that rely on few frugivore species for seed dispersal, such as the large-seeded palms. There is increasing evidence that neotropical, large-seeded palms – including several *Astrocaryum* species – rely mainly on scatter-hoarding rodents (e.g. Hoch & Adler, 1997; Peres & Baider, 1997; Asquith *et al*., 1999; Brewer & Rejmanek, 1999; Charles-Dominique *et al*., 2003). Indeed, 19 species (or 45%) of Atlantic forest palms are dispersed chiefly by scatter-hoarding rodents, especially agoutis, or by the endangered lowland tapir (*Tapirus terestris*) (Galetti *et al*., 2001; M Galetti, unpubl. data), including several endemic species and one endemic genus (*Polyandrococos*). Both scatter-hoarding rodents and the tapir are vanishing in small, defaunated areas (Chiarello, 1999), and the Atlantic forest is now a mosaic of small fragments with a few, large blocks of forest.

Our study provides a testable model for other large-seeded species where seed removal and legitimate dispersal by large frugivores is a function of both forest size and defaunation level (Fig. 3). The large-bodied frugivores, which are preferred game species, affect dispersal only in lightly hunted areas, while spiny rats and squirrels might act as legitimate dispersers only in extremely defaunated areas. Successful dispersal of large-seeded palms relies on scatter-hoarding by agoutis (*Dasyprocta* spp.), but this mutualism collapses in moderately hunted areas where the agoutis have been extirpated. The fraction of undispersed seeds increases as the probability of dispersal decreases, so that in relatively small, highly defaunated areas most seeds are preyed upon by insects. The sharp decline in the probability of successful dispersal may occur at
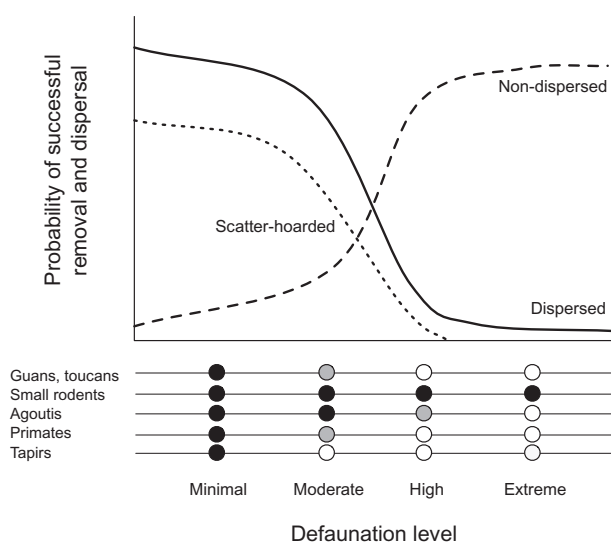

Figure 3. A conceptual model for the probability of successful seed removal and dispersal of large-seeded palms dispersed by vertebrates in tropical forests under variable defaunation intensity. Filled dots indicate the presence of different frugivorous taxa at each defaunation level; greyed dots indicate marginal abundances.

different defaunation levels depending on how hunting pressure covaries with area size. Successful dispersal events might be retained in large but severely hunted areas or in small fragments located close to larger, less defaunated areas. In any instance, local extirpation of agoutis is a key factor promoting the collapse of palm recruitment.

We expect a sharp collapse of scatter dispersal for *A. aculeatissimum* and other large-seeded species, due to the simultaneous effect of loss of the main seed disperser and the disproportionate increase in insect abundance in defaunated sites, which are usually also severely fragmented.

Current management practices including palm extraction, fragmentation and hunting pressure have a lasting effect on Atlantic forest palm regeneration by severely limiting successful recruitment of prereproductive individuals. The future of the populations of several palm species will depend on intense management, especially in small forest fragments.

ACKNOWLEDGEMENTS

REFERENCES

Asquith NM, Terborgh J, Arnold AE, Riveros CM. 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *Journal of Tropical Ecology* **15:** 229–235.

Benitez-Malvido J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* **12:** 380–389.

Brewer SW. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* **92:** 245–255.

Brewer SW, Rejmanek M. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science* **10:** 165–174.

Bruna EM. 2003. Are plant populations in fragmented habitats recruitment limited? Tests with an Amazonian herb. *Ecology* **84:** 932–947.

Carvalho FA. 2005. Efeitos da fragmentação florestal na florística e estrutura da Mata Atlântica submontana da região de Imbaú, município de Silva Jardim, RJ. MSc. dissertation, University of North Fluminense.

Chapman CA, Chapman LJ. 1995. Survival without dispersers: seedling recruitment under parents. *Conservation Biology* **9:** 675–678.

Chapman CA, Onderdonk DA. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* **45:** 127–141.

Charles-Dominique P, Chave J, Dubois MA, De Granville JJ, Riera B, Vezzoli C. 2003. Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. *Global Ecology and Biogeography* **12:** 237–248.

Chiarello AG. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation* **89:** 71–82.

Cordeiro NJ, Howe HF. 2001. Low recruitment of trees dispersed by animals in African forest fragments. *Conservation Biology* **15:** 1733–1741.

Cordeiro NJ, Howe HF. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the Natural Academy of Science, USA* **100:** 14 052–14 056.

Cullen L, Bodmer RE, Valladares-Pádua C. 2000. Effects of hunting in habitat fragments of the Atlantic forest, Brazil. *Biological Conservation* **95:** 49–56.

Donatti CI. 2004. Consequências da defaunação na dispersão e predação de sementes e no recrutamento de plântulas da palmeira brejaúva (Astrocaryum aculeatissimum) na Mata Atlântica. Unpublished Masters thesis, University of São Paulo.

Fa JE, Peres CA, Meeuwig J. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology* **16:** 232–237.

Fleury M, Galetti M. 2004. Effects of microhabitat on palm seed predation in two forest fragments in southeast Brazil. *Acta Oecologica* **26:** 179–184.

Forget PM. 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. *Tropical Ecology* **32:** 155–167.

Forget PM, Milleron T. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* **87:** 596–599.

Fragoso JMV, Huffman JM. 2000. Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *Journal of Tropical Ecology* **16:** 369–385.

Fragoso JMV, Silvius KM, Correa JA. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* **84:** 1998–2006.

Galetti M, Aleixo A. 1998. Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology* **35:** 286–293.

Galetti M, Fernandez JC. 1998. Palm heart harvesting in the Brazilian Atlantic forest: changes in industry structure and the illegal trade. *Journal of Applied Ecology* **35:** 294–301.

Galetti M, Keuroghlian A, Hanada L, Morato MI. 2001. Frugivory and seed dispersal by the lowland tapir (*Tapirus terrestris*) in southeast Brazil. *Biotropica* **33:** 723–726.

Galetti M, Paschoal M, Pedroni F. 1992. Predation on palm nuts (*Syagrus romanzoffiana*) by squirrels (*Sciurus ingrami*) in south-east Brazil. *Journal of Tropical Ecology* **8:** 121–123.

Galetti M, Ziparro VB, Morelatto LPC. 1999. Fruiting phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic Forest of Brazil. *Ecotropica* **5:** 115–122.

Guimarães PR, Lopes PFM, Lyra ML, Muriel AP. 2005. Fleshy pulp enhances the location of *Syagrus romanzoffiana* (Arecaceae) fruits by seed-dispersing rodents in an Atlantic forest in south-eastern Brazil. *Journal of Tropical Ecology* **21:** 109–112.

Harrington GN, Irvine AK, Crome FHJ, Moore LA. 1997. Regeneration of large-seeded trees in Australian rainforests fragments: a study of higher order interactions. In: Laurance WL, Bierregaard, RO, eds. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. Chicago: University of Chicago Press, 292–303.

Henderson A, Galeano G, Bernal R. 1995. *Field guide to the palms of the Americas*. Princeton, NJ: Princeton University Press.

Herrera CM, Jordano P, López Soria L, Amat JA. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* **64:** 315–344.

Hoch GA, Adler GH. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* **13:** 51–58.

Kiltie RA. 1981. Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* **13:** 141–145.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* **16:** 605–618.

Lorenzi H, Sousa HM, Costa JTM, Cerqueira LSC, Ferreira E. 2004. *Palmeiras Brasileiras: nativas e exóticas cultivadas*. Nova Odessa, SP: Instituto Plantarum.

Myers N, Mittermeier RA, Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403:** 853–858.

Oliveira-Filho A, Fontes MAL. 2000. Patterns of floristic differentiation among Atlantic forests in south-eastern Brazil, and the influence of climate. *Biotropica* **32:** 793–810.

Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* **15:** 1490–1505.

Peres CA, Baider C. 1997. Seed dispersal, spatial distribution and population structure of Brazil nut trees (*Bertholletia excelsa*) in southeastern Amazonia. *Journal of Tropical Ecology* **13:** 595–616.

Pimentel DS, Tabarelli M. 2004. Seed dispersal of the palm *Attalea oleifera* in a remnant of the Brazilian Atlantic Forest. *Biotropica* **36:** 74–84.

R Development Core Team. 2003. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

São Bernardo CS, Galetti M. 2004. Densidade e tamanho populacional de primatas em um fragmento florestal no sudeste do Brasil. *Revista Brasileira de Zoologia* **21:** 827–832.

Scariot A. 1999. Forest fragmentation effects on palm diversity in central Amazonia. *Journal of Ecology* **87:** 66–76.

Silman MR, Terborgh J, Kiltie RA. 2003. Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* **84:** 431–438.

Silva MG, Tabarelli M. 2001. Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. *Acta Oecologica* **22:** 259–268.

Smythe N. 1989. Seed survival in the palm *Astrocaryum standleyanum*, evidence for dependence upon its seed dispersers. *Biotropica* **21:** 50–56.

SOS Mata Atlântica, INPE. 1998. *Atlas da Evolução dos Remanescentes Florestais e Ecossistemas Associados no Domínio da Mata Atlântica no Período 1990–95*. São Paulo: INPE.

Souza AF, Martins FR. 2004. Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic Forest. *Biodiversity and Conservation* **13:** 1611–1632.

Tabarelli M, Silva MJC, Gascon C. 2004. Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodiversity and Conservation* **13:** 1419–1425.

Terborgh J. 1986. Keystone plant resources in the tropical forest. In: Soulé ME, ed. *Conservation biology*. Sunderland, MA: Sinauer, 330–340.

Venables WN, Ripley BD. 2002. *Modern applied statistics with S*. New York: Springer.

Wang BC, Smith TB. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* **17:** 379–385.

Wright SJ. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology Evolution and Systematics* **6:** 73–86.

Wright SJ, Duber HC. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyracea*, with implications for tropical tree diversity. *Biotropica* **33:** 583–595.

Wright SJ, Zeballos H, Dominguez I, Gallardo MM, Moreno MC, Ibanez R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* **14:** 227–239.

Zona S, Henderson A. 1989. A review of animal-mediated seed dispersal of palms. *Selbyana* **11:** 6–21.