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Original article

Effects of frugivore impoverishment and seed predators on the recruitment of a keystone palm

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ABSTRACT

Many plant species are threatened as a result of extinction of their large-bodied frugivores all over the world. Additionally, introduced herbivores and seed predators may cause severe pressure on early stages of plant recruitment. We studied the seed dispersal and seed predation of the keystone palm *Euterpe edulis* on a land-bridge island with a highly impoverished frugivore fauna and overabundant seed predators, and in a continuous Atlantic forest in Brazil. While the diversity of avian seed dispersers and predators was higher on the mainland, the abundance of seed dispersers was 4-fold higher on the island. *Turdus flavipes* was responsible for 72% and 96% of seeds removed in the island and mainland, respectively. However, the higher density of *T. flaviceps* on the island did not result in higher seed removal. In fact, seed removal rate was 1.7 times lower there than on the mainland, probably due to the aggressive behavior of the major seed disperser who defend palm fruits. Seed predation, on the other hand, was markedly higher on the island, where nearly 100% of seeds were preyed upon, but only 0.3% on the mainland. As a consequence of higher seed predation the population of *E. edulis* has few numbers of seedlings and saplings on the island. Therefore, management of the seed predator populations on the island is a key priority for recovering the natural population of this keystone palm and the frugivores that depend on its fruits.

1. Introduction

Tropical rainforests have been suffering increasing species extinctions over the last few decades (Alcover et al., 1998; Sodhi et al., 2004). One of the main causes of species loss is forest fragmentation followed by hunting and the introduction of exotic species (Wright and Duber, 2001; Courchamp et al., 2003). Most plants are affected directly by microclimate changes in fragments (Benitez-Malvido, 1998; Laurance et al., 2002), and indirectly by the changes in composition and abundance of animal communities, such as mutualists (i.e. pollinators, seed dispersers) (Cordeiro and Howe, 2003; Galetti et al., 2006) or antagonists (i.e. seed predators, herbivores) (Dirzo and Miranda, 1991; Fleury and Galetti, 2004,

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2006). In fact, the local extinction of some animal populations, or their reduction to the point of becoming functionally extinct, can have dramatic consequences in terms of regulating and supporting ecosystem services, especially in mutualisms, such as pollination and seed dispersal (McConkey and Drake, 2002; Wang and Smith, 2002).

In the Neotropics, large frugivorous birds, such as toucans, guans and some cotingas have been extirpated from most of their former distribution (e.g. Galetti et al., 1997; Sekercioglu et al., 2004). The decline of these large-gaped frugivores may negatively affect plant communities by reducing seed dispersal and thus reducing seedling establishment (Chapman and Chapman, 1996; Muller-Landau et al., 2002), plant distribution (Bleher and Böhning-Gaese, 2001), and local plant diversity (Webb and Peart, 2001; Wright et al., 2007). Additionally, in areas where large-bodied frugivores have become extinct, herbivores and small generalist seed predators, favored by the absence of large carnivores or competitors, increase their abundance dramatically (Terborgh et al., 2001).

The Anchieta Island in south-east Brazil is an off-shore island that has suffered intense defaunation of native frugivore birds and introduction of alien vertebrates (Bovendorp and Galetti, 2007; Alvarez et al., 2008). In 1983, the São Paulo Zoo introduced 15 mammal species, both exotic and native (Bovendorp and Galetti, 2007). Currently, the Anchieta Island presents the highest density of mammalian herbivores (capybaras, agoutis), seed and nest predators (agoutis, coatis, marmosets, and armadillos) in the Atlantic forest (Bovendorp and Galetti, 2007; Bovendorp et al., 2008), and its avian seed disperser fauna is highly impoverished with fewer than 75 bird species (Galetti et al., unpublished data).

Therefore, we could expect that the recruitment of seedlings would be negatively affected due to the high rates of seed predation, and that plant species that rely on large-gaped frugivores would be more susceptible to mutualism disruption than species dispersed by small birds, given that large fruits limit the potential seed disperser fauna (Howe, 1989; Silva and Tabarelli, 2000; Staggemeyer and Galetti, 2007).

One of the plants that may be affected by the loss of dispersers is the palm-heart or ''palmito'' *Euterpe edulis*, whose seeds are dispersed by several frugivores, but mainly by large-sized birds and mammals (Galetti et al., 1999; Galetti et al. 2000). Here we tested four predictions comparing Anchieta Island and the nearest mainland in a two-part study. First, we compared the patterns of seed dispersal and seed predation in both sites and predicted that: 1) fruit removal will be lower in Anchieta as a consequence of lower diversity of seed dispersers; 2) seed predation will be higher in the island due to the higher abundance of seed predators and, as a consequence 3) population structure in the island is not self-regenerating. In addition, we compared areas with and without *E. edulis* at Anchieta to test whether seed predation pressure would be higher in sites where this species occurs, in comparison with sites where it is less common. We tested this prediction experimentally by placing seeds in sites with and without adults of *E. edulis*. If seed predation is density-dependent, planting seeds in areas without *E. edulis* would enhance plant survivorship and therefore it would be a reasonable strategy to recover the population of this palm species.

2. Materials and methods

2.1. Study sites

The first part of this study was carried out from October 2003 to February 2005 at Ilha Anchieta State Park, Ubatuba (Anchieta hereafter; 45°02′ to 45°04′ W, 23°27′ to 23°34′ S) and at the Serra do Mar State Park – Caraguatatuba (Caraguá hereafter; 45°20′ to 45°44′ W, 23°32′ to 23°42′ S), in the north-east of São Paulo State, south-east Brazil (Fig. 1).

The second part was carried out in August 2006 and February 2007 as an a posteriori hypothesis test only at Anchieta. The climate and elevation of both sites studied are similar, with rainfall up to 2500 mm and elevation between 50 m and 200 m.

Anchieta is a land-bridge island with 806 ha separated from the continent by approximately 400 m and located 38 km from our study area in the mainland. Anchieta suffered from intense human occupation in the past and 70% of its area are covered by native secondary rainforest with distinct successional stages and many exotic species (Alvarez et al., 2008). The population of *E. edulis* is concentrated in a small portion of the island, where human activities were less intense. Since the creation of the park in the 1970s, the population of *E. edulis* has not being harvested. The avifauna is highly impoverished; large fruit-eating birds, such as toucans, guans and cotingas are absent (except for rare summer visitors *Procnias nudicollis* and *Pyroderus scutatus*). Mammals are represented mostly by introduced non-native species, which have reached high densities since they were introduced in the island in 1983, such as agoutis, capybaras, marmosets, coatis and armadillos (Bovendorp and Galetti, 2007).

The 39,800 ha study area on the mainland (Caraguá) has a high plant diversity and more than 250 forest-dwelling birds (C. Gussoni and R. Fadini, unpublished data) and several large-bodied mammals, such as tapirs, peccaries and howler monkeys. Large frugivorous birds also exist, such as guans (*Penelope obscura, Aburria jacutinga*), toucanets (*Pteroglossus bailloni*, *Selenidera maculirostris*), toucans (*Ramphastos vitellinus*, *Ramphastos dicolorus*) and cotingas (*P. scutatus*, *P. nudicollis*) (R. Fadini, personal observation). Therefore, all possible vertebrate seed dispersers and predators of *E. edulis* are present in the Caraguá site. In the last years, illegal harvesting is dramatically threatening the populations of *E. edulis* in this area (R. Fadini, personal observation).

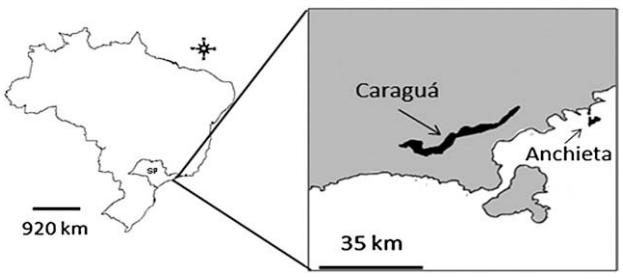

Fig. 1 – Location of Anchieta (island) and Caraguá (mainland) in São Paulo State (SP), Brazil.

2.2. Study species

E. edulis is a single-stemmed palm, 8–12 m tall, and is a dominant species in pristine areas of the Brazilian Atlantic forest (up to 500 adult palms/ha; Reis et al., 2000). The fruits are black drupes with one seed (mean ± SD = 13.5 ± 1.3 mm length, 14.2 ± 1.2 mm width) (Pizo and Vieira, 2004) and ripe fruits peaked in April and May (Castro et al., 2007; Genini et al., 2008). The pulp is rich in lipids and at least 30 birds and 13 mammal species are known to consume *E. edulis* fruits in the Atlantic rain forest, including guans, toucans, trogons, cotingas, agoutis, pacas and peccaries (Galetti et al., 1999). The main seed predators are rodents and peccaries (Keuroghlian and Eaton, 2008), and scolytid beetles (*Coccotrypes palmarum*, Scolytidae) (Pizo and Simão, 2001). The species reproduces annually and maintains a large seedling bank with more than 12,000 seedlings ha^{-1} in some sites (Reis et al., 2000). Despite its importance, the species has been over harvested for palm-heart, and large populations only remain in a few protected reserves (Galetti and Aleixo, 1998; Galetti and Fernandez, 1998).

2.3. Bird census

We compared the abundance of *E. edulis*' avian dispersers in Anchieta and Caraguá using bird point counts. We established several point counts spaced by 150 m in four trails in Caraguá (18–25 points each month) and in three trails in Anchieta (12–22 points each month) to sample the frugivorous birds from October 2003 to August 2004. The number of points varied each month due to weather constrains. We selected the birds to be sampled using information from a compilation of previous studies (Galetti et al., 1999). The points were sampled between 6:00 to 10:00 h, in periods of 5 min each (see Raman, 2003).

We used a randomization procedure to compare the relative bird abundances (number of records $point^{-1}$) among sites. In this case our datasheet was composed of two columns, corresponding to the sites, and a variable number of lines, corresponding to the points. Each point contained the number of birds sighted or heard at that point. We first calculated the mean number of birds per point at each site, and then subtracted one mean from another to obtain an observed difference. We shuffled the numbers to obtain a random distribution of the mean differences and then repeated this procedure 1000 times to obtain P values by counting the number of times the observed mean appeared in the random distribution (Manly, 1991).

2.4. Frugivory and seed dispersal

Records of frugivorous birds consuming fruits of *E. edulis* were conducted from April to May 2004 at Anchieta and from May to July of the same year at Caraguá, in the peak of fruit production on both sites. Observation sessions lasted 5 h in which we recorded: bird species; number of fruits carried in the bill, swallowed, dropped or regurgitated; and visit length. The total period of observations was 90 h (18 trees) in Anchieta and 100 h (13 trees) in Caraguá. Only visits in which the bird interacted with the plants were used in the analysis (Jordano and Schupp, 2000). We selected trees with high fruit production to minimize the effect of fruit quantity on the estimates of fruit removal among trees and sites. We compared the number of visits made for each bird species and number of fruits consumed per visit among the two sites using Mann–Whitney *U* tests.

2.5. Post-dispersal seed predation

We tested experimentally whether seed predation by mammals in Anchieta would be higher than in the mainland. Along the same trails where we carried out the bird census in each site, we set up 20 open cages (a box with 20 × 20 cm made of steel and opened in the four sides and on the top), 5 m aside the trails and 150 m apart, each containing 20 cleaned seeds at the center of the cage. Seeds were collected in April 2004 in Anchieta and June 2004 in Caraguá. Survivorship of seeds was checked after 30 days, sufficient to allow seed predation in the Atlantic Forest (Fleury and Galetti, 2004, 2006; Galetti et al., 2006), and minimize the effect of moonlight on the activity of small mammals (Longland and Price, 1991; Bowers and Dooley, 1993).

Due to the large difference in the local abundance of *E. edulis* inside Anchieta, we suspected the seed predators could be resource-oriented and therefore we tested whether post-dispersal seed predation differed among areas where the species is present or absent. To test this prediction we set up 20 stations along two transects (present vs. absent) consisting of 3 seeds per station, a number based on the quantity normally found dispersed together by large birds in the environment (Galetti et al., 1999). The proportion of seeds removed was checked after 30 days (see above). We assessed the fate of seeds by drilling them, attaching threads to the seeds and following their fate through a modification of the spool and line method (Fleury and Galetti, 2006; Galetti et al., 2006). Each seed was threaded with a line spool that was fixed parallel to the soil by a steel stick, allowing the line to easily unroll when the seed was removed. Additionally, we analyzed marks on predated seeds or sign on site that could indicate us the presence of 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 both during dry and wet season (August–September/2006 and February–March/2007 respectively). The proportions of seed predation in presence/absence of *E. edulis* were analyzed by likelihood χ^2 (G)-tests with the main effect of site. A nominal logistic test was used in order to detect differences on seed predation between sites (palm absence and presence) and season (wet and dry season). We ran both analyses on JMP 7.0 (SAS Institute, 2002).

2.6. Population structure

At each site we randomly demarcated 40 plots of 50 × 4 m totaling 0.8 sampled hectares, along the same four trails used for bird census. All seedlings, juveniles and adults of *E. edulis* were counted; individuals less than 0.5 m high were considered seedlings (Losos, 1995; Vormisto, 2002). Those with evidence of current or past flowering and/or fruiting signals were considered adults, while those higher than 0.5 m and

without flowering and/or fruiting were considered juveniles (Scariot, 1999). We compared the number of individuals per plot on each stage among the two sites using Mann–Whitney *U*-test. Because the number of seedlings and saplings could be influenced by the number of adults, we also compared the ratio of number of seedlings and saplings per adult among sites. Because many plots had no adults, we added one to conduct the analyses. For comparisons, we also used a Mann–Whitney as before. In Caraguá, where illegal harvesting is taken place recently, we avoid sampling palmitos in areas with harvesting activities.

3. Results

3.1. Bird census

Several frugivorous birds were found in Caraguá but not at Anchieta during our censuses (Table 1). The relative abundance of *Turdus flavipes*, the main seed disperser of *E. edulis* at both sites, was nearly 4-fold higher at Anchieta than Caraguá (two-tailed randomization test: $p = 0.006$; 1000 randomizations). Since most species were not important seed dispersers (see above), we did not compare their relative abundances among sites.

3.2. Frugivory and seed dispersal

We recorded seven bird species dispersing the fruits of *E. edulis* in Caraguá and only three in Anchieta (Table 1), including data from the focal-tree method and *ad libitum* observations. Of the 18 trees observed in Caraguá, three were not visited by any frugivore (17%), while in Anchieta, 4 of 13 trees did not have any visit (30%).

We also recorded three bird seed predators in Caraguá, all Psitacines: *Trichlaria malachitacea*, *Pionus maximiliani* and *Pyrrhura frontalis*. A pair of *Trichlaria* visited *E. edulis* only once and dropped 344 fruits under the tree crown. Further, four individuals of *Pionus* also visited *E. edulis* only once, but the number of fruits dropped could not be recorded.

The mean number of visits per plant was similar between the study sites (Mann–Whitney *U* test: $\chi^2 = 0.53$, $p = 0.46$), but the number of fruits consumed per visit was, on average, 1.7 times lower in Anchieta than Caraguá (Mann–Whitney *U* test: $\chi^2 = 13.86$, $p < 0.001$). *T. flavipes* was by far the most important frugivore in both sites, dispersing nearly 72% of the fruits in Anchieta, and 96% in Caraguá. Therefore, large frugivores were not important dispersers of *E. edulis* at either site during our study period.

3.3. Post-dispersal seed predation

Nearly all seeds were removed from exclosures in Anchieta. Three exclosures in Anchieta and five exclosures in Caraguá could not be found. In the remaining exclosures (17 in Anchieta and 15 in Caraguá), just one seed survived in Anchieta (survivorship: 1 seed/340 = 0.3%). In Caraguá only one exclosure had all seeds removed, while another two exclosures each had one seed removed (survivorship: 278 seeds/300 = 92.6%).

Table 1 – Frugivores birds observed feeding on *Euterpe edulis* at Anchieta (island) and Caraguá (mainland) in the Atlantic rain forest, Brazil. NP = species is not present; P = species is present but not registered on point counts. "No. of visits/plant" considers only visited plants. N = 13 for Anchieta and 18 plants for Caraguá.

Species	Abundance (individuals/point)		Mean no. of fruits eaten/visit (% of visits)		No. of visits/plant (% plants visited)	
	Anchieta	Caraguá	Anchieta	Caraguá	Anchieta	Caraguá
Large frugivores						
Trogonidae						
Trogon viridis	NP	0.33	–	1 (2)	–	1 (5)
Momotidae						
Baryphthengus ruficapillus	NP	P	–	1 (2.5)	–	6 (5)
Ramphastidae						
Ramphastos dicolorus	NP	P	–	–	–	0
S. maculirostris[a]	NP	0.05	–	–	–	0
P. bailloni[a]	NP	0.17	–	–	–	0
Medium frugivores						
Turdidae						
Turdus flavipes	0.7	0.27	0.85 (78)	1.65 (93.5)	15 (53.8)	10.8 (83)
Turdus albicollis	0.57	0.39	1.5 (9)	1 (2)	1.3 (53.8)	0.5 (11)
Cardinalidae						
Saltator similis	0.21	P	0.84 (13)		5.5 (15)	–
Total			0.90	1.56	12.5	10

a Species eating fruits of *E. edulis* on *ad libitum* observations.

3.4. Seed predation on the presence and absence of E. edulis at Anchieta

We only recorded one secondary seed dispersal event in the habitat where *E. edulis* occur (during the wet season), and all other removed seeds that we located were evidently destroyed. Higher seed predation was found in the habitat where the species occurs (likelihood χ^2 (G)-test, $\chi^2 = 15.72$, $p < 0.0001$). In these areas we registered 71.67% of seed predation, compared to 28.33% in areas where *E. edulis* is absent. However this difference was a consequence of a strong difference between areas during the dry season ($\chi^2 = 50.42$, $p < 0.0001$, present 91.67% and absent 31.67%), once we found no differences between areas on wet season ($\chi^2 = 1.22$, $p = 0.27$, present 51.67% and absent 61.7%). In summary, we found a strong seasonal effect on seed predation where the species is present (Nominal Logistic model, $\chi^2 = 19.08$, $p < 0.0001$), being more intense during the dry season.

3.5. Population structure

Seedlings and saplings were, on average, almost 14 times more abundant at Caraguá than in Anchieta (seedlings: $\chi^2 = 44.8$, df = 1, $p < 0.001$; saplings: $\chi^2 = 48.2$, df = 1, $p < 0.001$). Similarly, adults were 2.4 times more abundant in Caraguá (Fig. 2). Seedlings varied from 0 to 21 individuals per plot in Anchieta and from 0 to 92 in Caraguá. Saplings varied from 0 to 15 in Anchieta and 0 to 62 in Caraguá, while adults varied from 0 to 5 in Anchieta and 0 to 22 in Caraguá. The ratio of seedlings and saplings per adult was 15- and 24-fold greater in Caraguá than in Anchieta, respectively, showing that the recruitment per capita is much higher in the mainland than in the island.

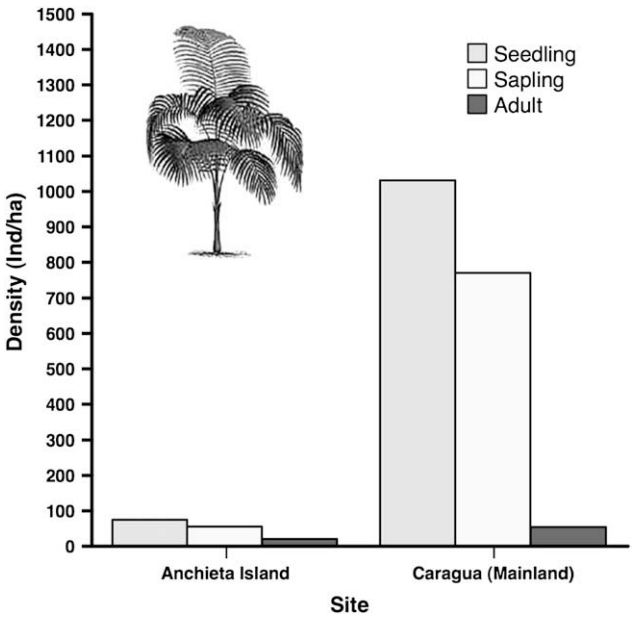

Fig. 2 – Density of *Euterpe edulis* (individuals ha^{-1}) at Anchieta Island and Caraguá, in the Atlantic forest, southeastern Brazil. Data were collected in 40 sample plots (4 × 50 m) on each study site.

4. Discussion

4.1. Bird diversity, density and seed dispersal

We found a depauperate frugivore assemblage where one species (*T. flavipes*) is the most important seed disperser of *E. edulis* in both Anchieta and Caraguá. The low diversity of large frugivorous birds observed eating *Euterpe* fruits at Caraguá maybe due to the high abundance of palms in that site which makes it more difficult to sample all species that feed on palm fruits (Galetti et al., 1999) or due to the impact of the illegal harvesting in some areas (Galetti and Aleixo, 1998). A low diversity of seed dispersers may have negative consequences for the quality component of seed dispersal, such as seed treatment and deposition (Schupp, 1993; Jordano and Schupp, 2000). Otherwise, because some large frugivores, such as toucans, travel across different habitat types, including degraded and fragmented forest areas (Holbrook et al., 2002), they may promote gene flow and help to maintain genetic diversity of *Euterpe* populations (Conte et al., 2003).

The yellow-legged Thrush *T. flavipes* is also an important seed disperser of *E. edulis* in other Atlantic forest sites, mainly in forest fragments, but its relative importance varies when compared to large-bodied avian frugivores (Table 2). Even though *T. flavipes* had higher visitation rates in Anchieta, its 4-fold increase in density at Anchieta did not result in higher seed removal. In fact, *Euterpe* at Anchieta had 1.7 lower removal rates than at Caraguá and fully one-third of the palms that we observed were not visited by any bird.

Staggemeyer and Galetti (2007) and Kirika et al. (2008) did not find compensation in dispersal services with an increase in disperser abundance of few species in areas with anthropogenic disturbance. This pattern is particularly evident when the major disperser is a territorial species. *T. flavipes* maintains winter feeding territories within which they defend fruit-laden trees and shrubs. *E. edulis* is by far the most important of the plants defended (Castro et al., unpublished data). Fruit defense associated with territoriality has been noted in some thrush species (Turdidae), such as the mistle thrush *Turdus viscivorus*, fieldfare *T. pilaris*, and robin *Erithacus rubecula*, which form winter territories in places with abundant berries and defend them as long-term resources (Snow and Snow, 1988). The high density of *T. flavipes*, the low availability of *E. edulis* and other fleshy fruits (Genini et al., 2008) and its aggressive behavior against frugivorous competitors may explain the lower fruit removal rate at Anchieta. Since large-bodied frugivores are absent from Anchieta and body size determines the dominance hierarchies in preferential fruiting trees in tropical frugivores (French and Smith, 2005), *T. flavipes* has no other frugivorous birds to displace it from fruiting patches.

4.2. Post-dispersal seed predation

We found the highest seed predation of *E. edulis* at Anchieta than any other area in the Atlantic forest (Table 3). This excessive predation is due to the high density of agoutis (19,753 ind/km^2, Bovendorp and Galetti, 2007). Only one other small rodent would be able to prey upon *E. edulis* seeds at

Table 2 – Main legitimate bird seed dispersers consuming fruits of *E. edulis* recorded in other studies through the Atlantic forest, and their relative importance for seed removal of this palm species on each site. The records of *Turdus* spp. are mainly composed of *T. flavipes*.

Study	Conservation condition	Frugivore size	No. of species[b]	Main seed dispersers	No. of fruits dispersed/visit[a]	% visits of total
Laps (1992)	Continuous (Pristine)	Medium	3	*Turdus* spp.	1.9 ± 0.4	25.7
		Large	6	Toucans, toucanets, cotingids and trogon	5.15 ± 3.4	65.7
		Large	2	Guans	46.2 ± 54.4	8.6
Matos and Watkinson (1998)	Fragment (Harvested)	Medium	5	*Turdus* spp.	1.9 ± 0.4	97
		Large	0	–	–	–
Côrtes (2006)[c]	Island (Pristine)	Medium	3	*Turdus* spp.	1.59 ± 0.4	75.7
		Large	4	Toucans, toucanets and cotingids	4.4 ± 3	24.3
Cerisola et al. (2007)	Fragment (Harvested)	Medium	4	*Turdus* spp.	Not shown	64
		Large	3	Toucan, cotingid	Not shown	Not shown
Von Matter (2008)	Contiguous (Pristine)	Medium	3	*T. albicollis*	3.1 ± 0.78	46
		Large	7	Cotingids, toucans and toucanets	7.27 ± 3.5	54
This study (Anchieta)	Island (Harvested)	Medium	3	*Turdus* spp.,	1 ± 0.38	100
		Large	–	None	0	0
This study (Caragua)	Continuous (Pristine)	Medium	2	*Turdus* spp.	1.3 ± 0.46	94
		Large	2	Trogon, Motmot	1 ± 0	6

a These numbers constitute the average of means for different species. Therefore, because of the difference in calculation, they are not the same as appeared in Table 1.
b There may be more species in the study sites. Except for this study, only the main seed dispersers were used here for simplicity.
c Due to spatial differences in frugivory within this study site, we only consider visits performed by frugivores in highlands.

Anchieta, the spiny rat *Trinomys iheringi*, but it is extremely rare in Anchieta (R. Bovendorp, unpublished data). Generalist herbivores such as rodents appear to feed less selectively at high than at low population densities (Pizo and Vieira, 2004), and thus are able to cause huge impacts in plant populations (Terborgh et al., 2006).

Typical populations of *E. edulis* form large seedling banks (average of 12,000 seedlings ha^{-1}) in swampy areas in both primary and secondary forest in the Atlantic forest (Conte et al., 2000), and depend on large seed production to recruit. Therefore, the high seed predation rates result in a lower population of seedlings and juveniles at Anchieta, potentially affecting negatively the recruitment of new adults. Additionally, we found a lower density of juveniles at Anchieta in comparison to Caraguá even if we had analyzed only swampy areas (Fadini, 2005), suggesting that seed

Table 3 – Seed predation of *Euterpe edulis* in the Atlantic Forest.

Study site	Conservation condition	No. of seeds	Time of exposition (days)	% of seeds preyed upon	Reference
Blumenau	Forest fragment	800	150	23.6	Reis (1995)[a]
Intervales	Continuous (Pristine)	300	365	7	Pizo and Simão (2001)[a]
Caetetus	Forest fragments	180	40	31	Fleury and Galetti (2004)
Mata São José		180	40	15	
Intervales	Contiguous to pristine (Harvested)	300	60	20–27	Pizo and Vieira (2004)[a]
	Continuous (Pristine)	300	60	20–22	
Santa Virgínia	Continuous (Pristine)	556	35	37.5	Voltolini (2004)
Intervales	Continuous (Pristine)	315	30	50	Von Allmen et al. (2004)[a]
Caraguá Anchieta	Continuous Island	340	30	**7.4**	This study
		340	30	**99.7**	

a When the study presented various treatments, we provide the results as ranges instead of means. Insects were always much more important seed predators than rodents (information gathered from box-and-whiskers plots). However, we could not provide this information because most of the papers gave the pooled estimates only.

predation and seedling herbivory is still overwhelming in this microhabitat.

4.3. *Management considerations*

The palm *E. edulis* is considered as one of the most important fruit sources for several frugivores in the Atlantic forest (Galetti and Aleixo, 1998; Galetti et al., 1999). Forest sites where this palm was not harvested produce about 173 kg ha^{-1} year^{-1} (or 80% of the overall fruit biomass; Galetti and Aleixo, 1998), but only 14 kg ha^{-1} year^{-1} at Anchieta (or 12% of the overall fruit biomass; Genini et al., 2008). This palm is considered a keystone species in fragmented forests (Mikich, 2002) and in continuous forests in La Niña years when the tree community fails to reproduce (M. Galetti et al., unpublished data). Therefore, an increase in density of palmito in Anchieta will increase the carrying capacity for frugivores and may attract large-bodied frugivores from the mainland, which, in turn, can disperse large seeds, such as *Virola* spp. and other species, and speed up the regeneration process of non-forested areas on the island.

We suggest three main alternatives to recover the population of *E. edulis* at Anchieta: 1) to sow seeds and exclude seed predators, 2) to plant juveniles and protect these from herbivory to enhance plant survivorship of earlier stages, and 3) to eradicate or control populations of major alien seed predators and herbivores.

Our study showed that planting seeds in sites without *Euterpe* is certainly the less expensive strategy to enhance seedling populations. Von Allmen et al. (2004) used a similar approach and did not find a distance-dependent response on seed predation. They suggest that because seeds were abundant and found everywhere, rodents have no necessity to search for them in particular microsites. Therefore, high seed survivorship in sites without *E. edulis* found in our study may suggest that agoutis are spatially oriented, concentrating their activities in sites with high fruit production (Silvius and Fragoso, 2003). Since overall seed predation is extremely high at Anchieta, planting seedlings and juveniles would be a better strategy, but will require plant protection in the earlier stages because of elevated herbivory, especially from capybaras (*Hydrochaeris hydrochaeris*, Alvarez et al., 2008).

Management of populations of agoutis and capybaras may be the more effective strategy, but also the most expensive and controversial. Agoutis usually prey upon most seeds with less than 3.5 g at Anchieta, but are important dispersers of large palm seeds (Galetti et al., 2006; M. Galetti, unpublished data). Additionally, they are known to prey upon ground nesting birds at Anchieta (Alvarez and Galetti, 2007). Therefore, maintaining their populations to a natural level would help to regenerate some important large-seeded plant species that were extirpated from Anchieta (such as of the Sapotaceae, Myristicaceae and Laruaceae families), and facilitate the recolonization of some fruit-eating birds from the mainland. Nowadays the population of agoutis in the island is at least 8 times higher than in the mainland of the Atlantic forest (Bovendorp and Galetti, 2007).

A specific legislation for animal management in Brazil is still poorly enforced. Moreover, animals such as capybaras and agoutis are charismatic to the general public (and even to the park administration), and the proposal of eradication of their populations may not be welcomed. Therefore, the fate of the *Euterpe* population at Anchieta Island is in jeopardy and its extinction will exacerbate the regeneration collapse of this island.

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