

Changes in Seed Predation of *Attalea dubia* in a Gradient of Atlantic Forest Disturbance in Brazil

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Many tropical forest biomes are now human-modified landscapes consisting of mosaics of forests under different degrees of anthropogenic disturbances immersed in a matrix of pastures and croplands (Melo et al. 2013). The conservation of the original plant diversity in these landscapes relies on the mechanisms that allow population persistence in the remnant patches such as adult survival and seedling recruitment (Portela et al. 2010). Plant population persistence may also rely on seed dispersal and predation that allow the colonization and recolonization of the patches (Tabarelli et al. 2010, McConkey et al. 2012).

Seed predators often control the abundance and spatial distribution of plants (Janzen 1971, Wright 2002), and seed predation may vary in different microhabitats (Christianini & Galetti 2007). It is not rare to find seed predators consuming all the seed crop and restricting plant regeneration to areas harboring low activity of granivores (Janzen 1971, Francisco et al. 2002, Wright 2002, Rodríguez et al. 2014).

For example, because granivorous rodents are more susceptible to predation by aerial and visually oriented predators in areas with less vegetation cover, they avoid foraging in these areas (Manson & Stiles 1998, Christianini & Galetti 2007). As a consequence, seed survival is less likely in closed canopy spots than in vegetation gaps (Manson & Stiles 1998). Resource abundance can also affect the

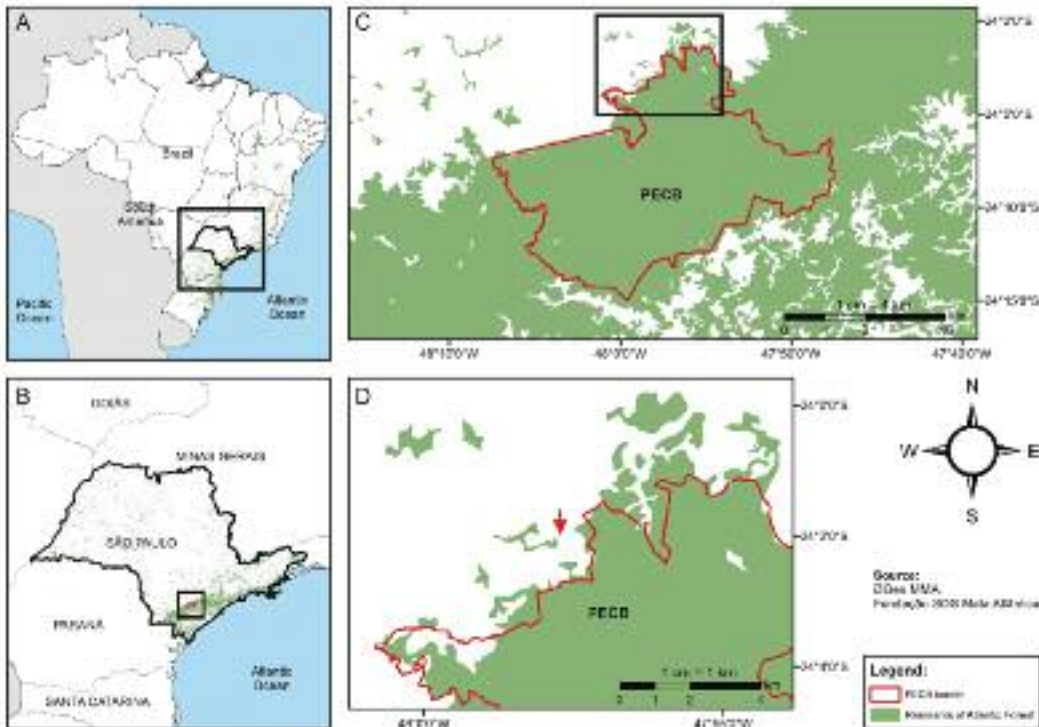
likelihood of seed predation since high seed production may satiate granivores, allowing more seeds to escape (Janzen 1971, Jansen et al. 2004, Wright 1990). Low food availability may force starved animals to forage in less favorable habitats and with a higher risk of predation (Lima & Dill 1990).

Forest disturbances such as habitat loss and fragmentation, edge effects, fire and hunting often change the abundance of pollinators, seed dispersers and granivores thus changing the likelihood of seed production, dispersal and mortality (Wright & Duber 2001, Aguilar et al. 2006, Galetti et al. 2006, Markl et al. 2012). Reductions in the abundance of vertebrate frugivores that perform seed dispersal and/or predation, such as lowland tapir (*Tapirus terrestris*), agoutis (*Dasyprocta* spp.) and peccaries (*Tayassu pecari* and *Pecari tajacu*), are common in tropical human-modified landscapes (Chiarello 1999, Peres & Palacios 2007, Galetti et al. 2009, Jorge et al. 2013). As a consequence many seeds are not dispersed and accumulate beneath parent plants, constraining plant regeneration to the vicinity (Dirzo & Miranda 1991, Cordeiro & Howe 2003, Galetti et al. 2006, Terborgh et al.

2008, Terborgh 2013). Specialized invertebrate granivores, such as weevils, may increase in response to an increase in food availability represented by undispersed seeds beneath parent plants (Wright 2003). In disturbed patches beetles may prey on a larger fraction of undispersed seeds, compensating for the decrease in seed predation by large vertebrate granivores. Such compensatory effects may constrain plant regeneration in disturbed patches but are seldom investigated (e.g. Wright & Duber 2001, Wright 2003, Galetti et al. 2006, Andreazzi et al. 2012).

The Brazilian Atlantic Forest (BAF) is a global hotspot of biodiversity consisting mostly of a mosaic of small forest fragments immersed in a matrix of agriculture, pasturelands and human settlements (Ribeiro et al. 2009). Current estimates of BAF cover varies between 11–16% of the original forest that once reached more than 1 million km² (Ribeiro et al. 2009). More than 80% of the remnants of the BAF consist of small, disturbed and isolated forest fragments smaller than 50 ha (Ribeiro et al. 2009). However, BAF still houses a rich diversity of palms including 10 genera and about 35–45 species, many of them endemics

1. Location of the study sites in São Paulo state, southeast Brazil (A, B). Atlantic forest remnants are in green. The study sites were near the northern border of an old-growth forest, the Carlos Botelho State Park (PECB) which is depicted in red (C). The red arrow in D indicates the location of the pastureland and nearby disturbed forest fragment studied.





2. View of the disturbed forest fragment from the adjacent pastureland, where some palms were sampled. The crown of several *Attalea dubia* is visible in the background (Photo: Ana Y.Y. Meiga).

(Henderson et al. 1995, Lorenzi et al. 1996). Palms often provide keystone food resources (fruit pulp and seeds) to frugivorous animals thanks to the abundance of nutritious crops and extended fruiting during periods of scarcity (Terborgh 1986, Genini et al. 2009). Palms may also out-compete other plants or create opportunities for plant recruitment thus affecting plant diversity at small scales (Aguiar & Tabarelli 2010, Correa et al. 2012). Meanwhile, palms influence the successional trajectories of disturbed sites. Disturbances often have negative effects on BAF palms, but the information available is restricted to few species (Lorenzi et al. 1996, Montúfar et al. 2011) with most studies concentrated on *Astrocaryum aculeatissimum* (Galetti et al. 2006, Donatti et al. 2009, Portela et al. 2010), *Attalea humilis* (e.g. Souza & Martins 2004, Andreazzi et al. 2012), *Euterpe edulis* (e.g. Fadini et al. 2009, Portela et al. 2010) and *Syagrus romanzoffiana* (Fleury & Galetti 2004, 2006). Surprisingly certain species of *Attalea* such as *A. oleifera* (Aguiar & Tabarelli 2010), *A. humilis* (Souza & Martins 2004, Andreazzi et al. 2012) and *A. dubia* (Ana Y.Y. Meiga pers. obs.) may increase in abundance after BAF disturbance. Mechanisms behind this apparent unusual response may include good competition performance (Aguiar & Tabarelli 2010), resistance to fire (Souza & Martins 2004),

increased seed production and reduced granivory by rodents (Andreazzi et al. 2012). The possible compensatory role of beetle seed predation in response to a potential decrease in seed eating by vertebrates mediated by environmental disturbance is poorly investigated in BAF palms (Galetti et al. 2006, Donatti et al. 2009, Andreazzi et al. 2012). We compared the fate of *Attalea dubia* seeds across a gradient of BAF disturbance including an old growth and protected forest, a forest fragment and a pastureland. We tested if rodents and weevils switched roles in seed predation across the gradient (i.e., compensation), if the number of seeds found beneath palms influences the chance of seed survival (i.e., predator satiation) and discussed the possible consequences for plant regeneration.

Methods

Study sites: Palm seed predation was sampled in three sites following a gradient of disturbance: A low disturbed forest (Carlos Botelho State Park, hereafter PECB), an intermediate disturbed forest fragment ca. 1 km from the park border and a heavily disturbed site represented by a pastureland adjacent to the fragment (Fig. 1). PECB is a 37,644 ha protected area covered by old-growth humid Atlantic forest in São Miguel Arcanjo, Southeast Brazil (24°00'–24°15'S,

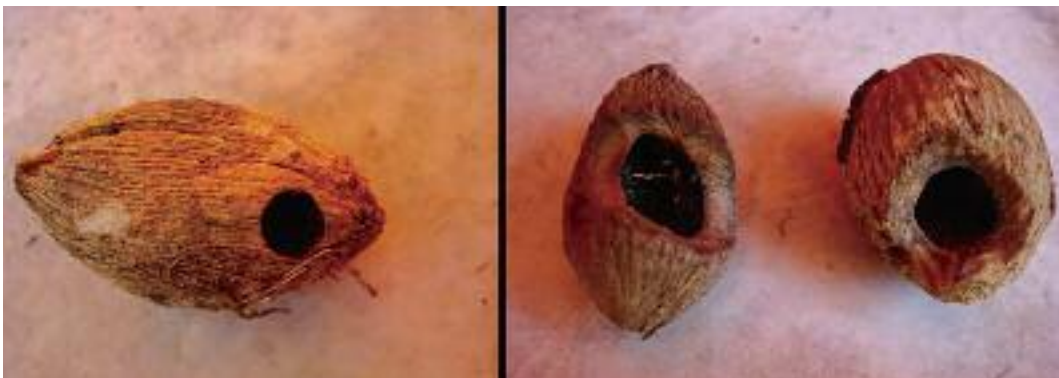
47°45'–48°10' W) (Fig. 1). PECB is a neighbor of other pristine areas that together encompass the largest continuous remnant of Atlantic forests (> 1200 km², Ribeiro et al. 2009). The park holds at least 1000 vascular plant species (Lima et al. 2011) and several threatened large frugivores such as Lowland tapirs (*Tapirus terrestris*) and Woolly spider monkeys (*Brachyteles arachnoides*) (Brocardo et al. 2012). Mean annual temperatures vary between 17° and 22°C and mean annual rainfall between 1700 and 2400 mm, with no clear dry season (São Paulo 2008). The disturbed fragment (24°01'S, 47°57'W) is a ca. 20 ha forest patch with evidence of past logging, an impoverished flora and lower trees compared to PECB (Fig. 2). The abundance of *Attalea dubia* is higher in the fragment compared to PECB (Ana Y.Y. Meiga pers. obs.). The fragment is surrounded by pastureland planted with the African grass *Urochloa* sp. (locally known as *braquiária*) used for cattle ranching. The pastureland is sprinkled with a few isolated *A. dubia* (Fig. 2).

Study species: *Attalea dubia* (Mart.) Burret (Arecaceae) is a ca. 20 m tall palm endemic to the humid Brazilian coastal forests (Henderson et al. 1995). In PECB, flowering occurs between February and April, while unripe fruits are presented throughout the year with ripe fruits peaking between September and October (Ana Y.Y. Meiga unpubl. data). The endocarp is covered with a fleshy, orange and fibrous pulp (mesocarp) surrounding one "seed." For easy interpretation we will refer to the seed plus endocarp as "seed." Seeds are 4.2 ± 0.4 cm in length and 2.4 ± 0.2 cm in diameter (mean ± SD, n=484), with 16 ± 4 g of fresh mass (n=12). In PECB, Capuchin monkeys (*Sapajus nigritus*) feed on the fruit pulp and thereafter drop the seeds beneath the palm. Squirrels (*Sciurus ingrami*) and unidentified Sigmodontinae

rodents prey on or scatterhoard the seeds and supposedly disperse and behave as seed predators (Ana Y.Y. Meiga unpubl. data), similar to what has been reported for *Attalea* species elsewhere (Carvajal & Adler 2008, Almeida & Galetti 2007). Larvae of boring beetles (*Pachymerus* sp.) prey on the seed of *A. dubia*, leaving a characteristically circular hole in the seed coat that enables us to discriminate predation between beetles and rodents (Steffler et al. 2008) (Fig. 3).

Measurements of seed predation: To evaluate seed predation, we collected all seeds found in quadrats under adult palms in November 2011. Only palms that finished fruiting were sampled. In PECB, we sampled seeds in a 2x2 m quadrat adjacent to each of ten adult palms. Sampled palms were at least 100 m away from one another and with a minimum distance of 10 m from the nearest conspecific fruiting palm. In the forest fragment, where adult palms and seed density were higher, we randomly selected four adult palms with a minimum distance of 40 m from one another and at least 5 m from the nearest fruiting palm. In the pastureland we sampled four palms with a minimum distance of 40 m from the nearest conspecific. In the fragment and pastureland we collected all the seeds found on a 1x1m quadrat adjacent to each palm. All seeds were carefully inspected and assigned to a category of fate: intact, preyed on by rodents, preyed on by beetles or rotten. We compared seed density among sites with one-way ANOVA. We evaluated if the proportion of seeds in fate categories differed among sites with sequential G-tests (Rice 1989). We tested if there was a relationship between seed predation by rodents and beetles with linear correlation (both variables Log transformed). To investigate the possibility of granivore satiation

3. Seeds of *Attalea dubia* preyed on by beetles (left) or by rodents (right) (Photos: Ana Y.Y. Meiga). Each seed has a mean length of 4.2 cm.



we regressed the number (Log) or proportion of intact seeds/m² against the total number of seeds/m² (Log). For correlations and regressions we pooled all palms and sites for the analysis to increase power. All tests followed Zar (1999).

Results

The density of seeds/m² under adult palms differed among sites (ANOVA: $F=7.3$, $df=2$, $p=0.006$). The PECB, fragment and pastureland had 6.3 ± 1.2 , 25.8 ± 13.3 and 43.8 ± 12.9 seeds/m², respectively (mean \pm SE of untransformed values). There were marked differences among seed fate categories and sites (G-test: $G=196.6$, $df=6$, $p<0.001$, Fig. 4). Intact seeds dominated samples at all sites (up to 87% in pastureland). Seed losses to rodents (up to 35%) were more common than those to beetles in PECB and in the fragment but not in the pastureland (Fig. 4). Beetles destroyed up to 16% of seeds at any given site. Rotten seeds were common in PECB (30%), rare in pastureland (<1%) and absent in the fragment (Fig. 4). Observations of the residual frequencies and sequential G-tests indicated that palms in the pastureland contributed significantly larger positive deviance than expected for intact seeds and negative deviances for seeds rotten, preyed on by rodents or beetles. Palms in PECB had a positive deviance for rotten seeds and a negative deviance for intact seeds. Finally, palms in the fragment had an excess of seeds preyed upon by rodents and a negative

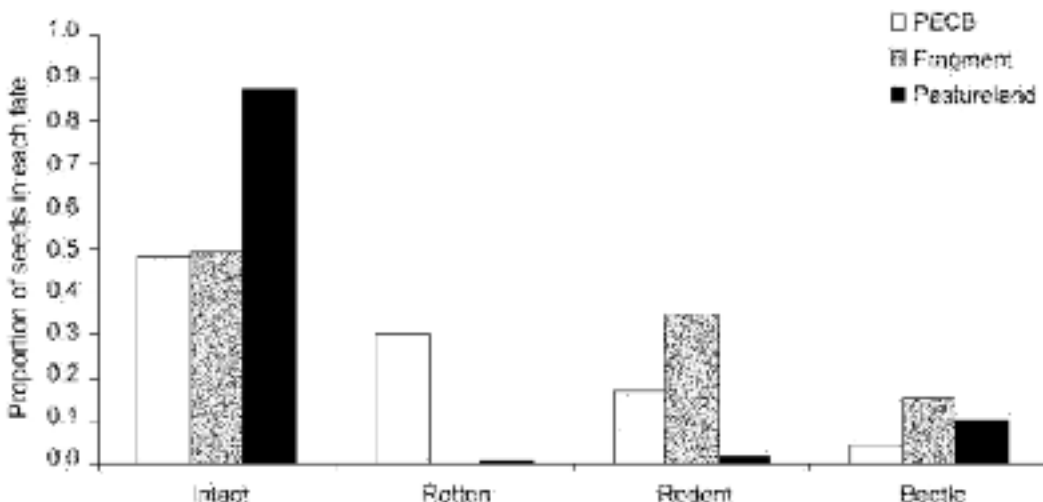
deviance of intact and rotten seeds. Seed predation by rodents and beetles did not vary between PECB and fragment ($G=1.51$, $df=1$, $p=0.22$).

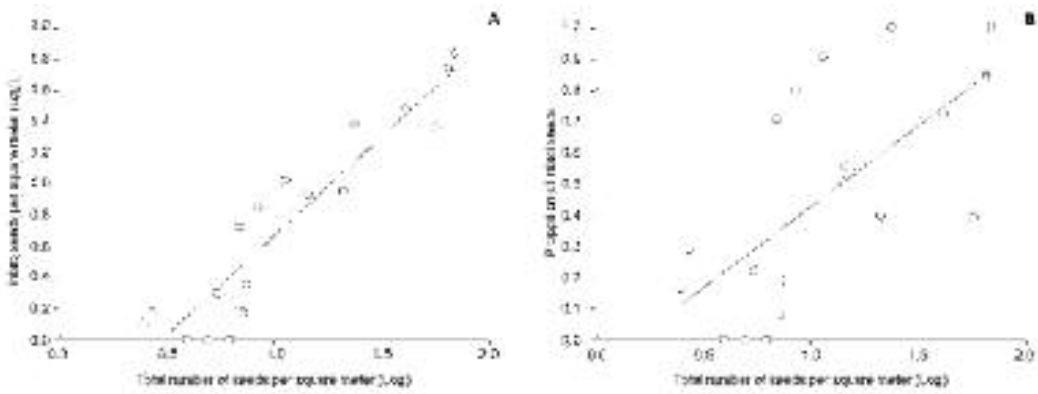
Contrary to expectations, seed predation by beetles and rodents did not show compensation and were positively related (Linear correlation on log-transformed data: $r=0.56$, $n=16$, $F=7.28$, $p=0.016$). Both the number of intact seeds/m² (slope= 1.28 ± 0.12 , $r^2=0.87$, $n=16$, $F=111.1$, $p<0.001$) and the proportion of intact seeds/m² (slope= 0.52 ± 0.15 , $r^2=0.44$, $n=16$, $F=12.6$, $p=0.002$) were positively affected by increments in the total number of seeds/m² under palms (Fig. 5).

Discussion

We found great variation in the main sources of mortality of the seeds of *Attalea dubia* across the gradient of forest disturbance. However, we detected no clear effect of compensation among the sources of mortality among and within sites. The more disturbed the site, the larger was seed density and survival under parent plants. Although we did not measure seed production, we expected a significant increase in crop size with increasing disturbance because there is evidence that forest palms, such as *Attalea speciosa* from the Amazon, invest more resources to reproduction whenever exposed to high light conditions such as in pasturelands (Barot et al. 2005). The congeneric *A. humilis* also shows increased reproductive output in disturbed BAF

4. Variability in the fate of seeds found under adult palms of *Attalea dubia* in a gradient of forest disturbance in southeast Brazil. The old growth forest found at Carlos Botelho State Park (PECB) had 253 seeds sampled, followed by 104 and 175 seeds in a nearby disturbed forest fragment and a pastureland, respectively. See text for details of sampling and results of comparisons.





5. Influence of the total amount of seeds on the number (A) or proportion (B) of seeds that escape predation beneath the palm *Attalea dubia* in a gradient of Atlantic forest disturbance in southeast Brazil. Each dot depicts data for one palm and all sites are pooled. Both relationships were significant suggesting that plants producing large seed crops attain higher seed survival.

compared to controls (Andreazzi et al. 2012). Thus, more seeds would be available for seed dispersers and predators in disturbed sites. We found indirect evidence for the same effect in *A. dubia*, with four- and seven-fold higher density of seeds/m² beneath palms in the fragment and pastureland, respectively, than in the old-growth forest (PECB). A lower removal of fallen fruits/seeds by vertebrates in disturbed sites could also contribute to these values (Cordeiro & Howe 2003, Galetti et al. 2006, Terborgh et al. 2008, Donatti et al. 2009).

High seed density beneath palms increases the number and proportion of intact seeds, suggesting predator satiation (Janzen 1971, Wright 1990). This surplus of intact seeds in disturbed sites may decrease seed limitation and increases the likelihood of plant regeneration, since plants producing large seeds like *A. dubia* are often more seed limited (Moles & Westoby 2002). We often found *A. dubia* seedlings around adult palms in all sites (A.Y.Y. Meiga and A.V. Christianini pers. obs.). Indeed, spatially aggregated patterns of palm recruitment are common in disturbed BAF sites suggesting the possibility of enhanced plant recruitment near parental palms following disturbances, as has been shown for *A. humilis* (Souza & Martins 2004) and *Syagrus romanzoffiana* (Sica et al. 2014). High seed output and low seed predation may thus explain the increases in the abundance of *Attalea* in disturbed forest fragments compared to old-growth forests (Wright & Duber 2001, Souza & Martins 2004, Andreazzi et al. 2012, this study).

Pathogens, rodents and beetles respond to the largest source of seed loss in the PECB,

fragment and pastureland, respectively. Low light and high humidity, typical of old-growth humid forests, often favor pathogen infestation of seeds (Augspurger 1984). Fragment edges and pasturelands are subject to high light conditions that are correlated with increased predation hazard to rodents that, consequently, avoid these areas (Stevens & Husband 1998). Rodent abundance and diversity are often reduced in BAF fragments (Pardini 2004), which may be followed by a decrease in interactions between rodents and palm seeds in small fragments (Fleury & Galetti 2004, 2006). However, contrary to this expectation we found relatively high seed predation by rodents in the disturbed fragment. It is possible that small and generalist species of granivorous rodents increase in abundance in disturbed and small fragments of BAF (Pardini 2004) in response to a decrease in top predators that control their abundance (e.g., Dirzo et al. 2014). The higher density of rodents in these areas would translate in increased seed predation by rodents (Dirzo et al. 2007). Low resource availability in fragments may also increase the likelihood of seed predation by rodents that otherwise would behave as scatterhoarders and seed dispersers (Jorge & Howe 2009). The effect of BAF disturbance on palm seed predation is rather complex and hard to predict, as it seems to be not a linear function of fragment size, distance to fragment edge, type of surrounding matrix and degree of defaunation, with palm identity also playing a role (Fleury & Galetti 2004, 2006, Galetti et al. 2006, Donatti et al. 2009, Fadini et al. 2009, Andreazzi et al. 2012).

Beetles are the only relevant source of seed mortality in all sites along the gradient of forest

disturbance. This result indicates that *Pachymerus* sp. is able to disperse, find and colonize available seed hosts in pasturelands away from forests, but they are unable to cause drastic reductions in the amount of intact seeds. Although a shift between rodent and beetle seed predation was observed in PECB and the pastureland, beetles did not compensate when seed predation by rodents fell to low values within a site, as demonstrated by the positive correlation between rodent and beetle seed predation. Fruit pulp may work as a barrier against seed boorers, and pulp removal by rodents may increase opportunities of oviposition by weevil beetles (Silvius & Fragoso 2002, Ríos & Pacheco 2006, Rodríguez et al. 2014). This may be the reason why seed predation of *A. dubia* by beetles is much higher in Cardoso State Park (48.9% of seeds preyed on by beetles, Steffler et al. 2008), a large and protected site where the abundance of large rodents such as agoutis (*Dasyprocta* spp.) is higher than many other BAF sites (Donatti et al. 2009). Therefore, in the face of a decrease in rodent activity in pasturelands, reproductive success of beetles may be limited, and they may be unable to take advantage of the high number of undispersed seeds available beneath parent plants.

Release from seed predation and increasing crop size in response to disturbances may underlie the unexpected increase in *Attalea* abundance in human modified landscapes (see also Barot et al. 2005, Andreazzi et al. 2012). From a community perspective, low palm seed predation rates following disturbances may create opportunities for exotic plant invasions that often impoverish the biodiversity value of human modified landscapes. For instance, low seed predation and high plant fecundity are among the possible causes of the successful invasion of disturbed BAF by the Australian palm *Archontophoenix cunninghamiana* (Christianini 2006). Low seed predation of competitive superior species, such as *Attalea* (Aguiar & Tabarelli 2010, Andreazzi et al. 2012), may also increase community dominance of these species and decrease plant diversity in the long run (Wright & Duber 2001, Wright 2003).

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