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Original article

Litterfall, seed size, and predator-free time window enhance survival of a keystone palm in an Atlantic forest restored site

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ABSTRACT

Although enrichment planting is recommended to increase biodiversity in restoration, environmental filters can prevent the establishment of sowed/planted species. *Euterpe edulis* is a keystone palm in the Brazilian Atlantic forest, whose fruits are consumed by many animals. We assessed the viability of direct seeding of this palm in an Atlantic forest restored site in Southeast Brazil, guided by these questions: 1) Does germinability vary among seeds covered and uncovered by litterfall and according to litterfall depth? 2) Can direct seeding be impaired by seed predation? 3) Does seed size affect seed predation and seedling vigor? We found litterfall favored germination by reducing soil evaporation, but litterfall depth did not affect germination. Seed predation was low, as seed location was probably unpredictable to rodents. Smaller seeds were more removed, possibly because the larger ones impose transportation costs on small rodents. By removing the smaller seeds, predators may favor the production of larger and more vigorous seedlings. Direct seeding of *E. edulis* can be successful if implemented in medium regeneration stages of Atlantic forest sites, where shade and moisture provided by litterfall, and absence of mid- to large-sized seed predators, allow seeds to overcome the constraints on germination and predation.

Keywords: direct seeding, enrichment planting, *Euterpe edulis*, forest restoration, germination, keystone palm, litterfall, population reinforcement, reintroduction, seed predation

Introduction

Many forest fragments in the tropical forest are under ecological succession (Hansen *et al.* 2013). So, secondary forests represent most of the vegetation in anthropized areas (Chazdon *et al.* 2009; Forbes *et al.* 2020). Intact forests have disappeared, causing severe habitat loss and the local extinction of several species throughout the world (Dirzo & Raven 2003; Powers & Jetz 2019). To mitigate this situation, foresters have used enrichment planting by adding species ecologically threatened or vulnerable, otherwise unable to colonize restored areas or forest fragments, improving the local biodiversity (Lamb *et al.* 2005).

Two main techniques have been used for forest enrichment and restoration: direct seeding and planting

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of seedlings (Palma & Laurance 2015). From an economic perspective, direct seeding is much more cost-effective than growing and planting seedlings (Meli *et al.* 2018). However, the success of this technique depends on knowing whether the seeds of the focal species can overcome environmental barriers to germination and establishment.

Germination is one of the earliest events in the life history of plants, eventually determining the vegetal community composition (Braz *et al.* 2014). This process is affected by a strong natural selection once the plant needs to overleap the seedling stage to express other adaptive characters (Donohue *et al.* 2010). Germination niche - a range of specific conditions under which seeds germinate (Grubb 1977) – is a key aspect of forest recovery, determining the spatial and ecological species distribution (Brändle *et al.* 2003; Donohue *et al.* 2010). Seeds are adapted to germinate on habitats in which the species reproduces. Understanding the relationships between germination and environmental requirements is essential to improve forest restoration actions (Baskin & Baskin 2001).

Several environmental filters can prevent seed germination. Particular characters of species allow their seeds to germinate at different places and times, occupying different niches (Grubb 1977). Generally, light and water are essential factors affecting this process (Baskin & Baskin 2001). In tropical forests, light is usually necessary for pioneer plant germination (Vazquez-Yañes & Orozco-Segovia 1993), but it is not strongly required for many later successional species. In this sense, litterfall on the forest floor can inhibit or stimulates germination (Vazquez-Yañes & Orozco-Segovia 1993). It avoids water vapor diffusion (Facelli & Pickett 1991), holding enough moisture for germination of large and recalcitrant seeds (Molofksky & Augspurger 1992). Conversely, a thick litter or soil layer covering positive photoblastic seeds may be sufficient to prevent germination (Monk & Gabrielson 1985).

Seed size is another relevant factor affecting seedling survival. Larger seeds have more energy reserves, allowing the radicular system of the seedlings to reach deeper into the soil, finding better water supplies, and enabling the aerial part to also reach higher into the light (Westoby *et al.* 1996). Contrary, seedlings from tiny seeds may not have enough energy to grow in darkness throughout the litter layer (Vazquez-Yañes & Orozco-Segovia 1993). Some studies showed a positive relationship between seed size and seedling vigor (Gonzalez 1993; Pizo *et al.* 2006; Ambika *et al.* 2014). At the same time, predation on larger seeds tends to be higher (Wenny 2001), resulting in fewer germinations. In this sense, rapid germination may be ecologically advantageous, minimizing seed exposure to rodents and other potential predators (Pizo *et al.* 2006; Xiao *et al.* 2007; Donohue *et al.* 2010; Braz *et al.* 2014). When environmental conditions are favorable, early germination provides a competitive advantage, enabling better growth to the plant before the reproductive stage (Donohue *et al.* 2010). Yet, in adverse conditions, a germination delay may benefit seedling survival and competition (Vazquez-Yañes & Orozco-Segovia 1993).

As germination is a crucial stage in forest recovery, field studies are increasingly necessary to understand how this process operates under natural conditions (Volis 2016). Therefore, we aimed to assess the viability of planting *Euterpe edulis* (Arecaceae) by direct seeding in areas under restoration in the Atlantic forest, guided by the following questions: 1) Does germinability vary among seeds covered and uncovered by litterfall and according to litterfall depth? 2) Can direct seeding be impaired by seed predation? 3) Does seed size affect seed predation and seedling vigor in this palm?

Material and methods

Species and study area

Euterpe edulis Mart. is a single-stemmed palm, 8-12 m in height, that has been considered a keystone food resource in many tropical ecosystems (Fadini *et al.* 2009; Montagna *et al.* 2018) since at least 58 bird and 21 mammal species consume their fruits (Galetti *et al.* 2013). With long fruiting periods, this species is an excellent source of nutrients for frugivores – especially during local fruit shortages (Henderson *et al.* 2000) – because the pulp has high concentrations of carbohydrates, lipids, and proteins (Galetti *et al.* 2011). Although *E. edulis* is a dominant species in old-growth areas of the Brazilian Atlantic forest (Reis *et al.* 2000; Guilherme *et al.* 2004; Emer *et al.* 2019), its population have declined in many forest fragments due to illegal harvesting (Favreto *et al.* 2010), leading the federal government to include it in the Brazilian List of Threatened Plant Species (Martinelli & Moraes 2013). Thus, the reintroduction of *E. edulis* in sites where it was extinct can help to restore or enrich degraded areas. The abundant fruit production attracts both seed predators and frugivores, whose concurrent presence contributes to the forest dynamics. Therefore, *E. edulis* can enrich secondary forests by accelerating the natural regeneration and the recolonization by fauna.

We conducted this study at Intermontes farm (24°11’41.67” S, 48°11’22.83” W), a 343 ha private area in São Paulo state, southeast Brazil, that belongs to a local cement company. In 2001, a restoration program was initiated in compliance with state regulations, aiming to restore 164.7 ha as an offset for mining activities (Busato *et al.* 2007). The climate is mesothermic with a variable seasonality, marked by a dry season from May to August and a wet season from September to April, with an average rainfall of 1,640 mm.

Before restoration, cattle ranching prevented natural regeneration. Vegetation was composed mainly of pastures, with and without regenerating shrubs, and few secondary forest fragments with different disturbance levels (Busato *et al.* 2007). From 2002 on, several restoration measures were taken: cattle were removed, fires were prevented, exotic grasses and ants were controlled, and native tree species were introduced by the planting of seedlings (Busato *et al.* 2007).

By the time of this study, the area was characterized by pastures, medium regeneration stage vegetation, and forest fragments. Pastures showed abundant grasses with some shrubs of less than 5 m in height. In the medium regeneration stage, trees had less than 15 m in height, the canopy was slightly open, and the understory was present. Finally, forest fragments were relatively well conserved, with arboreal stratum higher than 15 m, closed canopy, and understory present. Since this study assessed the enrichment planting in areas under restoration and considering that *E. edulis* seeds are recalcitrant (Panza *et al.* 2004; Panza *et al.* 2007; Cursi & Cicero 2014), we conducted the experiments in medium regeneration stage sites.

Generally, a high density of *E. edulis* is observed in well-preserved Atlantic forest areas. For example, phytosociological research in the Parque Estadual Intervales, Base Saibadela, located at 35 km from our study site, found a density of 318.6 mature individuals of *E. edulis* per hectare (Guilherme *et al.* 2004). However, in our study site, we recorded only one immature adult and very few scattered juvenile individuals, which corresponds to an estimated density of 0.09 individuals per hectare, including seedlings, juveniles, and adults. Such remarkable absence probably is due to the intense exploitation of this palm in the past, as well as the conversion of forests to pastures.

Other palms are also rare in the study site. The only recorded species was *Syagrus romanzoffiana* (Cham.) Glassman, which also occurs in a very low density. Concerning to fauna, a previous survey of mammals found many small rodent species, mainly *Oligoryzomys nigripes*, but mid- and large-sized vertebrate seed predators, as *Dasyprocta* sp., *Cuniculus paca*, and *Tayassu pecari*, were not recorded (Castilho 2015), as these animals are usually absent in degraded areas (Galetti *et al.* 2015a).

Seed collection and processing

The fruits were collected from a private property located 13 km from the study area in July 2015. Fruits were immersed in water for 24 h and then were de-pulped in running water, by scraping them against a steel-net sieve. We dried the seeds at room temperature for three hours and stored them in sealed plastic bags in a refrigerator at 15°C for five days. We weighted all seeds by a semi-analytical balance and measured them with a digital caliper to the nearest 0.1 mm. As diameter and mass were strongly correlated (Pearson correlation, $P < 0.0001$, $r = 0.80$, $N = 490$), we used only the diameter values for analysis. To test the viability of seeds used in the field experiment, we randomly separated 90 seeds to germination in the laboratory. These seeds were sowed in Petri dishes, on filter paper, and were brought to a germinator at 30° C by day and 20° C by night, in a 12 hours photoperiod, simulating the natural variation in the field. As we found 86.6 % of germination, we assumed the seeds were viable.

Seed germination and predation

We selected 40 sampling points in the restored area, with at least 50 m between them. As *E. edulis* is an ombrophilous species (Reis *et al.* 2000), we avoided sites with very little or no shade. At each point, we installed two 1 m^2 plots, 10 m apart from each other, with five seeds per plot: one in each corner and one in the center of the square plot. In one plot, the seeds were individually protected by wired cages (7.5 cm in diameter x 3 cm in height), which excluded the access of vertebrate predators and prevented seeds from being directly covered by litterfall. In the other plot, seeds were individually placed inside a PVC ring (10 cm in diameter x 2 cm in height), allowing the removal by vertebrates and the covering by litterfall, although preventing rain wash. We sowed the seeds in July 2015, in mid-dry season, and monitored them monthly until August 2016 to check for germination and seed predation. We considered the radicle emission as evidence of germination. Seeds damaged by rodents or not found inside the plot or its vicinity were considered removed by vertebrates. Predation by invertebrates was indicated by a typical hole left by the adult beetles (Pizo *et al.* 2006). We assessed the relationship between seed diameter and seed removal. Litterfall depth was also measured monthly at four points per plot (excluding those with seeds protected by cages), from August 2015 to March 2016, when there was no further germination. We take the measures by a thin-tipped graduated wooden stick that passed through the litterfall, reaching the soil surface.

Seedling size and seedling vigor

To assess the relationship between seed diameter and seedling vigor, we measured 90 seeds and sowed them in pots (8 cm in diameter x 10 cm in height) filled with sterile potting soil, keeping them under room temperature in the laboratory. After six months, we dried the whole seedlings (aerial part and root) in a drying oven at 60°C for 24 h and weighed them with a semi-analytical balance. We used dry mass as a proxy for the seedling vigor (Pizo *et al.* 2006; Snider *et al.* 2016).

Statistical analysis

We analyzed the relation between seed germination and litterfall presence by Generalized Linear Models with random effect and binomial distribution, assuming the sampling points as the random factor and excluding the seeds removed by vertebrates. The same test was also applied to verify the influence of litterfall height on germination and the effect of seed size on removal by vertebrates. We also compared the velocity of germination between treatments (seed covered by litterfall and uncovered seeds) by the Germination Velocity Index (GVI) (Maguire 1962), by the formula:

$$GVI = \sum(n_i/t)$$

Where,

n_i = number of germinated seeds in the month i.

t = number of days since the beginning of the experiment.

We calculated a GVI value per sampling plot, excluding those with removal by vertebrates, and compared both treatments by a paired t-test. Finally, the effect of seed size on the dry mass of seedlings was assessed by Linear Regression. As the weights of the aerial part and root were correlated, we used the total dry weight of the seedlings for the analysis. All the analyses were made by R software, version 3.5.1 (R Development Core Team 2016).

Results

The germination of seeds covered by litterfall was greater than uncovered ones (87.8 % for covered seeds and 70.5 % for uncovered, P < 0.001, Fig. 1), but the variation in litterfall depth (2.39 ± 0.78 SD) did not influence the germination (P = 0.22, Tab. 1). By comparing the GVI for both treatments, we recorded a delay in the germination of seeds deprived of litterfall (t = 4.90, df = 59.14, P = 0.0001, Fig. 2). We found only one seed preyed on invertebrates, while about 17 % were consumed or removed by vertebrates. There was a negative relation between seed size and seed removal, indicating that smaller seeds were more removed (P = 0.04, Tab. 1). Seed mean diameter was 12.15 ± 1.07 cm, ranging from 9.75 to 13.75 cm, and the mean dry weight of seedlings was 0.32 ± 0.14 g. We found a positive relation between seed size and seedling vigor (R^2 = 0.39, *P* < 0.001, Fig. 3).

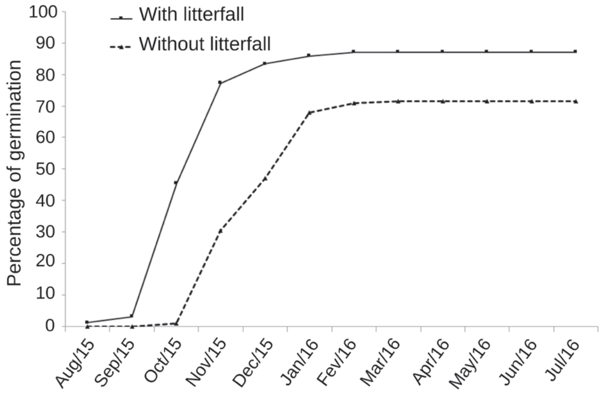

Figure 1. Cumulative monthly germination of *Euterpe edulis* from seeds protected by wired cages (without litterfall coverage) and unprotected (with natural litterfall coverage).

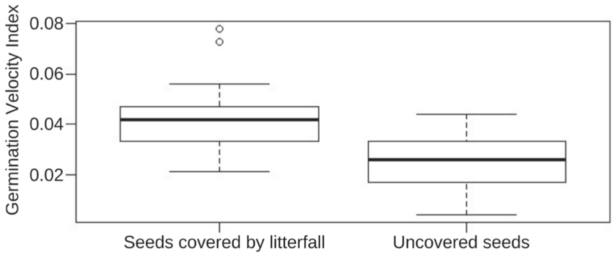

Figure 2. Velocity of seedling emergence of *Euterpe edulis* from seeds with litterfall coverage and uncovered seeds compared by the Germination Velocity Index (GVI).

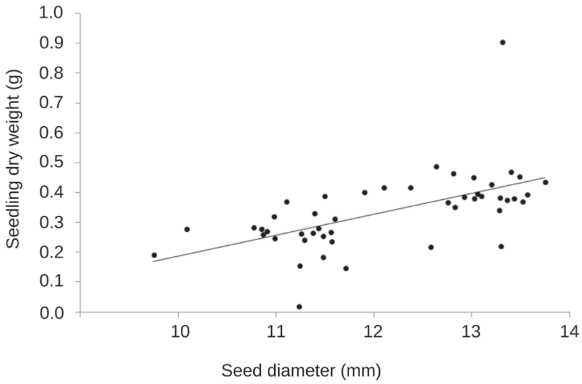

Figure 3. Relationship between seed diameter (mm) and total dry mass (g) of *Euterpe edulis* seedlings cultivated in the laboratory.

Table 1. Results of Generalized Models with random effects applied to the experiments testing litterfall presence and depth in seed germination and size effect on seed removal. When the difference between DAICc is lesser than two (for each pair of models), the models are equivalent. *Weights* express the relative likelihood of each model, and *DF* corresponds to the degree of freedom.

Model	ΔAICc	DF	Weight
Seed germination ~ litterfall presence			
Null model	16.7	2	<0.001
Litterfall presence	0.0	3	1
Seed germination ~ litterfall depth			
Null model	0.0	1	0.57
Litterfall depth	0.5	2	0.43
Seed removal ~ seed size			
Null model	2.1	2	0.26
Seed size	0	3	0.74

Discussion

Seed germination was high for both treatments, suggesting a broad germination niche for *Euterpe edulis* (Braz *et al*. 2014). In another experiment (Zaniratto & Silva, data not published), we monitored all individuals after radicle extrusion for two years and we found that almost 80 % of plants were alive. Since survival chances progressively increase according to the ontogenetic stage (Matos 2000) and considering the broad amplitude of germination niche for this species, direct seeding can be a feasible technique to perform populational reinforcement or reintroduction in areas where populations of this palm have been declined or extinct.

Litterfall plays a relevant role in seed germination, as the germinability of seeds covered by litterfall was higher. The seeds of this palm are recalcitrant and sensitive to dehydration (Panza *et al.* 2004; Panza *et al.* 2007; Cursi & Cicero 2014), losing their germinative ability as they desiccate (Martins *et al.* 2009). Litterfall is composed of overlapping layers of leaves and leaf fragments, producing coverture that reduces the vapor flow (Facelli & Pickett 1991; Marthews *et al.* 2008). We sowed the seeds in the dry season, the fruiting period for this species in that region of the Atlantic forest. Being covered by litterfall immediately after dispersal helps keep the seed moist, increasing the chances of germination, even when there was no rainfall in the following days after sowing (authors' pers. obs.).

Possibly, moisture conserved by the litterfall also influences the germination velocity, as the seeds covered by litterfall germinated faster than uncovered seeds. For the studied species, moister conditions can accelerate germination, which, in turn, is affected by the presence of litterfall. Usually, seed germination is synchronous under optimal conditions but tends to be asynchronous under suboptimal situations (Marques *et al.* 2014). In the prevalence of low humidity, as in our caged seeds, germination may be delayed until more suitable conditions occur. Braz *et al.* (2014) also found a delay in *E. edulis* seed germination in soil with low water potential and rapid germination at the onset of flooding. This broad niche breadth amplitude is advantageous because a delay in germination under adverse conditions can ensure a greater probability of seedling emergence when the environmental conditions are appropriate. On the other hand, rapid germination minimizes predation risks (Evans *et al.* 2007), a tradeoff that may be considered a bet-hedging strategy (Wilbur & Rudolf 2006; Evans *et al.* 2007).

Although litterfall coverage increased germinability and germination rates, litterfall depth did not affect seed germination. A dense litterfall layer may reduce light input (Daws *et al.* 2005). However, it is not a filter for *E. edulis* seeds since this species can germinate in a range of light conditions (Braz *et al.* 2014; Aguiar *et al.* 2017). The low light and high moisture conditions posed by litterfall coverage may promote the ideal environment for fungi development, which affects the seed germination of many plant species (Souza *et al.* 2015). Besides, a deep litterfall layer may reduce seedling recruitment, as it creates a physical barrier for seedling emergence (Facelli & Pickett 1991). However, only six out of 200 seeds showed signs of fungi contamination. Rother *et al.* (2013) also found that fungal activity was not a mortality factor for *E. edulis* seeds. Litterfall depth also did not prevent seedling emergence, as the very hard and pointed first leaf can drill its way through the litterfall, allowing seedling emergence (authors' pers. obs.).

Seed predation by vertebrates was low and possibly overestimated since we considered seeds removed as consumed without knowing their fate. Scatter hoarding is a usual behavior among small (Forget 1999; Lichti *et al.* 2017) and mid-sized mammals (Forget & Vander Wall 2001). This behavior consists of burying seeds in many spots for later consumption (Forget & Vander Wall 2001; Wenny 2001; Lichti *et al.* 2017). Sometimes, these animals store more food than they require, and as a result, some seeds escape predation and can germinate (Forget & Vander Wall 2001). In our experiment, some of the removed seeds may have been secondarily dispersed by small rodents.

We found a small percentage of predation or removal compared to other studies in areas with a low density of *E. edulis* (Pizo & Vieira 2004, for a harvested site; Fadini *et al.* 2009, for an island). Conversely, our results are similar to those found in well-preserved ecosystems, where the palm occurs in dense populations (Pizo & Vieira 2004, for an unharvested site; Fadini *et al.* 2009, for the mainland). Lower predation rates in areas where *E. edulis* is very abundant probably reflect the predator's satiation effect, resulting in a lower predation pressure (Pizo & Vieira 2004). On the other hand, in areas where this palm is less abundant, these seeds would constitute a more valuable food item, resulting in heavier predation rates when found by seed predators (Fadini *et al.* 2009).

The low seed predation or removal in our study site possibly is not due to the predator's satiation effect since there were no fertile individuals of this palm in the area. The seeds we sowed represented an unpredictable and potentially novel food resource so that those removed or consumed were probably found at random by seed predators, which reduces the chances of predation. This situation seems to favor the reintroduction or the population reinforcement of *E. edulis* in degraded areas by direct seeding because rodents are spatially oriented and concentrate their activities in sites with high fruit production (Silvius & Fragoso 2003; Fadini *et al.* 2009). Furthermore, mid-sized and large vertebrate seed predator, as agoutis, pacas, and peccaries, are usually absent in degraded areas (Galetti *et al.* 2015a). The probability of seed predation sharply increases with the body mass of the seed predator (Galetti *et al.* 2015b). Thus, the time frame before these mammals colonizes a restored site should be the right time for the reintroduction or the population reinforcement of *E. edulis* seeds due to the low predation risk and the increased chances of germination and seedling establishment. The time frame can be determinant to avoid seed predation in other forest palm species (Ramírez *et al.* 2009).

Only one seed out of 400 was attacked by invertebrates. Post-dispersal seed predation in this and other palms is usually associated with the scolytid beetle *Coccotrypes palmarum* (Pizo & Simão 2001). Although we did not conduct an invertebrate census, this beetle species may be absent in our study site due to the absence of fertile individuals of *E. edulis* and to the low density of any other palm species (authors' pers. obs.), a situation that represents another time frame favoring the reintroduction or the population reinforcement of *E. edulis* by direct seeding in areas where this palm was locally extinct. The richness of some beetle species increases according to the restoration age but is almost always limited compared to pristine forests (Derhé *et al.* 2016).

Smaller seeds were more removed than larger ones. This result contrasts with previous studies suggesting that seed predators usually prefer large seeds, which offer higher nutritional content (Janzen 1969; Brewer 2001; Vander Wall 2003). Working in an Atlantic forest site with a complete set of seed predator mammal species, Pizo *et al.* (2006) found no relation between seed size and predation in *E. edulis*, which suggests the variation in seed size in this palm is negligible and would not highlight differences in seed exploitation by predators. Small rodents are more resilient to the drivers of defaunation, proliferating in areas where large mammals were extinct (Galetti *et al.* 2015a). In our study site, small rodents probably are the main predators of *E. edulis*, a guild that may be more sensitive to seed size variation.

Most of the seeds preyed on in our experiment were removed and not locally consumed, suggesting that seed size may be a limiting factor for the removal by rodents. Larger seeds offer a higher nutrient content to predators. However, the costs of transporting them are also positively related to seed size, which may impose upper limits on the seed size carried by small rodents (Muñoz & Bonal 2008). As reported in other studies (Pizo & Simão 2001; Pizo *et al.* 2006), we also found that larger seeds generate more vigorous seedlings. Seedling size is especially relevant because it may determine plant success under competitive conditions (Galetti *et al.* 2013). In this regard, the predation of smaller seeds in our study site may indirectly contribute to the germination of larger ones, which will produce seedlings with higher chances of survival.

Our results showed that the direct seeding of *E. edulis* in areas with a populational decline or extinction of the species might be feasible. We recommend the direct seeding of de-pulped seeds to avoid a decrease in germination caused by the fruit mesocarp (Aguiar *et al.* 2017). Because this palm is an ombrophilous species (Reis *et al.* 2000), we do not recommend direct seeding in open areas or young restored sites, where the canopy layer can be absent or very discontinuous. Rather, that should be implemented in more humid and shaded areas, like those along with watercourses or mid- and old-aged restored sites, where litterfall plays a role in preserving moisture. Our study makes us confident that the reintroduction or the population reinforcement of this ecologically valuable palm is feasible, cheap, beneficial to the animal community, and essential to recover the structural and functional state of some Atlantic forest areas.

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