Original article

Bamboo thickets alter the demographic structure of *Euterpe edulis* population: A keystone, threatened palm species of the Atlantic forest

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ABSTRACT

The rapid spread of bamboos can strongly affect forest structure by interfering plant regeneration and reducing local biodiversity. Considering that bamboos exert a negative influence on the plant community, our main goal was to investigate how this influence manifests at the population level. We compared the demographic structure of the threatened palm *Euterpe edulis* between bamboo and non-bamboo dominated patches within the Atlantic forest. In the study site, the native bamboo *Guadua tagoara* has created a marked patchiness and heterogeneity in the vegetation. Plots were set up randomly in bamboo and non-bamboo patches and the heights of all *E. edulis* individuals were measured. Data from canopy openness and litter depth were collected for both patches. Greater number of *E. edulis* was recorded in bamboo patches. However, frequency distribution of the height classes differed between patches revealing a predominance of seedling and sapling I classes in bamboo patches, in comparison to a more evenly distribution of height classes in non-bamboo patches. The canopy in bamboo patches was more open and the litter depth was thicker. Our analyses evidenced *G. tagoara* is functioning as a demographic bottleneck of natural population of *E. edulis* by arresting its later stages of regeneration and in high densities that bamboos may limit recruitment of this palm species.

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1. Introduction

Bamboo establishment within areas of tropical forest can occur rapidly due to its naturally invasive ecology, which is facilitated by vegetative reproduction and occur even when the bamboo is native to the forest (Wong, 1991). The rapid spread of bamboos can strongly affect forest structure, either through interfering with plant regeneration and reducing local biodiversity (Lima, 2007; Lima et al., 2012; Oliveira-Filho et al., 1994; Rother, 2006; Rother et al., 2013a) or by altering the structure of vegetation (Fantini and Guries, 2007; Guilherme et al., 2004; Lima, 2007; Lima et al., 2012; Oliveira-Filho et al., 1994; Rother, 2006; Rother et al., 2013a; Tabarelli and Mantovani, 1999).

Bamboo promotes structural changes in vegetation through either direct damage to other plants or indirectly via impacts on regenerating plants through changes in the forest microclimate and increased litter deposition (Araujo, 2008). As a consequence of its establishment, bamboo may influence the vegetation in different ways: affecting the abundance of seeds entering a site via dispersal mechanisms (Rother et al., 2009), the regeneration of tree species (Carvalho, 1997; Oliveira-Filho et al., 1994; Fantini and Guries, 2007), the growth of trees (Oliveira-Filho et al., 1994) and subsequently forest succession more generally (Griscom and Ashton, 2003; Lima, 2007).

Most of the studies involving bamboo dominance of tropical forests are concentrated within a few sites in the Amazon and Atlantic Forests. Oliveira (2000) found that larger trees were the least common size class present within forests dominated by *Guadua weberbaueri* in the northern state of Acre. Also in north Brazil Silveira (2000) noted that local floristic composition was reduced to almost 40% of the initial species richness as a result of *G. weberbaueri* colonization.

In the Atlantic forest, which is threatened by habitat loss and fragmentation (Ribeiro et al., 2009), researchers and

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conservationists see *Guadua tagoara* (Nees) Kunth and other bamboo species as a major threat (Araujo, 2008). In certain protected areas, bamboo presence is considered to be one of the major factors related to the reduction of species richness (Lima et al., 2012). Despite being a native species, concerns exist because evidence that *G. tagoara* populations are expanding (Alves, 2007). At sites where *G. tagoara* naturally occurs, changes in forest dynamics have been observed when the species is able to find suitable conditions to establish and dominate (Alves, 2007; Fantini and Guries, 2007; Morokawa, 2008).

Due to the fact that it is a pioneer species and can quickly occupy disturbed areas (Judziewicz et al., 1999), some authors associate the current abundance of *G. tagoara* to anthropogenic disturbances, such as the extraction of palm heart from *Euterpe edulis*, a usually dominant tree species in non-disturbed areas (Araujo, 2008; Fantini and Guries, 2000).

Bamboo dominance and its subsequent effect on plant and bird communities is well studied in Carlos Botelho state park (Lima et al., 2012; Rother et al., 2009, 2013a, 2013b). Recent research indicates that seed rain is not greatly altered by the presence of *G. tagoara* (Rother et al., 2009), which, however, exerts a negative influence on seedling establishment, a crucial stage for plant regeneration (Rother, 2006; Rother et al., 2013a). Interestingly, this finding did not apply to seedlings of *E. edulis*, which were found to be present in greater density within bamboo dominated patches (Rother, 2006). Bamboo effects upon the early recruitment of non-bamboo species were thus demonstrated to be patchy and species-specific, with patches of bamboo dominated succession exerting a far-reaching influence over the heterogeneity of plant species composition and abundance (Rother et al., 2013a).

E. edulis is the dominant species of palm in the understory of the Atlantic forest. It is also threatened by illegal overexploitation (Galetti and Fernandez, 1998). Within Carlos Botelho State Park, *E. edulis* populations are reducing rapidly as a result of this intense exploitation (Muler et al., 2014; Rother et al., 2009). Bamboo expansion has also been linked to this exploitation (Araujo, 2008, Fantini and Guries, 2000).

E. edulis has characteristics that amplify its ecological importance in the forest ecosystem. Its historic abundance lends the species a central place in the vegetation structure and dynamics of the Atlantic Forest, rendering it a priority species within forest management plans and conservation efforts. It also plays a key role concerning the attraction and retention of seed dispersers by annually producing large quantities of fruit, most crucially within the food shortage period (Castro et al., 2007; Fadini et al., 2009).

As the only species in the local plant community which did not suffer any limitation by bamboo in the early stages of the regeneration cycle, the study of *E. edulis* population structure in bamboo dominated forest has the potential to function as a model for evaluating the consequences of bamboo thickets on forest dynamics (Rother et al., 2013a).

In the literature, there are plenty of studies that investigate the effects of a plant species population on other plant species population (Wang and Augspurger, 2004, 2006). Nonetheless, remain scarce studies focusing on the influence of bamboo species on plant populations. Considering that bamboos exert a negative influence on the plant community, our main goal was to investigate how this influence manifests at the population level. We compared the demographic structure of *E. edulis* between bamboo and non-bamboo dominated patches within the Brazilian Atlantic forest where *G. tagoara* has created a marked patchiness and heterogeneity in the vegetation (Muler et al., 2014; Rother et al., 2013a).

The demography of natural populations of *E. edulis* has been well studied (Melito et al., 2014; Meyer and Dornelles, 2009; Raupp et al., 2009; Reis et al., 2000; Silva, 1991; Silva et al., 2009). We

are interested here, however, in evaluating whether different habitats characterized by the extent of bamboo dominance can lead to different demographic structures of *E. edulis*. Also, we are interested in characterize both patches regarding canopy openness and litter depth. After considering the pre-existing literature, we hypothesized that bamboo dominated patches would show an arrested recruitment of *E. edulis* in the later stages due to a possible physical barrier to the growth of this palm. Finally, we discuss the influence of bamboo dominance and microhabitat characteristics on the future of *E. edulis* populations in the Atlantic forest.

2. Materials and methods

2.1. Study site

The study took place in a 10-ha permanent research plot located within Carlos Botelho state park (Fig. 1), a reserve of over 37,000 ha of well-preserved Atlantic rain forest (*sensu* Morellato and Haddad, 2000) located in the state of São Paulo, SE Brazil. The study site (24° 10′ S, 47° 56′ W; 350–450 m a.s.l.) is covered by tall (20–30 m) lowland old-growth forest with an opened understory. During the study period, the mean temperature was 21.1° C (range 17.4–25.2° C), and the site received 3384 mm of rainfall. Rains are well distributed throughout the year, but the rainiest and hottest season occurs from December to March.

Approximately 3 ha of the study area is covered by *G. tagoara* which form scattered patches throughout the plot. *G. tagoara* is a perennial plant with woody stems 8–15 (–20) m high, 5–10 cm diameter, erect at the base but scandent at the apex. Stems have spines on nodes, more developed in the lower nodes, hollow internodes, and deciduous leaves sometimes persistent in the basal nodes. The genus *Guadua* is widely distributed throughout the Neotropics and contains around 30 species (Londoño, 1998; Young and Judd, 1992). *G. tagoara* occurs within the Brazilian Atlantic forest in areas of secondary growth (Fantini and Guries, 2007). The reproductive behavior of this species needs further studies, but there are indications that the populations die after fruiting period (Alves, 2007).

In non-bamboo dominated patches vegetation is characterized by the presence of trees, woody lianas and epiphytes in an abundance that differentiate them from other vegetation formations (Dias, 2005; Veloso and Oliveira Filho, 1992). It is similarly covered by a tall (20–30 m) lowland old-growth forest with an opened understory where the palms *E. edulis* (269.8 individuals.ha-1; unpubl. data) and *Geonoma* spp., and arborescent ferns (Cyatheaceae) are common. Myrtaceae, Lauraceae, Rubiaceae, Fabaceae and Sapotaceae are the richest plant families (Dias, 2005).

2.2. Species

E. edulis (hereafter *Euterpe*) is one of the most abundant understory tree species in the Atlantic Forest, occurring at an approximate density of 224 individuals.ha^{-1} when counting trees with diameter at breast height (DBH) > 4.8 cm (Rodrigues, 2006). Individual palms produce 1–5 infructescences annually bearing on average over 3000 fruits each (Mantovani and Morellato, 2000). *Euterpe* fruits are globose drupes containing a single rounded seed which averages 12 mm in diameter (Pizo and Vieira, 2004). Fruits are eaten by a variety of animals, including birds and mammals, which disperse the seeds (Galetti et al., 1999).

2.3. Data collection

2.3.1. Euterpe demography
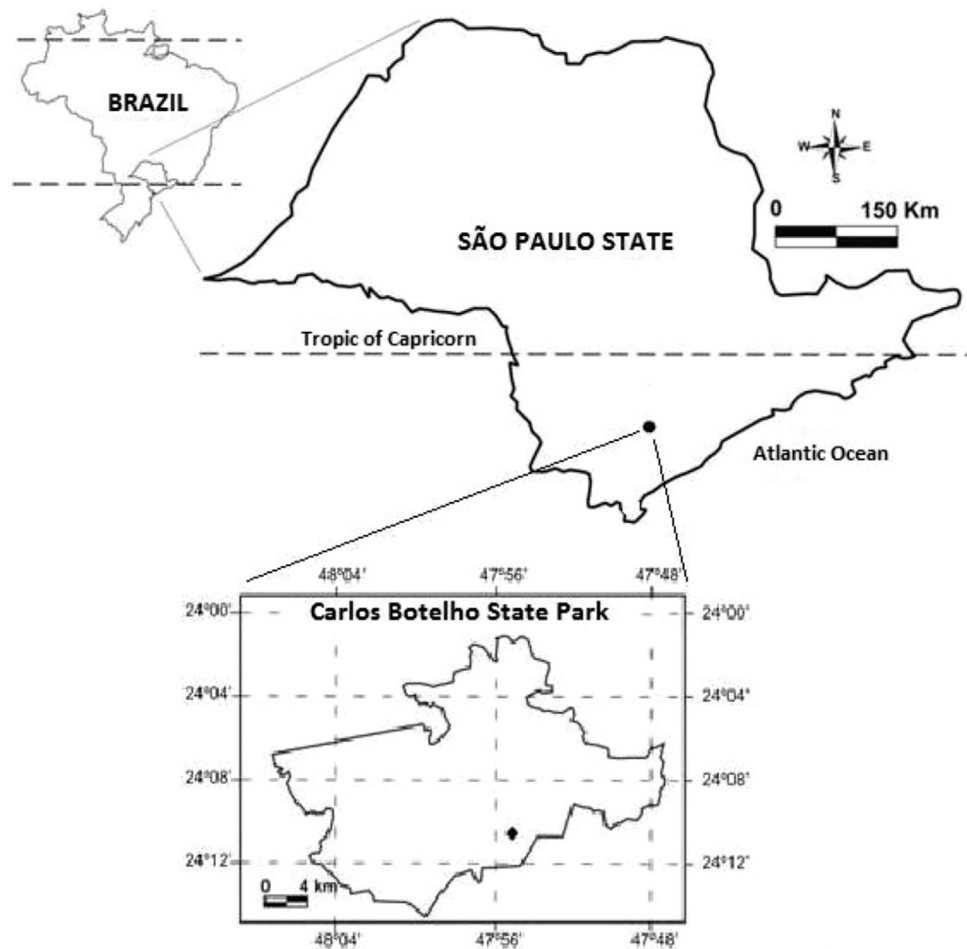Twenty 10 × 10 square plots were set up randomly in bamboo

Fig. 1. Study site at Carlos Botelho State Park, Sete Barras municipality, São Paulo State, Brazil. The point represents the location of Permanent Plot.

and non-bamboo patches, amounting to a total of 40 plots. The heights of all *Euterpe* individuals within the plots were measured at the apex, i.e. the point where the youngest leaf intersects with the stem. Following the classification of Silva (1991) and Reis (1995), with adaptations, individuals were assigned to one of the following classes based on their heights: seedling ($\leq$0.30 m), sapling I (0.31 m—1.00 m), sapling II (1.01 m—2.00 m), sapling III (2.01 m—6.00 m), and adult ($\geq$6.01 m or with reproductive signal, i.e., scar or drooping of inflorescences and infructescences under the plant). Heights were measured with a measuring tape, except to the adults that were estimated using a straight stick of 2 m length. Those data were collected in July 2005.

2.3.2. Microhabitat characteristics

To characterize bamboo (hereafter B) and non-bamboo (hereafter NB) patches we measured for canopy openness and litter depth in both patches. Canopy openness is a surrogate measure for the amount of light reaching the forest floor, an important factor for plant performance, especially during early recruitment (Swaine, 1996). Litter depth, in turn, has been demonstrated to influence the predation and germination of seeds, and thus seedling establishment rates (Molofsky and Augspurger, 1992; Schupp, 1988). Data from canopy openness and litter depth were collected in 40 points at each patch totaling 80 points in the permanent plot to characterize the microhabitats. Canopy openness was estimated above each point with a spherical densiometer (Forestry Suppliers Inc.; Lemmon, 1957). Four densiometer readings were made facing

outward at each side of each point and averaged for analyses. Litter depth was estimated by pinching the leaf litter with a slender stick and counting the number of leaves pinched. Five pinches were made in each point and the average was used for analyses.

2.4. Data analyses

To study population structure of *Euterpe* we used the statistical parameters: mean, confidence interval (confidence level at 95%) and variance. To compare the abundance and density of *Euterpe* between B and NB patches we used the F-test, and to evaluate frequency differences among height classes between patches we performed the Kolmogorov—Smirnov test.

To characterize the B and NB patches we firstly performed a Spearman Correlation to prevent collinearity between variables. Finally we compared each variable between patches using a Mann—Whitney test. All analyses were performed through using the PAST program (Hammer et al., 2001).

3. Results

3.1. Euterpe demography

A total of 285 and 724 *Euterpe* individuals were sampled within the non-bamboo and bamboo patches respectively. In bamboo patches seedling abundance was considerably greater than non-bamboo patches. Seedlings within bamboo patches represented

80.25% (581 seedlings) of all height classes recorded, whereas in non-bamboo patches seedlings represented only 33.68% (96 seedlings) of all height classes. Descriptive data is provided in Table 1. Variance of *Euterpe* population varied significantly in NB patches, resulting in a greater variation in height classes within the *Euterpe* population ($F = 10.92$, $p < 0.001$) (Table 2).

Frequency distribution of the height classes differed between patches ($D_{max} = 0.46$; $p < 0.01$), revealing a predominance of young individuals in the seedling and sapling I classes in bamboo patches, in comparison to a more evenly distribution of height classes in non-bamboo patches (Fig. 2). In short, bamboo presence exerted an important influence on the height classes of *Euterpe*.

3.2. Microhabitat characteristics

The variables of canopy openness and litter depth were not significantly correlated ($r_s = 0.14$; $p = 0.20$; $n = 80$). Overall, the canopy in bamboo patches was more open ($U = 466$, $p = 0.001$, $n = 40$), and the litter depth was thicker ($U = 509$; $p = 0.005$; $n = 40$) (Fig. 3A and B, respectively).

4. Discussion

Populations in both patches showed the expected reverse J-shaped curves with certain small deviations from this shape (Fig. S1). These small differences may have resulted from past harvests of palm heart at the studied site (Muler et al., 2014). The reverse J-shaped curve is usually taken as an indicator of self-replacing populations but this is discussed by Virillo et al. (2011). These authors evaluated populations over time and found that not all species with reverse J-shaped curves are effectively stable or increasing in population. They also conclude that for management purposes it is necessary consider the variation on demographic rates over time and the factors that influence this variation.

Natural populations of *Euterpe* typically have a pyramid-shaped demographic structure with a large base of seedlings and saplings and a small number of reproductive individuals (Reis et al., 2000). Despite this, in our study bamboo presence clearly lead to differences in *Euterpe* height class distribution. Individuals from the early recruitment stage (i.e, seedling and sapling I) were the most common individuals in bamboo patches, indicating that there is a potential seedling bank and juveniles up to 1.0 m tall for forest regeneration. The typical reproductive strategy of *Euterpe* includes the maintenance of a large seedling bank (Reis et al., 1996; Raupp et al., 2009).

Within bamboo dominated patches, distinctive physiognomic characteristics can limit the seed rain of *Euterpe*, most likely because frugivores seem to be the least common fauna by dietary category (Rother et al., 2013b). On the other hand, bamboo provides suitable conditions for germination and seedling establishment as previously reported by Rother et al. (2013a). In developing a manipulative experiment, these authors were able to establish that

Table 1

Descriptive data for *Euterpe edulis* populations in each height classes at bamboo (B) and non-bamboo dominated patches (NB) in Carlos Botelho State Park, Sete Barras municipality, São Paulo, Brazil.

Height classes	Abundance		Density (m²)	
	B	NB	B	NB
Seedling	581	96	0.291	0.048
Sapling I	123	121	0.062	0.061
Sapling II	7	23	0.004	0.012
Sapling III	13	37	0.007	0.019
Adult	0	8	0	0.004

Table 2

Parameters for population structure for *Euterpe edulis* at bamboo (B) and non-bamboo dominated patches (NB) in Carlos Botelho State Park, Sete Barras municipality, São Paulo, Brazil.

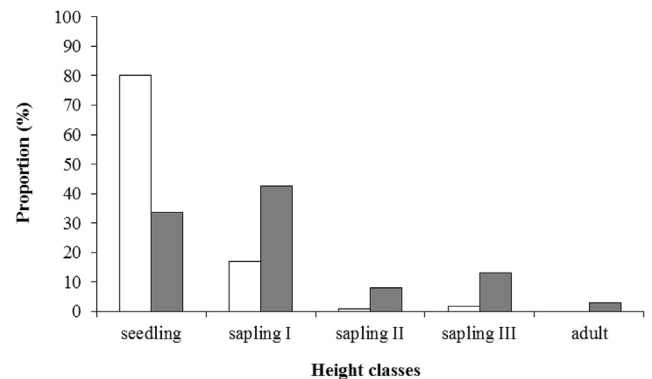| Parameters	B	NB
Abundance	724	285
Mean	0.29	1.05
95% Confidence interval	0.25–0.32	0.87–1.23
Variance	0.22	2.41

Fig. 2. Frequency distribution of *Euterpe edulis* in height classes at bamboo (white bars, n = 724) and non-bamboo dominanted patches (grey bars, n = 285).

Euterpe emergence and seedling survival is greater within bamboo dominated patches.

Non-bamboo patches naturally receive a greater density of *Euterpe* seeds (Rother et al., 2013a). Nevertheless, if dispersal is not a problem for *Euterpe* seeds in non-bamboo sites, the authors contended that its success in early recruitment is then strongly constrained by post-dispersal mortality factors in these patches, especially seed removal and predation. In the literature, some authors found that action of fungi due to humidity (Janzen, 1970; Connell, 1971), the fall of canopy trees leaves (Cintra, 1997; Svenning, 2001; Raupp and Cintra, 2010) and the percentage of rocky outcrop (Raupp et al., 2009) are also factors that limit the development of seedlings.

Despite the seedling recruitment is very variable through time, it is worth noting that there is a kind of complement of height classes between environments. Although smaller classes were less represented within the *Euterpe* population in non-bamboo patches, these patches contained a larger stock of individuals with the potential to reach adulthood. According to our results, after the critical seed-seedling stage, non-bamboo sites seems to be suitable for the successful recruitment of *Euterpe*.

A distinct pattern was observed within bamboo patches, due to the fact that the tangled *G. tagoara* stems form thickets that act as a physical barrier preventing *Euterpe* individuals from reaching the later stages of growth and regeneration. In summary, *Euterpe* within bamboo dominated patches must overcome significant barriers to reach the reproductive stage, and thus ensure any continued regeneration of the population. Other studies have confirmed this pattern, attributing these results to bamboo mechanical damage on the plants (Lima et al., 2012; Griscom and Ashton, 2003). Griscom and Ashton (2003) established that *Guadua sarcocarpa* dominated patches within the Peruvian Amazon reduce the survival and recruitment of all other plant species, as well as causing physical damage via the fall of culms that fold up on themselves. Using the same permanent research plot employed by this study, Lima et al. (2012) recorded that *G. tagoara* patches contained a lower density of adult trees (DBH > 5 cm) and greater
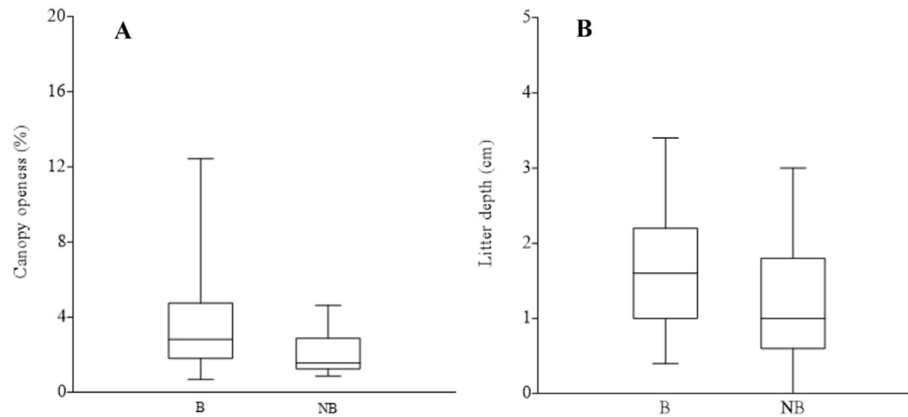
Fig. 3. Boxplots for microhabitat characteristics (canopy openness and litter depth) at bamboo (B) and non-bamboo dominated patches (NB) in Carlos Botelho State Park, Sete Barras municipality, São Paulo, Brazil. The upper and lower border of the box are the 75th and 25th percentiles, respectively, the black horizontal line within the box is the median and the error bars are the 10th and 90th percentiles.

concentration of small-sized trees. Authors relate these differences to higher mortality rates, lower rates of recruitment, mechanical damage caused by culm fall and a higher frequency of resprouting individuals (of other plant species) within bamboo dominated patches.

Euterpe is a palm of the Atlantic Forest and Cerrado Biomes (Martinelli and Moraes, 2013) that occurs predominantly in soils with high water availability (Brancalion et al., 2012). At the permanent plot the soils occupied by bamboos are predominantly more fertile and clayey, whilst the soils in non-bamboo dominated plots are typically sandy loams (Lima et al., 2012). As clay soils have very small, electrically bonded particles, the micropores between them usually retain more water (Osman, 2013). These soil differences could offer an alternative explanation as to why *Euterpe* form a higher seedling bank in bamboo dominated patches.

Microhabitat characteristics (Vásquez-Yánes and Orozco-Segovia, 1993) and interspecific interactions (Dirzo and Dominguez, 1986) are able to influence seed germination and, consequently, the differential establishment of the species in the environments. Establishment limitation has been reported as a result of high rates of seed predation (Fleury and Galetti, 2006; Santos and Tellería, 1994) and reduction or absence of suitable sites for the establishment (Bruna, 2002; Jordano et al., 2004; Meiners et al., 2002). In this case, abiotic variables such as light and litter can affect the establishment and recruitment pattern of species in the forest. Light availability is known to be an important factor for growth in tropical plants (Howe et al., 1985; Swaine, 1996), whilst litter characteristics can influence patterns of seed predation or seed germination (Molofsky and Augspurger, 1992; Schupp, 1988).

In the current study, understory under bamboos had a higher light incidence. This may negatively influence the germination and establishment of shade tolerant understory species, as *Euterpe*. Despite being a shade tolerant understory species, *Euterpe* still requires the presence of a forest microhabitat with sufficient light for successful regeneration and initial growth (Klein, 1974). *Euterpe* can benefit from small gaps appearance for regeneration (Nakazono et al., 2001). Thus, contrary to our hypothesis, bamboo dominated patches offered suitable lighting conditions for the initial recruitment of *Euterpe* seedlings. Light is a central limiting factor on the general growth and presence of forest palms. A higher investment in vertical growth can lead to a vertical position in the forest canopy that provides the greater benefits of increased illumination (Alves et al., 2004). This may be related to the greater number of adults found at non bamboo patches. Similarly, litter depth was greater upon soil from within bamboo dominated patches, a characteristic that can also affect seed germination and seedling establishment. This did not, however, exert any statistically significant influence upon the early regeneration of *Euterpe* in bamboo dominated patches.

According our results, *G. tagoara* is functioning as a demographic bottleneck of the later stages of *Euterpe* regeneration, which corroborates with our initial hypothesis. These patches in the forest are changing the demographic structure of natural population of *Euterpe* through arresting its regeneration cycle.

5. Conclusions

Natural populations of *Euterpe* have dependence of a large population, as the base of the demographic structure with a large base of juvenile plants (especially, seedlings and saplings) and a small number of reproductive individuals (Reis, 1995; Reis et al., 2000). However, survival in later stages is crucial for predicting patterns of *Euterpe* population persistence in tropical forests.

As the adults are the reservoir of genetic structure, the demographic population of this palm species is a matter of concern because, besides the presence of bamboo, illegal harvesting of reproductive adults frequently occurs in the study area. This illegal activity, however, creates gaps that favor bamboo proliferation (Fantini and Guries, 2007). Here, we have a complex system that deserve more studies because if the density of *Euterpe* adult's decreases with time as a consequence of both arrested regeneration in the later stages and the perpetuation of the bamboo dominance, recruitment limitation within bamboo patches tends to enhance.

Recruitment limitation has also negative consequences for ecological interactions between *Euterpe* and species that depend on it for feed. In a changing world, more important than focusing on a single species, it is important to conserve networks of interacting species and rethink management options to maintain the community functions.

Author contributions

Conceived and designed the experiments: DCR, RRR, MAP. Performed the experiments: DCR. Analyzed the data: DCR, MAP. Contributed reagents/materials/analysis tools: RRR. Wrote the manuscript: DCR, RRR, MAP.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2015.11.008.

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