Original article

What is the influence of anthropogenic impact on the population structure of *Attalea speciosa* Mart. ex Spreng. in the Brazilian Amazonian region?

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ABSTRACT

Attalea speciosa (babassu) is a native palm of the primary forest from Amazonian and Cerrado biomes, and has multiple economic and cultural uses. However, this palm can become dominant in open areas, with a long-term persistence in the community. The objective of this study was to compare the population structure and morphology of babassu in three habitat types characterizing forest succession: primary forest, pasture, and babaçual (babassu-dominated secondary forest). For this purpose, we monitored 6,333 individuals for three years at six life stages in 11 sites with 25 plots located in PA-Benfica, Itupiranga-Pará, Brazil. The morphological parameters showed differences between secondary environments (pasture and babaçual) and primary forests, suggesting that this species has a high capacity for phenotypic plasticity. The inverse J-shaped distribution was observed only in primary forests, with the density of all stages constant along the whole study, unlike pastures and babaçual areas. While the density of seedlings is highest in primary forests, stage 4 and 5 juveniles and adults are most numerous in babaçuals. Our results suggest that the higher dominance of *A. speciosa* in babaçual areas can be associated with the resilience of this species to anthropogenic disturbances.

Keywords: Amazon, *Attalea speciosa*, population structure, anthropogenic impact

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Introduction

Land use change is currently recognized as one of the main causes of biodiversity loss (IPBES 2019). As Serres (2020) pointed out "We recently learned, at the risk of our survival, that we now depend on things that depend on us". Thus, while humanity depends on the resources of the biosphere, collective land use practices degrade ecological conditions (Foley *et al.* 2005). The deforestation process has been shown to negatively affect forest species, including Neotropical palms, mainly due to microclimatic changes (Anthelme *et al.* 2011). Although native to primary forest, some species of the genus Attalea, such as *Attalea speciosa* Mart. ex Spreng. (babassu) and *Attalea maripa* (Aubl.) Mart. (inajá), can become invasive and establish in open areas (Kahn *et al.* 2003; Santos & Mitja 2011; Coelho *et al.* 2012), because deforestation promotes the growth of surviving palms, and fires do not usually kill acaule young individuals whose underground stipe is protected (Mitja & Ferraz 2001; Souza & Martins 2002; Kahn *et al.* 2003). However, frequent habitat disturbances may threaten even disturbance-adapted species. While palm babassu exists in both closed and open environments, such as forests and pastures, morphological differences have been observed between individuals from the two sites. Indeed, Barot *et al.* (2005) observed that the size of the reproductive individuals was lower in pastures than in forests, due to exposure to light in open environments. In addition, Campos *et al.* (2017) showed that babassu produce more bunches and fruits per adult individual, in pastures and crops than in seasonal semideciduous forests.

Given the increasing frequency and intensity of anthropogenic disturbances, it is essential to understand species responses (Feeley *et al.* 2007) and characterize the effects of these disturbances on their demography. Palm babassu are economically, culturally and ecologically important, but they can also have certain negative impacts when they become dominant. While their presence allows the conservation of a certain biodiversity in pastures and crops, when their density is very high, they can also limit biodiversity by competing with other species, for example in babaçual areas where they are still dominant sometimes even after several decades. Therefore, the demographic study of the babassu population can provide two contrasting and important management actions. The first is the conservation of the species, which is considered extremely important from an economic and cultural point of view for the extractive communities of northern and northeastern Brazil (Campos *et al.* 2015; Almeida *et al.* 2016). This action can support the management policies for sustainable harvesting. The second is the control of the palm, in areas where it has become invasive, such as open areas, since its dominance can generate negative impacts for rural landowners. In this case, demographic studies support the actions of selective cutting or cleaning. These two actions, conserving babassu for use, and controlling it because it invades agrosystems, seem contradictory, but could be part of the same strategy for the sustainable management of this species.

Comprehensive demographic studies of long-lived species require relatively long-term measurement and observation periods (Feeley *et al.* 2007). These studies can address fruit production, mortality, recruitment, and growth of individuals over many years. These time-consuming and expensive studies are sometimes faced with the urgency of management decisions (Wiegand *et al.* 2000; Cousins *et al.* 2014). A study on the population structure is the first step in a demographic study. It is a point-in-time measure of the demographics of a species in a particular environment that does not predict future population trends (Condit *et al.* 1998; Feeley *et al.* 2007). Furthermore, it is only recommended as a basis for management decisions when combined with measures of demographic rates over time (Virillo *et al.* 2011). However, it can be used to compare the point responses of the same species to different situations of anthropogenic pressure. Previous studies have already described the population structure of different palm species in different habitats, providing evidence of regeneration status (*e.g.*, Giroldo *et al.* 2012; Costantin *et al.* 2013; Negrelle 2013; Oliveira *et al.* 2014).

Babassu palm is one of the species whose population structure, as well as the different sites occupied, have been described. Anderson (1983), in the state of Maranhão, showed that the primary forest (deciduous forest) had the least total density (seedlings, youngs and adults) of babassu individuals, in contrast to pastures and particularly secondary forest, which had very high total densities of babassu. Campos *et al.* (2017), in the state of Ceará, also observed lower total babassu densities in semi-deciduous forest, while croplands and particularly pastures had higher total babassu densities. In contrast, Barot *et al.* (2005), in the PA-Benfica, state of Pará, showed that primary forest had a higher total density of *A. speciosa* than babaçual (babassu-dominated secondary forest) and pastures areas, due to a higher seedling density in the lower stratum of the primary forest. Therefore, depending on the locality, it is not the same land use types that present the highest total densities of this species. However, these values measured at a one point in time may vary across a period, and little is known about the trend in the babassu population structure over time.

The aim of this study was to verify the anthropogenic impact on the population structure and the potential resilience of this useful species in a highly diverse tropical forest. To do so, we compared the population structure and morphology of babassu palms in three different habitats characterizing a secondary forest succession: pasture areas (initial successional stage) established after deforestation of the initial primary forest (initial natural vegetation of the study area), babaçual areas (babassu-dominated secondary forest, intermediate successional stage) resulting from abandonment of pastures. The final successional stage does not exist on the PA-Benfica because human occupation is too recent.

Materials and Methods

Study area

This study was conducted in small farmlands at the Benfica Settlement Project - PA-Benfica (S 05°16′20′′, W 49°50′25′′), located in the municipality of Itupiranga, in the southern part of Pará state, eastern Amazon (Fig. 1). The area of the Project is 9501 ha, and its occupation began in 1986. The latest estimate indicated 183 agricultural establishments and approximately 1000 people in the community (Ritter *et al*. 2009).

The climate is humid tropical, with a 7-months rainy season, between October and April, and a 5-months dry season (Reynal *et al*. 1995). According to the annual meteorological data from the National Institute of Meteorology (INMET 2017), valid for the study area, there were important climatic variations during the last 16 years, which included the study period (2013-2015, Fig. 2). The average annual precipitation is 1776 mm (min. 1335 mm, max. 2240 mm) and the average annual temperature is 28.3 °C (min. 27.7 °C, max. 29.5 °C). Like most arable land in the Amazon region, the study area has low soil fertility, and the conversion of forest into pastures has caused a rapid change in the chemical, physical, and biological soil properties (Dosso *et al*. 2005; Ritter *et al*. 2009).

Across the three studied habitats, the babassu palm was subjected to contrasting microclimatic conditions. Although we do not have measurements of microclimatic conditions, it was clear that episodes of drought or high temperature did not affect juveniles and seedlings in the forest understory in the same way as they did in the pasture. In forest environments, juveniles and seedlings, present in the undergrowth, are also subjected to low light intensity (*e.g.*, Chazdon & Fetcher 1984; Svenning 2002). Adult individuals, which can reach up to 30 m in height (Lorenzi 2010), have their crowns in the canopy. In pastures, babassu seedlings, juveniles and adults are subjected to direct sunlight. In addition, it is common in pastures the occurrence of periodic fires and manual weeding practices that can damage aerial parts (leaves) of seedlings and young individuals of *A. speciosa*, slowing their growth without eliminating them (Mitja *et al*. 2018). In babaçual areas, resulting from pasture abandonment, babassu individuals are also subjected to high levels of light, however, usually there is no weeding or fires (except in exceptional cases of escaped fire from cultivated areas). After a few years, it is possible that babaçual lands are cleared to be transformed into pasture. In PA-Benfica, chemical weeding and clear-cutting of adult individuals began to occur; however, these activities did not occur in 2013 when we set up our study. In 2015, the babaçual areas had undergone partial cuts: in the B01 area, some stage 5 individuals were cut, and in the B02 area some stage 5 and 6 individuals were cut.
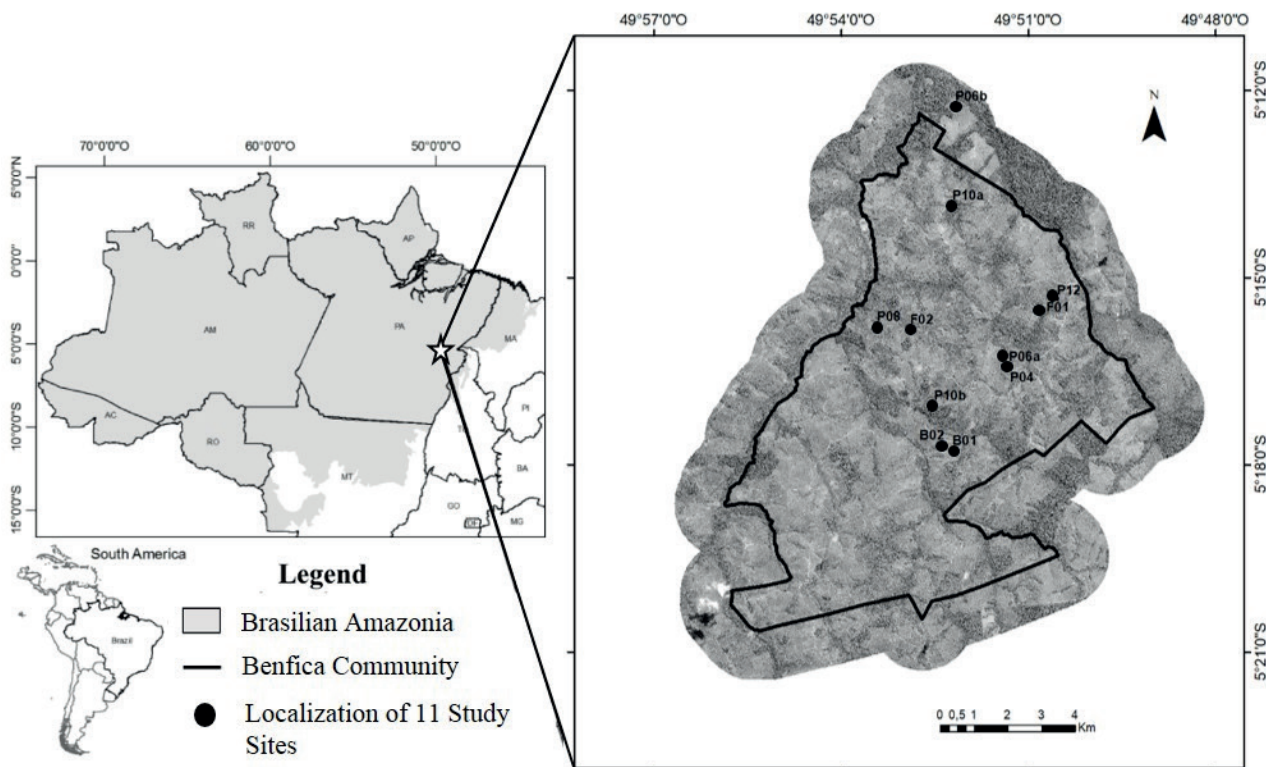

Figure 1. Location of the PA-Benfica and the studied sites (satellite image Pléiades of June 18, 2018).

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The sampled primary forests are tropical "terra firme" forests, with low adult babassu palm abundance. Another habitat sampled was the pasture areas, which was a tropical native forest (terra firme) that was slashed and burned for pasture formation in the past, and then was seeded with *Brachiaria brizantha* cv. Marandu, which is sometimes associated with the grass species *Panicum maximum* cv. Mombaça. During deforestation, the farmers remove most of the trees and retain most of the arborescent palms. Only the very tall palms are cut down because they can fall and represent a danger for cattle and people. The other habitat sampled was the babaçual, a secondary forest with a monodominance of babassu palm, formed after the abandonment of pastures. In these areas, babassu density can increase, and this species can become dominant (Mitja & Ferraz 2001). Babassu is a particular native species which becomes a super-dominant species following a change in land use (Pivello *et al.* 2018). In our paper, in agreement with Simberloff (2011) and Heger *et al.* (2013), we will also use the term invasive species for this palm.

In PA-Benfica, fires occur soon after deforestation by farmers, but subsequently, other intentional or unintentional fires may occur (Tab. 1).
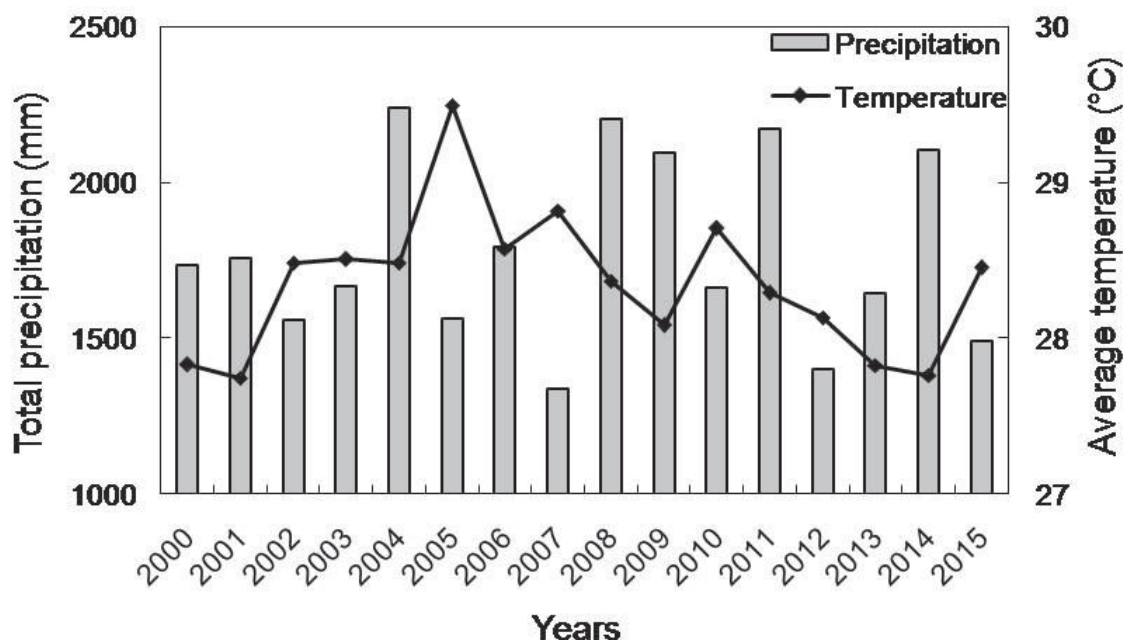

Figure 2. Annual meteorological data of the study area in the 2000-2015 period, obtained from the INMET station in Marabá-Pará.

Table 1. Habitat types history of the studied sites at the Benfica settlement, Pará.

Plots	Trajectory	IPDe	N° Burn	N° Clean	Area-m²/N (st 1 to 6)	Area-m²/N (st 5 to 6)
Flo1	Primary forest	-	0	0	760/2	11578/1
Flo2	Primary forest	-	0	0	560/2	274/1
Pas-04	Primary forest → Annual crops (rice) → Pasture	9	2	1	940/3	9338/1
Pas-06a	Primary forest → Annual crops (rice) → Pasture	7	1	1	600/2	21730/1
Pas-06b	Primary forest → Annual crops (rice) → Pasture	7	3	2 to 3	860/2	1534/1
Pas-08	Primary forest → Annual crops (rice) → Pasture	5	2	1	1540/3	13593/1
Pas-10a	Secondary forest → Annual crops (maize) → Pasture	3	1	1	640/2	18314/1
Pas-10b	Primary forest → Annual crops (rice) → Pasture	3	2	1	6720/2	13738/1
Pas-12	Primary forest → Annual crops (rice) → Pasture	1	1	0	1820/3	840/1
Bab1	Primary forest → Various crops→ Pasture → Babaçual	>30	>3	1	720/2	_
Bab2	Primary forest → Various crops→ Pasture → Babaçual	>30	>3	1	1200/2	_
				TOTAL	16360/25	90939/9

IPDe: Age of the 1st deforestation (years) in 2013; N° Burn: Total number of burning since 1st deforestation; N° Clean: Number of clearings/year; N° Plots.

Study species

In Brazil, *Attalea speciosa* Mart. ex Spreng. (babassu) occurs in the Amazon rainforest, in the gallery forests of the Cerrado (Brazilian tropical savanna), at the interface between the Amazon rainforest and the Caatinga (xeric shrubland and thorn forest), and in the Atlantic Forest (Mitja *et al.* 2018). In Brazil, this species has a wide distribution range, occurring over an area of 200,000 km² (May *et al.* 1985), across 13 states (Anderson *et al.* 1991; Henderson 1995; Shiraishi-Neto 1999; Rufino *et al.* 2008; Araújo & Lopes 2012). It has an optimal development in secondary environments (Anderson & Anderson 1985; May *et al.* 1985; Barot *et al.* 2005; Santos & Mitja 2011; Coelho *et al.* 2012), where it can become dominant (Anderson 1983; Pinheiro 2004; Mitja *et al.* 2018).

Babassu is a monoecious species and its reproduction is solely sexual (Anderson *et al.* 1991). Its stipe is erect and single. It has cryptocotylar germination (Anderson *et al.*1991; Mitja & Ferraz 2001) and its terminal meristem is thus protected in the soil at the beginning of its growth, before becoming aerial. Babassu produces large, indehiscent fruits (~ 200 g) that fall to the ground at the foot of the parent palm (Mitja *et al.* 2018) and may contain many large seeds. Between 1 and 4 seeds were observed by Mitja & Ferraz (2001), up to 6 seeds by Carvalho *et al.* (1988), up to 7 seeds by Uhl & Dransfield (1987), and up to 11 seeds by May *et al.* (1985). Farmers in Benfica reported the presence of wild animals such as agouti (Dasyprocta spp.) and paca (Cuniculus spp.), which disperse babassu fruits. In addition, we observed babassu fruits in the pastures and forest that were distant from an adult babassu, whose epicarp had been torn off and the mesocarp was consumed.

The life cycle of babassu has been divided into six different life stages based on morphological analysis (Tab. 2, Fig. 3; Mitja *et al.* 2018; Mitja *et al.* 2019).

Table 2. Life stages of the babassu individuals studied.

Stages	Characteristics
1	Seedling with the lamina of all leaves not yet divided
2	Juvenile with at least 1 leaf with a divided lamina, or in the process of division, and no petiole exceeding 50 cm in length (measured above the surface of the ground);
3	Juvenile with lamina of leaves divided or in process of division, petiole of at least 1 leaf greater than 50 cm and with the terminal meristem underground
4	Juvenile with the terminal meristem at the soil surface level (with well-visible leaf sheaths)
5	Juvenile with an aerial stipe (regardless of sheath coverage) and without the signs of male or female reproductive organs
6	Adult with an aerial stipe and signs of male or female reproductive organs

In Brazil, the babassu has economic, cultural, and ecological importance. This palm is frequently exploited, with potential benefit for the populations using it. Araujo *et al.* (2016) described 60 uses, including oil production from the seeds, the use of the leaves for roof construction, and palm heart for human food. Among the Kayapó Indians, the leaves are used to make masks representing animals, such as monkeys, for various traditional festivals (Mitja *et al.* 2019). The ecological importance of the babassu lies in the fact that it exists in the long term in environments that are different from primary forests and pastures, and in these environments, its fruits are an important resource for wildlife.
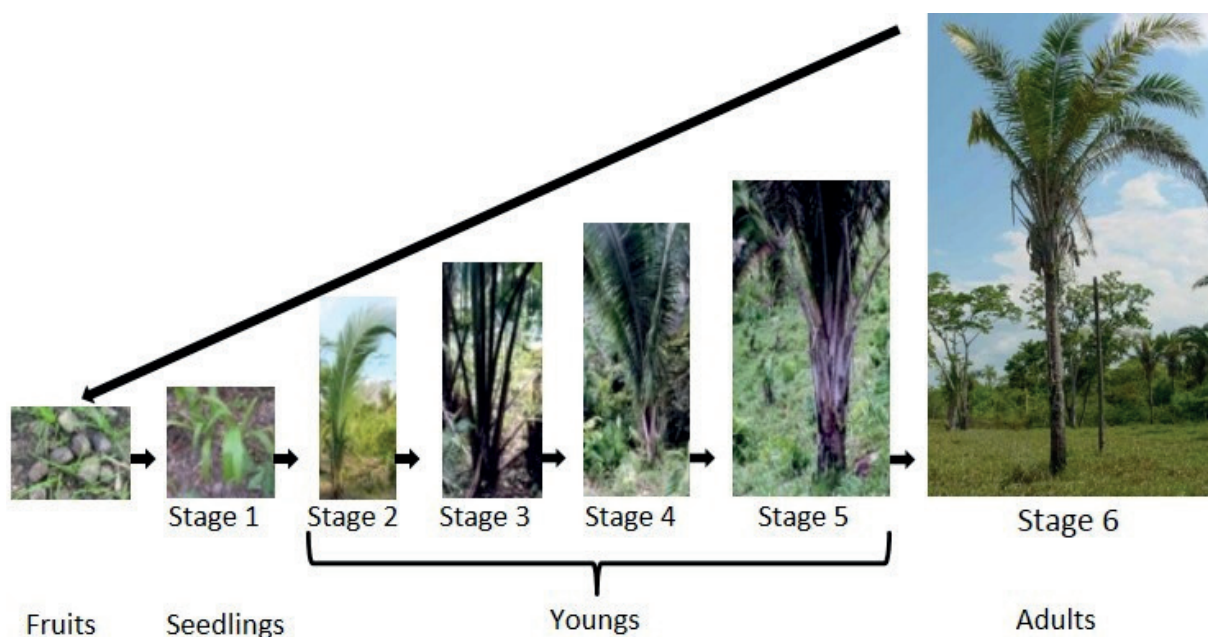

Figure 3. Life cycle stages of the babassu palm trees studied in Benfica.

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Field survey

Selection of the study site

Although babassu exists in PA-Benfica, only a few people use it regularly. We therefore chose this region to carry out this research, as we wanted to study the population structure of babassu without major modifications due to fruit or leaf harvest actions. The study sites were chosen in collaboration with the volunteer farmers from PA-Benfica. A visit with the farmers was undertaken to select the primary forests, pastures of various ages, and babaçual areas. We chose plots where, according to the farmers based on their knowledge, harvest actions (fruits and leaves) had not been carried out. Thereafter, during the three years of measurement, there were no harvest actions.

Plot selection and sampling

In 2013, 7 pastures of the following ages were chosen: 1 year (n=1, P12), 3 years (n=2, P10a and P10b), 5 years (n=1, P08), 7 years (n=2, P06a and P06b) and 9 years (n=1, P04); 2 primary forests (F01 and F02); and 2 babaçual areas: dense (n=1, B01) and less dense (n=1, B02) (Tab. 1). In these 11 sample sites, a total of 25 permanent plots were installed, 17 of them in pastures (2 in P10a, P10b, P06a, P06b and 3 in P12, P08, and P04), 4 in forests, and 4 in babaçual areas, where all individuals from stages 1 to 6 were marked with numbered stainless steel labels. In addition, 9 other plots were installed to sample a sufficient number of individuals from stages 5 and 6: 7 plots in pastures and 2 plots in forests. Our choice was to have a similar number of individuals in each pasture age, therefore, the size of the plots was different at each site due to differences in babassu densities. For the 25 surveys, the sampled areas varied between 560 and 6,720 m², and for the 9 additional transects, between 274 and 21,730 m². A total of 10.7 ha was sampled, 9.2 ha in pastures, 1.3 ha in forests and 0.2 ha in babaçual areas (Tab. 1). The data were transformed into numbers of individuals per hectare (density = ind. ha^{-1}). In 2013, 4,977 babassu individuals were measured: 1,002 in forests, 989 in babaçual areas and 2,986 in pastures.

Morphological characterization of life stages in the habitat types

To describe the morphological variation between habitats, the following morphological characteristics of the individuals were measured: petiole length (for stages 1 to 4 only), number of leaves, total height (for all stages), stipe height, diameter at 30 cm aboveground (only if the stipe is free, i.e., without leaf sheaths), diameter at breast height (DBH only if the stipe is free), and crown circumference (stages 5 and 6 only). These measurements were repeated once a year in 2014 and 2015 during the dry season. In addition, the new plants (stage 1) from recruitment were included in the survey, increasing the number of individuals measured. The individuals that were not found after two surveys (2014 and 2015) were considered dead.

Data analysis

The normality of all data was tested using the Shapiro-Wilk test; as the data were not normal, nonparametric tests were used. All morphological measurements, such as total height, petiole length, stipe height, diameter at the base, and breast height and crown circumference, taken during the three survey years (2013, 2014, and 2015) were compared between habitat types using the Kruskal-Wallis test with Bonferroni adjustment for a general characterization of the profile at each of the six life stages, and the densities of individuals in each habitat were compared between years using a similar analysis. To verify if the density of each life stage varied across different habitat types along the study, we used the Friedman test.

The structural similarity of the plots at different sites was tested using hierarchical cluster analysis based on the total density data at each life stage in each plot. For this analysis, the Euclidean distance and the unweighted pair group method with arithmetic mean algorithm (UPGMA) were used for clustering.

Analyses were performed using the R-Studio interface to R (R Development Core Team 2014), using the packages 'agricolae' (Mendiburu 2015) and 'vegan' (Oksanen *et al.* 2020).

Results

Morphological characterization of life stages in the habitat types

In general, the morphological characteristics differed across habitat types (primary forests, pastures and babaçual areas) for each life stage. For stage 1 (seedlings), the number of leaves was significantly higher in the babaçual areas and petiole length was significantly higher in the primary forests, and was significantly different between the three habitat types, while the total height was significantly greater in the forests than in the pastures and babaçual areas (Tab. 3). Morphological characteristics at stage 2 also differed significantly among the three habitat types, with total height and petiole length both significantly higher in the pastures, except for the number of leaves, which was significantly higher in the pastures and forests. For stage 3, there was a significant difference between primary forests and the other habitat types (pastures and babaçual areas) in total height, number of leaves, and petiole length, which was significantly higher in the forests. At stage 4, all the morphological characteristics also differed significantly between the three habitat types, with total height and number of leaves significantly higher in the forests. In stage 4, petiole length, which was significantly higher in the forests but was similar in the pastures and the babaçual areas. Stage 5 was characterized by a significant difference between the three habitat types only with respect to the crown circumference being significantly higher in the forests.

Finally, for adults (stage 6), Table 3 shows that the plants in forests differ significantly from those in babaçual areas and pastures in (i) higher total height, (ii) higher stipe height, (iii) lower number of leaves, (iv) lower diameter aboveground, and (v) lower DBH. The adults were all similar in all areas in terms of crown circumference (Tab. 3).

Density of *A. speciosa* individuals during the 3 years study period

After seedling recruitment, the 4,977 individuals marked in 2013, 650 and 706 new individuals were recruited in 2014 and 2015, respectively, bringing the total number of marked individuals to 6,333.

In the primary forest areas, the average densities in stages 1, 2, 4, 5, and 6 were not significantly different during the 3 years, (p = 0.18, 0.61, 0.73, 0.16, and 0.40, respectively); only stage 3 had a significantly different mean density during the study period (p = 0.05), significantly increasing from 2013 to 2015 (Fig. 4). In the pastures, the mean densities of stages 1, 4, and 5 were not significantly different during the study (p = 0.39, 0.73, and 0.59,

respectively); the stages 2, 3, and 6 differed significantly (p = 0.04, 0, and 0, respectively). The density of stage 2 was lowest in 2015, while stages 3 and 6 were highest in 2015. In the babaçual areas, the average densities of stages 2, 3, and 6 were not significantly different (p = 0.11, 0.11, and 0.15, respectively); stages 1, 4, and 5 differed significantly (p = 0, 0.02, and 0.03, respectively). The density of stage 1 and 5 were lowest in 2015, while stage 4 was highest in 2015 (Fig. 4).

In a comparison of the density of individuals by stage between habitat types in each year, we observed significant differences between the habitat types along the study period for stage 1 (seedlings) (2013: p = 0.004; 2014: p = 0.02, and 2015: p = 0.04, Fig. 5). The highest density of seedlings was observed in primary forests and the lowest in pastures, while babaçual areas had an intermediate value. For stages 2 and 3, the differences in densities were not significant between habitat types across three years of study (2013: p = 0.77 (St2, stage 2) and p = 0.15 (St3), 2014: p = 0.39 (St2) and p = 0.83 (St3), 2015: p = 0.58 (St2) and p = 0.72 (St3). For stages 4 and 5, the differences in densities were significant across the three years of study (2013: p = 0.05 (St4) and

Table 3. Mean (± Standard Deviation) of morphological measures of six stages of life of *Attalea speciosa* (babassu) in different habitats in the southeast of Pará, considering the three surveys (2013, 2014, and 2015).

Stages of life	Total height (m)			Number of leaves			Petiole length (cm)		
	Forest	Pasture	Babaçual	Forest	Pasture	Babaçual	Forest	Pasture	Babaçual
Stage 1	0.36±0.14[a]	0.29±0.15[b]	0.29±0.14[b]	2.5±1[B]	2.4±1.1[C]	2.6±1.1[A]	6.5±3.8[a]	4±3.3[c]	4.3±3[b]
	n=2210	n=2698	n=1070	n=2210	n=2698	n=1070	n=2210	n=2698	n=1070
Stage 2	0.89±0.44[b]	1.03±0.55[a]	0.80±0.48[c]	3.4±1.1[A]	3.3±1[A]	3.2±1[B]	18.6±10.8[b]	21.3±12.7[a]	15.6±11.2[c]
	n=400	n=4736	n=1202	n=400	n=4736	n=1202	n=400	n=4736	n=1202
Stage 3	3.67±1.55[a]	2.45±1[b]	2.35±0.87[b]	4.8±1.3[a]	3.8±1.1[b]	3.8±0.9[b]	139.6±72[A]	73.1±35.3[B]	68±28.9[B]
	n=192	n=1794	n=425	n=192	n=1794	n=425	n=192	n=1794	n=425
Stage 4	8.83±1.7[a]	5.67±1.7[b]	3.48±1[c]	7.7±1.2[a]	6.2±2[b]	4.4±1.3[c]	344.4±51.3[a]	75±74[b]	56.7±41.2[b]
	n=9	n=71	n=51	n=9	n=71	n=51	n=9	n=71	n=51
							Diameter breast height (cm)*		
							Forest	Pasture	Babaçual
Stage 5	10.09±1.7[A]	8.86±2[B]	9.46±1.7[A]	10±1.9[a]	10.7±4.6[a]	11.7±3.9[a]	40.7	50.2±10.6	-
	n=32	n=145	n=56	n=32	n=145	n=56	n=1	n=6	
Stage 6	19.16±6.1[A]	12.68±3.9[B]	11.53±1.1[B]	12.6±3.8[b]	18.2±6.2[a]	16.4±3.4[a]	35.9±5[b]	41.7±7[a]	43.1±6.5[a]
	n=88	n=330	n=52	n=88	n=330	n=52	n=85	n=166	n=18
	Stipe height (m)*			Crown circumference (m)			Diameter-30 cm aboveground (cm) *		
	Forest	Pasture	Babaçual	Forest	Pasture	Babaçual	Forest	Pasture	Babaçual
Stage 5	1.2±0.8[A]	1.1±0.3[A]	-	32±5.3[a]	21.6±5.4[c]	26.2±7.7[b]	49.2±8.3[a]	50.8±10.3[a]	-
	n=3	n=22		n=32	n=144	n=57	n=3	n=22	
Stage 6	11.8±7.1[a]	4.1±5.5[b]	1.7±1.1[c]	32.7±5.3[A]	32.9±7.1[A]	33±5.4[A]	44±7.4[b]	53.4±10.4[a]	53±9.8[a]
	n=85	n=225	n=33	n=88	n=330	n=52	n=85	n=224	n=32

The different letters indicate that the means are significantly different (Kruskal-Wallis test, p<0.05, using the Bonferroni adjustment method and the Wilcoxon test, p<0.05 only for dual average comparison in stage 5 "Stipe height" and "Diameter-30 cm aboveground").

*Only individuals with free stems (not enveloped by sheaths) were used to calculate the average of these morphological features.
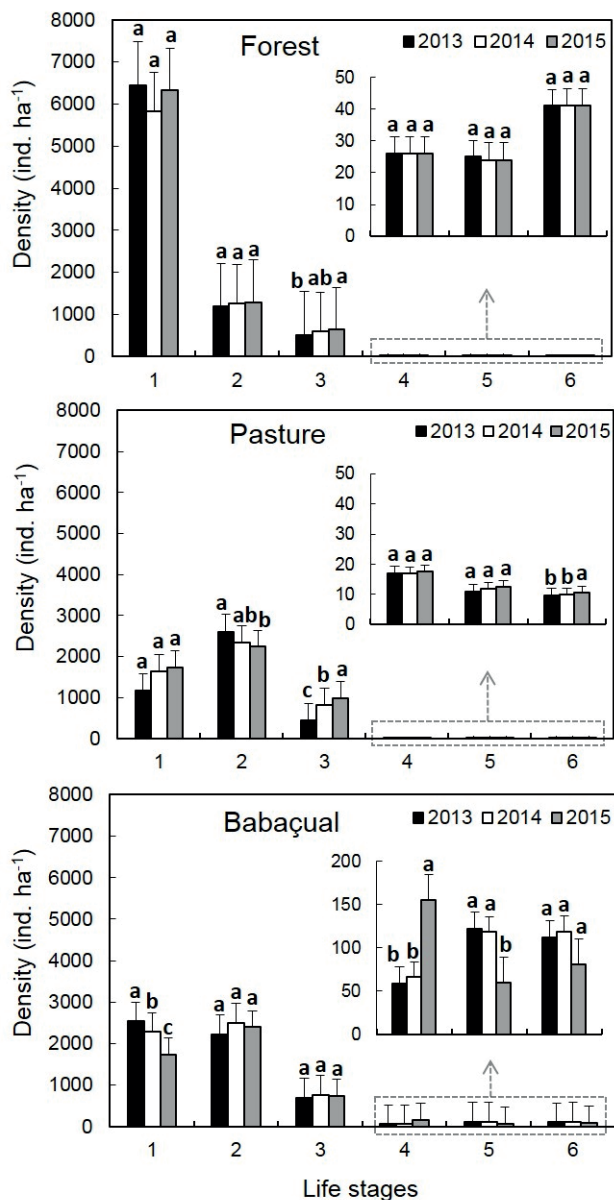
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Figure 4. Density of individuals per stage of life during the years 2013, 2014, and 2015 in the primary forests (n=4), pastures (n=17) and babaçual areas (n=4) of the Benfica Settlement Project.
Note: Common lowercase letters indicate that there is no difference between the treatments within each stage of life, over time (Friedman test, p<0.05). Standard error is represented for each histogram.

p = 0.005 (St5), 2014 p = 0.03 (St4) and p = 0.006 (St5), 2015: p = 0.008 (St4) and p = 0.008 (St5)); for these stages, the babaçual areas had higher significantly densities and the pastures had lower significantly densities, while the forests had an intermediate value. For stage 6, the densities were significantly different across habitats in the first two years (2013: p = 0.003, 2014: p = 0.002), with a higher density in the babaçual areas. In 2015, no significant differences were observed for stage 6 densities across habitat types (Fig. 5).
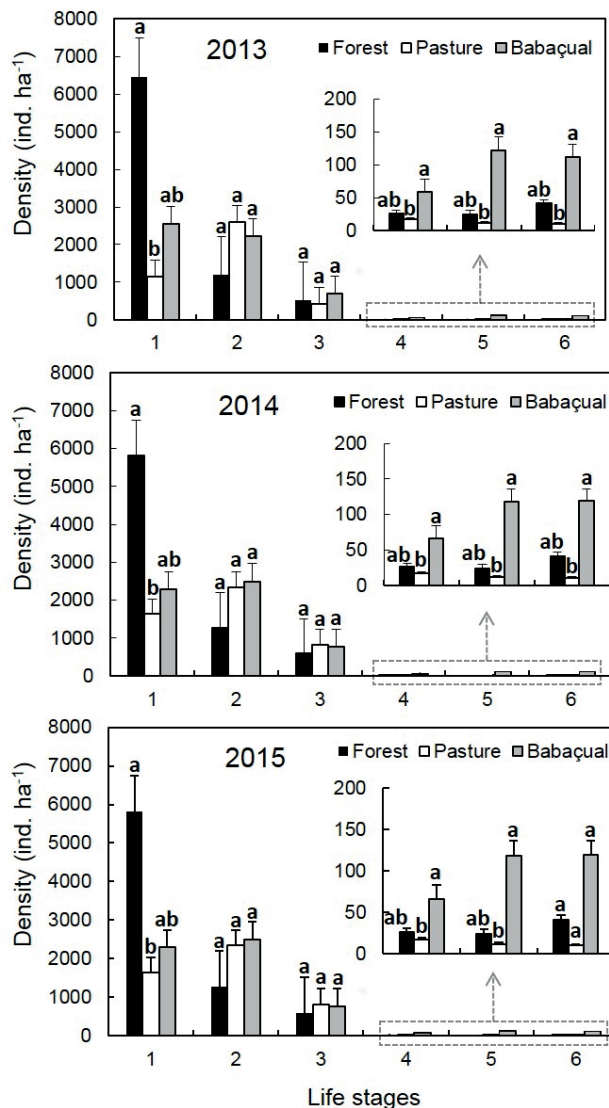

Figure 5. Density of individuals by life stage in the primary forests (n = 4), pastures (n = 17) and babaçual areas (n = 4) of the Benfica Settlement Project, in each year (2013, 2014, and 2015).
Note: Common lowercase letters indicate that there is no difference among areas for each ontogenetic stage (Kruskal-Wallis test, p<0.05, using the Bonferroni adjustment method). Standard error is represented for each histogram.

Similarity among study sites

The areas sampled in 2013 were separated into three groups (Fig. 6): a group formed by primary forests (F01 and F02), a group containing only the 9 years pasture (P04), and a group formed by 1 to 7 years pastures (P06, P10, P08, and P12) and babaçual areas (B01 dense and B02 less dense). The group formed by the two forests (F01 and F02) remained identical in 2014 and 2015. In 2014, the babaçual areas became different, the less dense babaçual (B02) became similar to 1 to 5 years pastures (P08, P10, and P12) and the more dense babaçual (B01) became similar to 7 to

9 years pastures (P04 and P06). In 2015, the groups were similar to those formed in 2014, but the 5 years pasture (P08) became similar to the group of 7 and 9 years pastures, since its density increased by 25 % between 2014 and 2015.

Figure 6. Structural similarity dendrograms between pastures (n= 5), primary forests (n=2) and babaçual areas (n=2), based on the density of individuals in each ontogenetic state, in the Benfica settlement, Pará in 2013, 2014, and 2015.

Note: The connection method was the unweighted pair group method with arithmetic mean algorithm (UPGMA) and the Euclidean Distance coefficient.

Discussion

Morphological characterization of life stages in the habitat types

The morphological characteristics of babassu palm individuals in life stages 1 to 4 were significantly similar between secondary environments (pastures and babaçual areas), but different in relation to primary forests. In the primary forest, the measured parameter values were usually larger, most likely due to variations in the environmental factors that influence individual performance and survival (Faleiro & Schiavini 2009). The development of initial-phase individuals (seedlings and juveniles) in forests is favored by litter, which provides relatively high levels of moisture and soil organic matter (Marcos & Matos 2003). The higher values of morphological characteristics of babassu seedlings (stage 1) were also observed by Gatti *et al*. (2011) for the palm *Euterpe edulis* Mart. These authors showed that the *E. edulis* palm produced larger leaves than those produced under higher solar radiation to compensate for the low solar radiation to which the seedlings were subjected in the forest understory.

In stage 5, the individuals present in forests became more similar in morphology to those in pastures and babaçual areas, except in crown circumference, which was larger within the forests. Adults (reproductive stage 6) from all three studied habitats were similar in morphology in terms of crown circumference. However, these adults had a higher overall height and stipe height in primary forests than in secondary environments (pastures and babaçual areas). Indeed, primary forest individuals must reach a certain height to access sufficient light to allow reproduction (Barot *et al*. 2005; Campos *et al*. 2017), while in secondary environments with high levels of light, this growth is not necessary. In secondary environments, the diameter at 30 cm above ground and DBH had higher values than those in the primary forests. In the primary forests, the density of stems of all tree and palm species protects the environment and the individuals against strong winds, and the babassu, which must mobilize its reserves to reach the height that allows it to reproduce, has certainly done so at the expense of the diameter of its stem. Contrasting this, in secondary environments, as the vegetation is less dense, the isolated babassu adult individuals can be more directly impacted by violent winds. In these environments, our hypothesis is that the babassu, which does not need to produce a tall stem to have access to high luminosity, mobilizes its resources to produce a wider stem that makes it more resistant to climatic disturbances.

The morphological variations observed in these contrasting habitat types suggest that babassu has a high phenotypic plasticity capacity. However, the upper limit of the basal area of palms may also be affected by physical soil restrictions in some areas (Emilio *et al*. 2013),
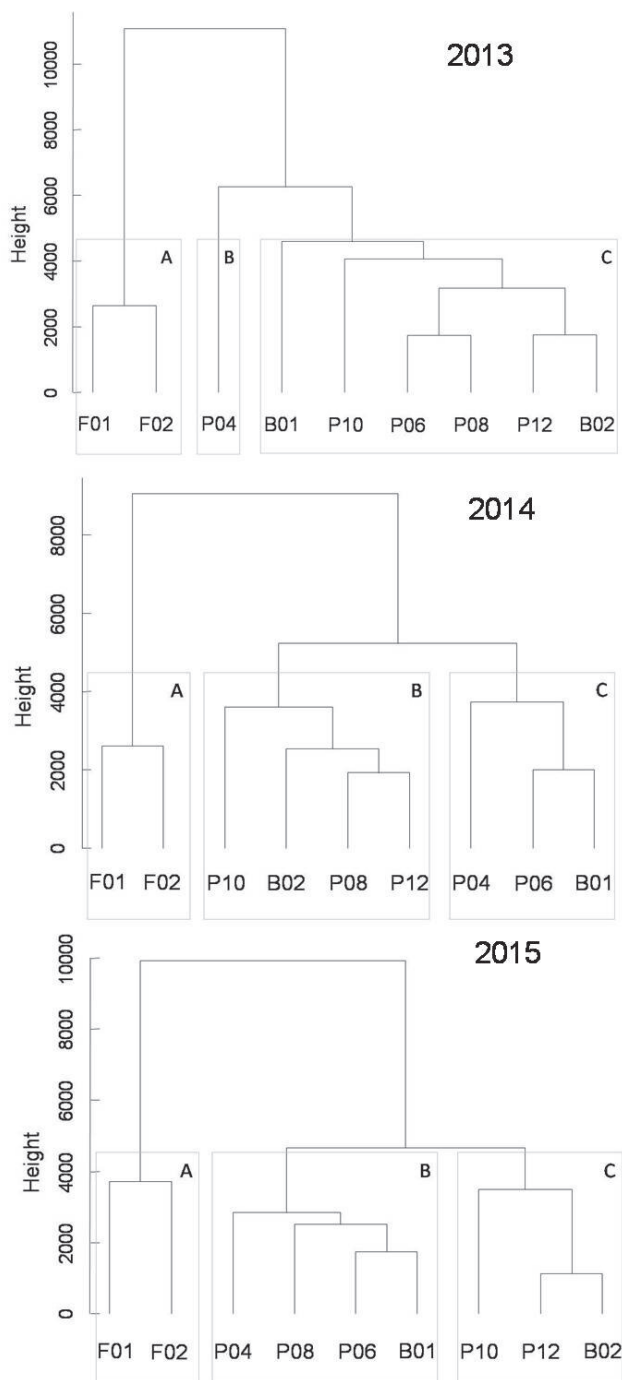
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an argument that we were unable to verify here because we do not have the necessary soil data. In the case of number of leaves, the low number of leaves in the primary forest may be the result of the difficulty in observing the leaves, due to the tall height of the palms and the impediment caused by other forest species. Since there was no leaf removal in the plots during our study, differences in leaf numbers cannot be attributed to this.

Population structure of *A. speciosa*

In primary forests, the distribution of individuals by stage showed a negative exponential shape (Fig. 4), known as an inverse J-shape, where the highest concentration of individuals per hectare was found in the early stages, a normal pattern observed in natural environments that are stable in density and self-replacing (Hall & Bawa 1993). Although Condit *et al.* (1998) questioned this interpretation, they admit that in the absence of an estimate of population size over time, it is reasonable to consider that these inverse J-shapes characterize stable populations, while those with a small number of young stages would correspond to declining populations. These authors have shown that the survival of the plant population would depend more on the individual growth rate in the different stages (Condit *et al.* 1998), which allows the maintenance of a sufficient density of adults, if the growth rates are relatively fast. Our measurements in the primary forests of PA-Benfica showed that in each stage, the densities were not significantly different between years. This reinforces the idea that the babassu population is stable in these forests, at least during the observed period, between 2013 and 2015.

Considering this, the lower seedling density (stage 1) observed in PA-Benfica pastures, compared to primary forests, is not necessarily related to a decline in the babassu population over time. In pastures, a decrease over time in the stage 2 density and an increase in stage 3 density suggests that the population is in a dynamic phase (accelerated individual growth of stage 2 moving to stage 3). The rapid growth of the seedling and juvenile stages in these pastures could explain the presence of a considerable adult population in these pastures. In pastures, the curve is not inverse J-shaped because of the higher density of stage 2 individuals than that of stage 1 individuals (Fig. 4).

Similar to our observations in PA-Benfica forests, Campos *et al.* (2017) observed the inverse J-shaped curve in a seasonal semi-deciduous forest in Ceará State, but unlike our results, these authors also observed this distribution shape in pastures and croplands. The pasture studied by Campos *et al.* (2017) was older than the pastures studied in PA-Benfica (more than 15 years old), and thus the density distribution of babassu had possibly reached a certain stable state. In PA-Benfica, the pastures studied were between 1 and 12 years old, and there were also differences between more recent pastures with lower babassu density and the oldest pastures with higher babassu density.

In the babaçual areas, as in the pastures, the curve is not inverse J- shaped, with the densities of stage 1 and 2 not significantly different (Fig. 5). The babaçual population structure is dynamic over time (the density decreased in stage 1 over 3 years, and increased in stage 4), despite the formation of a relatively closed environment, with limited light in the understory. The age of the babaçual areas studied exceeded 30 years, and farmers still consider these areas as active pastures, where the babassu densities of all life stages are periodically managed. In these babaçual areas, the decrease in babassu density in 2015 is strongly linked to an unforeseen event: the cutting of individuals of stages 5 and 6, which overlapped with the palm's own successional dynamics. Overall, it is in the babaçual areas where the babassu density of stages 2 to 6 was the highest. After the abandonment of pastures, in the young babaçual, the babassu densities of all stages increased (except for seedling stage), since we observed the highest densities of individuals in stages 2 to 6. In these areas, most other species are being phased out, therefore, they are considered as monodominant babassu forests (Almeida *et al.* 2016).

The population structure of babassu palm in the two primary forests studied in PA-Benfica is similar, as shown by the structural similarity study that groups the two forests and also differentiates them from other habitat types (Fig. 6). A progression of total density could be observed in the pasture plots, moving from the more recent pastures (lower density) to the oldest pastures (higher density). Our results showed that there is a tendency for the density of the babassu to increase with the age of the pastures. In these pastures, over time, the young individuals gradually develop across stages and become mature, which increases the density of adults. We expected that the two babaçual areas would have similar densities, but this was not observed. As early as 2014, the more dense babaçual showed a stronger similarity to the oldest pastures, also more dense. In contrast, the less dense babaçual was grouped with the more recent pastures, also less dense. This highlights the importance of surveying multiple sites within each habitat type, when possible, to better characterize them.

The population structure of the babassu palm can also be influenced by fruit harvesting, which limits the production of seedlings, influences the life cycle, and therefore, the future density of adults. In our study, there was no fruit harvesting in the plots studied, and the population structure observed was the result of the ability of babassu to develop in natural conditions found in primary forest, pasture, and babaçual.

Changes in density of individuals during forest succession

Primary forest

We observed that babassu exists in the primary forests of PA-Benfica, with a life cycle characterized by an inverted J-shaped population structure (numerous seedlings)

and densities of individuals that remain stable over time (at least during the 3 years of the survey). These primary rainforests, such as those in the Maranhão state, are an ideal habitat for babassu palm germination, where soils are moist and shaded (Anderson 1983). The experiments by Mitja & Ferraz (2001) showed that in forests, the rate of germinated seeds is very high and that the number of multiple germinations per fruit (2 to 4 seeds, each having produced 1 germination) was more frequent than in open environments; this partly explains the high density of seedlings observed in the forest undergrowth. The same experiments showed that after 18 months, the seedlings which had produced fewer leaves, apparently grew less rapidly than the seedlings in open areas. If growth is slower, individuals will take longer to develop across stages, and the density of stage 1 will be higher. It can be assumed that the microclimatic conditions of the forest undergrowth, humidity, and low luminosity contribute to this slow growth. The same applies to the subsequent stages. Anderson *et al.* (1991) estimated a period of 38 years between the germination of the babassu palm and the initial vertical growth of its stipe in primary forests and more than 70 years for the individual to become reproductive. They estimated the age of the tallest babassu encountered in their study as 184 years.

Previous studies have shown that species that are more capable of germinating in shaded habitats have relatively large seeds (Puig 2008). As babassu also has larger seeds, this trait can contribute to higher seed germination and seedling recruitment in the primary forest. In addition, its slow growth and long life span (Anderson *et al.* 1991) give it all the characteristics of a sciaphilous (or shade-tolerant) species (*e.g.*, Brown & Witmore 1992; Puig 2008), also called primary species (Chandrashkara & Ramakrishnan 1993).

Pastures

Pastures are established after clearing and burning the forest. This slash-and-burn system significantly alters the environment because the undergrowth is cleared, most of the trees are cut, and this vegetation once dried is burned, leaving the soil exposed to the sun and the rains. Some adult babassu palms that were present in the original forest were cut, while others with the lowest stipes were retained (Mitja *et al.* 2018). Generally, seedlings, juveniles, and adults resist fire, rapidly producing new leaves (Mitja *et al.* 2018). Although large seeds, such as babassu seeds, have greater nutritional reserves and therefore a better chance of establishment (Salm 2005), fruits encountered in pastures, unlike those in forests, are unprotected and exposed to sunlight and fire, which may result in seed destruction (Mitja & Ferraz 2001). This could explain the lower number of seedlings (stage 1) in these open environments, while fruit production is higher in pastures than in forests (Campos *et al.* 2017). However, the presence of the livestock that tread on babassu fruits and bury them can also protect the seeds

and prevent their destruction (Mitja & Ferraz 2001). In fact, the effect of fire is complex and contradictory: on the one hand, it destroys unprotected seeds; on the other, it eliminates competition from other species in the pasture by promoting greater growth of this species, which inherently has a faster growth rate than other species (Mitja *et al.* 2018). In pastures, *A. speciosa* seedlings exposed to a higher light availability grow faster than those inside forests (Mitja & Ferraz 2001). Two effects are cumulative: first, fewer seeds germinate in the pasture than in the forest, resulting in a lower seedling competition. Second, the babassu seedlings from these germinated seeds grow faster due to higher light availability in pasture, resulting in a higher transition to the subsequent stage. This explains the lower number of seedlings in pastures compared to that in the forest. This much faster growth in pastures than in the forest was reported by Anderson *et al.* (1991), who estimated at 8 to 12 years as the period needed for a babassu to become fertile (stage 6) in the Maranhão pastures. Pastures can be maintained in production for many years, but some may be abandoned for different reasons, such as weed invasion, disease contracted by the pasture owner, or migration.

Babaçual areas

The pastures that are abandoned can, over time, become babaçual areas, with a higher babassu density. Usually, when pastures are abandoned, periodic maintenance is interrupted. Occasionally, the cattle graze there, but this is no longer systematic, as in the active pastures. Some of these areas become secondary forests that are almost monospecific with babassu. In these environments, the babassu grows without competition with other species that are not present. While the average density of seedlings in babaçual areas was intermediate between forest and pasture, the density in stages 2 to 6 was higher. However, the density can vary from one babaçual to another. This is probably due to the state of the population at the time of abandonment of the area. This is the case for the two babaçual areas that we studied. In our study, we were not able to obtain the historic information that would have allowed us to confirm this hypothesis.

Resilience of *A. speciosa*

Certain studies have already reported the excellent development of babassu palm in secondary environments (*e.g.*, Anderson & Anderson 1985; Mitja & Ferraz 2001; Santos & Mitja 2011; Coelho *et al.* 2012). The high density of this palm in these areas results from its resilience to natural and anthropogenic disturbances (fire and cutting for young acaule stages) (Mitja *et al.* 2018). This resilience is linked to endogenous factors specific to the species and to exogenous factors that influence the species in secondary environments, which sometimes favor it. Among the endogenous factors, Barot *et al.* (2005) pointed out its great reproductive plasticity, with rapidly maturing

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individuals in open environments. Specifically, Anderson *et al.* (1991) estimated that 70 years are required for babassu individuals to be reproductive in the forest, whereas 8-12 years are sufficient in pastures. Our hypothesis, which is yet to be proven, to explain this difference is that babassu can grow more rapidly in pastures than in forests. Moreover, this palm tree has an underground stipe during the first stages of its development, which can increase the survival of these individuals during fire and pasture cleaning events. Previous studies also found that an underground stipe can increase the survival of palm species in habitats with the occurrence of anthropogenic disturbances (Barot *et al.* 2005; Montúfar *et al.* 2011). Indeed, the location of the meristem approximately 0.5-1 m below ground provides the potential for extremely vigorous regrowth of the babassu (Sousa *et al.* 2016). The thick roots of the babassu palm are deeper than other species (natural or cultivated), although a high percentage of its fine roots share the same niche as other species, placing this palm in interspecific competition situations (Sousa *et al.* 2016). These authors highlight the importance of the root system of babassu, which explains its great competitiveness and the increase in its density.

Resilience exhibited by the babassu palm has also been observed in numerous other species of arborescent palms (Montúfar *et al.* 2011). Sanín *et al.* (2013) studied the performance of *Ceroxylon quindiuense* (Karst.) H. Wendl. in pastures and concluded that the permanence of this palm species was associated with not only deforestation, which spares the palm, but also with the resilience of juveniles that grew up to adults. Similar resilience has also been observed in other studies with the species *Ceroxylon echinulatum* Galeano (Anthelme *et al.* 2011) and *Attalea humilis* Mart. ex Spreng. (Souza & Martins 2002; 2004). The subterranean apical meristem in juveniles of these species is generally protected by the sheaths and surrounding leaves, preventing its exposure to fire or cutting (Souza & Martins 2002; 2004; Anthelme *et al.* 2011; Sanín *et al.* 2013).

In pastures, the exogenous factors that favor the development of babassu are directly or indirectly linked to humans. When the forest is cleared for pasture, some adult individuals are retained by the farmers. Large fruits that fall under the adult babassu can be dispersed by wild animals (zoochory), especially agouti (Dasyprocta spp.) and paca (Cuniculus spp.). These animals are considered fruits dispersers because of their habit of burying fruits after removing their mesocarps (Anderson 1983; Andreazzi *et al.* 2009), a behavior that favors germination. These dispersers are usually active in forests and in cultivated areas close to forest remnants or secondary forests. In pasture areas, fruit dispersal is also accomplished by cattle (Kahn *et al.* 2003) and floods, especially in compacted soils, where fruits can be transported up to 25 m away from the matrix (Anderson 1983). Cattle that move throughout the pastures and sometimes rest under the palms, can also bury the fruits

in the pastures soil, which can increase the germination's success in this environment (Mitja & Ferraz 2001).

Due to its resilience and because of anthropogenic disturbances, the babassu, a native species of primary forests, can become dominant by invading open environments. It is one of the Brazilian species cited by Pivello *et al.* (2018) that have become super-dominant as a result of unusual disturbances mostly of anthropogenic origin, such as *Mikania micrantha* Willd., *Tabebuia aurea* (Manso) Benth. & Hook f. ex S. Moore, *Pteridium arachnoideum* (kaulf.) Maxon or *Curatella americana* L.

In conclusion, our study showed that agricultural practices related to the establishment of pastures influence the population structure of the babassu palm by decreasing its density. Despite this, the density of babassu tends to increase in older pastures and in some babaçual areas due to the high resilience of this palm. This resilience is related to the presence of an underground stipe in the early stages of development, and the faster development of babassu individuals in open environments, reducing the time period to start fruit production. A better understanding of the mechanisms that lead to the proliferation of babassu palms in open environments will make it possible to envisage the management of the adult stages as well as the initial stages. Continued acquisition of these data will make it possible to propose population dynamics models capable of providing simulations related to specific anthropogenic impacts.

Acknowledgments

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