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DEMOGRAPHY OF *Mora paraensis* (DUCKE) DUCKE IN THE ESTUARINE FLOODPLAIN FORESTS OF THE AMAZON RIVER

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Abstract: Trees of *Mora paraensis* (known as *pracuúba*) accumulate most of the commercial volume of the estuarine floodplain forests in the Amazon River, which are being pressed by disordered logging. To verify if their demographic rates are balanced and vary according to their proximity to the Amazon River, we analyzed the population dynamics of this species for 5 years in 240 plots of 10 m x 25 m. Half of the plots were in areas near the Amazon River and half were in more distant areas (3 ha in each site). The annual measured DBH from 2011 to 2015 was used to construct integral projection models (IPMs), based on the variation in the size of individual trees in that period. Tree survival was high in both populations, but only the population closest to the Amazon River showed mortality in trees of greater than 50 cm DBH. This population has a higher pracuúba density and basal area, but a smaller diameter average because there is a greater proportion and predominance of smaller trees. Both the population near and distant from the Amazon River exhibited increasing population growth rates in all sampling intervals. Population growth rates (λ) ranged from 1.02 to 1.25. The survival of *M. paraensis* populations showed a strong dependence on size and the distance of the Amazon River changes the density and demography of specie in estuarine forests population increases were maintained throughout the evaluation period, with no atypical year causing shrinkage in the populations.

Keywords: elasticity; integral projection model (IPM); lowland forests; population dynamics; survival.

INTRODUCTION

Species distributions typically vary across environmental factors (Ashcroft *et al.* 2011, Peterson *et al.* 2011). In turn, these environmental gradients often cause changes in vital rates (survival, decline, and fecundity) and vary between populations (Villellas *et al.* 2015). Knowing how vital rates respond to environmental drives would help predict shifts in species geographical ranges of species induced by climate change (Villellas *et al.* 2015). In the floodplain forests of the Amazon, flooding is one important environmental factor that varies spatially and over time and may generate different plant morphological and physiological responses in flooded areas (Ferreira *et al.* 2009, Grandis *et al.* 2010). It has been already reported in the literature that flooding induced large morphological changes in *Himatanthus sucuuba* (Apocynaceae), a tree species that is found in the floodplain (*várzea*) and upland (*terra firme*) forest of the Amazon (Ferreira *et al.* 2009). These two habitats imposed a selective pressure strong enough to result in large phenotypic differences between populations in terms of long-term flood tolerance.

In addition to environmental factors, logging is another component that can cause changes in vital rates in tree species subject to selective timber extraction in the tropical region (Fortini & Zarin, 2011, Darrigo *et al.* 2016). The removal of individuals in a population alters the processes of natural regeneration, changing the demographic parameters of the tree species susceptible to timber extraction (Sebbenn *et al.* 2008, Yamada *et al.* 2013). Yamada *et al.* (2013) studying 130 tree species in a Malaysian lowland forest showed a significantly faster growth rate of trees in the logged forest than in the primary forest with little difference in mortality rates between the two forests. However, recruitment rates in the logged forest were significantly lower than those found in the primary forest. Consequently, population growth rates were significantly higher in the primary forest. Thus, demographic studies lead to many contemporary challenges in ecology, from understanding species distributions to the destination of biodiversity under anthropogenic disturbance. However, analyzing data from temporal processes has always been a "bottleneck" for understanding and defining demographic patterns (Caswell 2001).

Demographic studies, through the use of demographic models, have become a useful tool for designing management strategies, estimating the approximate proportion of resources that can be collected without exhausting the population and subsidizing long-term planning (Morris & Doak 2002). Such models are useful to estimate population growth rates (lambda) as well as to identify which demographic parameters impact more lambda. These parameters, in turn, are used to define which individuals should be prioritized in management actions (Isaza *et al.* 2016, Isaza *et al.* 2017, Zucaratto *et al.* 2021). Most studies have used matrix models to produce such predictions (Crone *et al.* 2011). The problem of matrix models for species that do not have ontogenetic stages lies in the arbitrary definition of individuals in size classes, which may generate inadequate estimates of population growth rates and affect the interpretation of disturbance analyses (Easterling *et al.* 2000, Zuidema *et al.* 2010). Integral Projection Models (IPMs) were developed to tentatively mitigate the problems of matrix models (Easterling *et al.* 2000, Ellner & Rees 2006, Zuidema *et al.* 2010). IPMs are extensions of matrix models that maintain the essential properties of matrices such as population growth rate, sensitivity, elasticity, and age estimates (Zuidema *et al.* 2010). However, instead of grouping the plants into classes, a continuous variable (plant height, diameter) produces more robust results (Ramula *et al.* 2009, Zuidema *et al.* 2010, Merow *et al.* 2014).

IPMs are rarely used for long-lived and slow-growing species such as *Mora paraensis* (Ducke) Ducke (Fabaceae family), popularly known as *pracuúba*, despite their potential for this purpose (Metcalf *et al.* 2009). *Mora paraensis* presents a high-density wood, with a diametric growth rate of 0.491 mm year^{1} and can live for more than 150 years in the Amazon River estuary forests (Miranda *et al.* 2018). It is a species with potential for management, as it has a high dominance and abundance in these forests (Queiroz *et al.* 2005, Queiroz & Machado 2007, Carin *et al.* 2008, Fortini & Zarin 2011). *Mora paraensis* was already the dominant species before most timber extraction in the Amazon River estuary forests (Fortini & Zarin 2011). *Mora paraensis* has only been harvested at low and commercial levels by smallholders in the last decade because of its heavy wood and low buoyancy that make ground and water transport difficult (Fortini & Zarin 2011). This broadens the possibilities of structuring management practices that may potentiate economic exploitation of the species, which is of interest to the timber industry.

This species still presents the remaining stock of 13 commercial trees (DBH ≥ 50 cm) per hectare and a commercial volume of 37 m^{3} ha^{-1} in the same region of the present study (Lima *et al.* 2014). In addition, it is the wood from the most commercialized lowland forest (Castilho 2013), justifying the focus of the work on this species. It has a high demand for use in the construction of structures in floodplain and wood houses. *Pracuúba* may represent the last opportunity to carry out sustainable polycyclic management for wood production in the lowland forest. The viability of logging in lowland areas where log transport is carried out by the river is dependent on the drainage network (Fortini & Zarin 2011, Fortini *et al.* 2015). The distance from the logging site to the watercourses directly influences the travel time by the rivers. In addition to affecting the viability of the exploitation, the geographic question and the river distance can also be associated with the demography of the species. Since *M. paraensis* is subject to the effects of flooding and timber extraction and such factors can alter the demography of the species, the following objectives were defined: 1) to verify if the individuals closest to the northern Amazon River channel, are subject to greater flooding, present higher mortality; 2) to analyze if the most distant areas of the Amazon River are more favorable to *pracuúba* tree establishment and their population growth; and 3) to quantify changes in demographic rates over 5 years, to check if there was any atypical year and whether changes could be associated with the temporal variation.

MATERIAL AND METHODS

Study area

The study was carried out in the municipality of Mazagão across the Mazagão, Maracá and Ajuruxi rivers (Figure 1), southwest of Amapá state, Brazil. These locations are arranged along the northern Amazon River channel and are characterized as floodplain areas of the Amazonian estuary, under the direct influence of the daily flow of ocean tides (Salomão *et al.* 2007).

The predominant vegetation in the region is high-level floodplain forest, with a high frequency of palm trees (Fortini *et al.* 2006), also classified as Alluvial Ombrophilous Dense Forest (IBGE 2012). The soil is classified as Gleysol and presents a predominantly silty and clayey texture (Pinedo-Vasquez 1999). The region has a hot and humid tropical climate, with an annual average temperature of 27.7 °C *(*INMET 2015). The average annual rainfall is 2,423 mm, irregularly distributed throughout the year, with higher precipitation between January and June (INMET 2015). This part of the Amazon River estuary is characterized by a tidal fluctuation of around 2 to 3 m, driven by the Atlantic Ocean's impoundment of the Amazon waters. Because of the variation due to the tides and the high level of the river, forests are flooded twice a day, mainly during the rainy season (Fortini & Carter 2014).

Data collection

Four transects were implanted in each studied region, forming a distance gradient in relation to the north Amazon River channel. Each transect was spaced at least 1 km from one another to guarantee independence between the samples (Figure 1). Within each transect, 20 plots of 250 m^2 (10 m x 25 m) were allocated. The plots of the two transects closest to the river from each region were grouped totaling 6 transects, 120 plots and a sample area of 3 ha for the population close to the Amazon River. The same sampling was done for the most distant areas from the junction of the other six transects, also totaling 3 inventoried hectares.

The *pracuúba* tree diameters from 4.7 cm in diameter at breast height (DBH) were measured annually from 2011 to 2015, using a tape measure with 1 mm of precision. Since it was very difficult to identify seedlings of the species, *pracuúba* individuals with DBH = 4.7 cm were considered seedlings recruited (fecundity) in the analyses. The place where the measurement was carried out was marked with red paint so that all the measurements were carried out exactly in the same place during the years. The inventory was done by traversing the transects and performing the measurements in the demarcated plots along the same transects, and all the *pracuúba* trees were identified and numbered with aluminum plates.

Data analysis

Structural parameters of the two populations (near and far from the northern Amazon River channel) were calculated at the beginning (2011) and at the end of the monitoring (2015) to

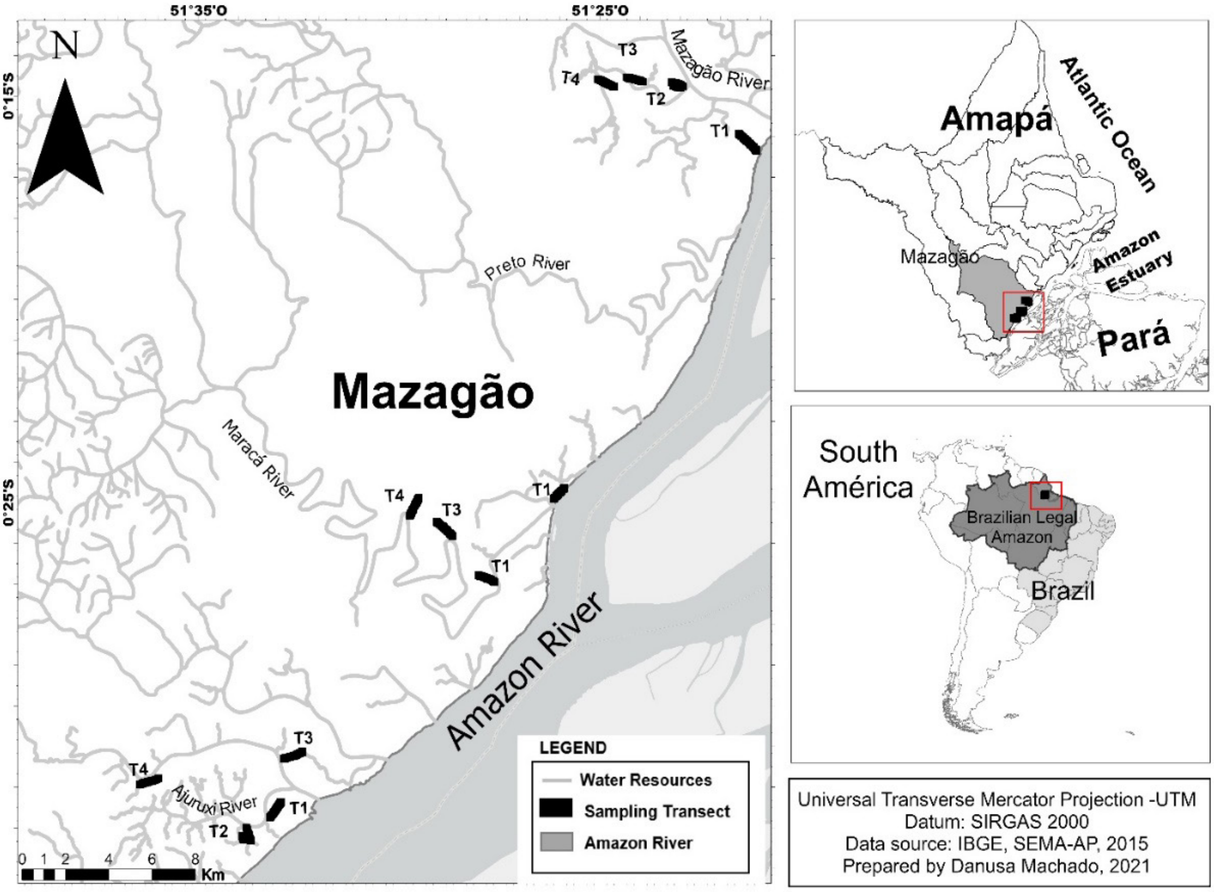

Figure 1. Location of the sampling transects at the three study sites in the municipality of Mazagão, southern Amapá state, defined 1 as a function of the confluence of the primary tributaries with the northern Amazon River channel. The four 2 transects located at different distances of the Amazon in each tributary/region can be observed.

subsidize the discussion about the differences and variations observed in the demographic rates. Relative frequency distribution curves of the pracuúba trees were constructed in classes of 10 cm in diameter, and the density, mean diameter, and basal diameter of each population were calculated.

For the demography analysis, we applied the integral projection model (IPM) proposed by Easterling *et al.*, (2000). In this model, as in the case of transition matrices, individuals in the population may die or survive, grow, and reproduce. Therefore, three functions of growth, survival, and fecundity of the individuals are initially necessary for applying the model. When combined, these functions form the kernel function that will be integrated. Thus, the matrix used in the matrix models is replaced by the Kernel function in the integral projection model. By performing the integral of this function, we can evaluate the vital rates for a population with very small classes (Easterling *et al.* 2000), which represents a continuous variation along the diametric distribution. Therefore, population dynamics are described by the equation:

$$n(y, t+1) = \int_{L}^{U} K(y,x)n(x,t)dx$$

K is the projection kernel that replaces the size matrix in matrix models (Easterling *et al.* 2000) and represents all the possible size transitions, including births, where x is the size at time t, y is size at time $t+1$. [L, U] is the range of possible sizes (or any other continuous descriptor of the demographic state) that an individual may have, and n is the distribution vector of the population. To build the kernel was used the midpoint rule integration method, evaluating the kernel at mesh points with a grid dimension of 300 for all IPMs. The smallest (4.7 cm) and the greatest (127.3

cm) diameter at breast height were used as the minimum and maximum limits of integration. The projection kernel is built from a *P* (which represents survival and growth) and an *F* (which represents fecundity) functions (Easterling et al. 2000, Ellner & Rees 2006, Zuidema et al. 2010). The *P* function used was the simplest case $P(z', z) = s(z)\, g(z', z)$ to the survival/growth kernel. The survival function $s(z)$ describes the probability of survival of an individual in the census interval (t and $t+1$) and, if that occurs, the distribution of probability for the size it may reach, the growth function $g(z', z)$ (Merow et al. 2014). The F function describes the number of recruits generated by reproductive individuals during the census interval and the size distribution of the new offspring. The fecundity was estimated as the ratio between the number of new recruits (individuals with DBH = 4.7 cm) in time $t+1$ and the number of reproductive *pracuúba* trees in time *t*. Reproductive *pracuúba* trees were those with DBH ≥ 34 cm (Fortini & Zarin 2011).

Alternative statistical relationships were calculated for growth and survivorship (vital rates) as functions of plant size (independent, size, $size^2$, $size^3$) and then model selection methods based on the Akaike Information Criterion (AIC) were used to determine which provided the best data fit the data. The following functions were tested: vital rate~1, vital rate~size, vital rate~size+$size^2$, vital rate~size+$size^2$+$size^3$ and chose the model with the lowest AIC score or the simplest model, using $\Delta AIC \leq 2$ (Table S1, Table S2). To avoid eviction in the *P* and *F* kernels was used *discretizeExtremes* argument correction to construct IPMPmatrix and IPMFmatrix. Population growth rates λ (dominant eigenvalue) for determining time intervals are obtained by the integral transform of the projection kernel. Values of $\lambda = 1$ indicate a stable population, $\lambda > 1$ indicate population increase, and $\lambda < 1$ indicate population decline. To estimate the proportional effect of each life cycle vital rates (survival, growth and fecundity) on the population growth rate λ were performed prospective analyses of elasticity (Caswell 2001). To compare different values for population growth rate was calculated confidence intervals (CI) through bootstrapping. Using the *sample* function was obtained a subset in which 5% of the individuals in the populations were removed, in a loop of 1,000 randomizations. Then, for each randomized subset the mean λ values were obtained and 95% confidence intervals were calculated. All analyses were performed in R v.3.5.1 environment (R Development Core Team 2018) using the package 'IPMpack' (Metcalf *et al.* 2013) 'popbio' (Stubben & Milligan 2007), gamm4 (Wood & Scheipl 2020), and 'fields' (Nychka *et al.* 2017).

RESULTS

The number of *M. paraensis* individuals varied between the studied areas (t = -3.3872, df = 8.3543, p = 0.008), with greater abundance in the areas near the Amazon River, being 218 ind. ha^{-1} quantified in the first year of measurement (2011), and 215 ind.ha^{-1} quantified in the last year (2015) ($R^2 = 0.4516$; $p = 0.033$). In the most distant areas of the Amazon River, the population density recorded were 102 ind.ha^{-1} in 2011 and 103 ind.ha^{-1} in 2015 ($R^2 = 0.5437$; $p = 0.023$) (Table 1). The DBH varied between 4.7 and 127.3 cm (Figure 2a, b). There is a predominance of young individuals in both, but the relative proportion in the first class is different ($R^2 = 0.4516$; $p = 0.033$). The population of the surrounding areas of the Amazon River showed higher density and basal area, but lower mean diameter (Table 1).

Table 1. Structural evaluation of populations of *pracuúba* trees at the beginning and end of the monitoring through an analysis of the density (D), mean diameter (medDBH) and basal area (G), in the close and far areas from the northern Amazon River channel.

Period	**D (ind. ha^{-1})**	**medDBH (cm)**	**G(m^2 ha^{-1})**
Near 2011	218	18.1	11.06
Near 2015	215	18.6	11.03
Distant 2011	102	23.0	7.6
Distant 2015	103	24.2	8.3

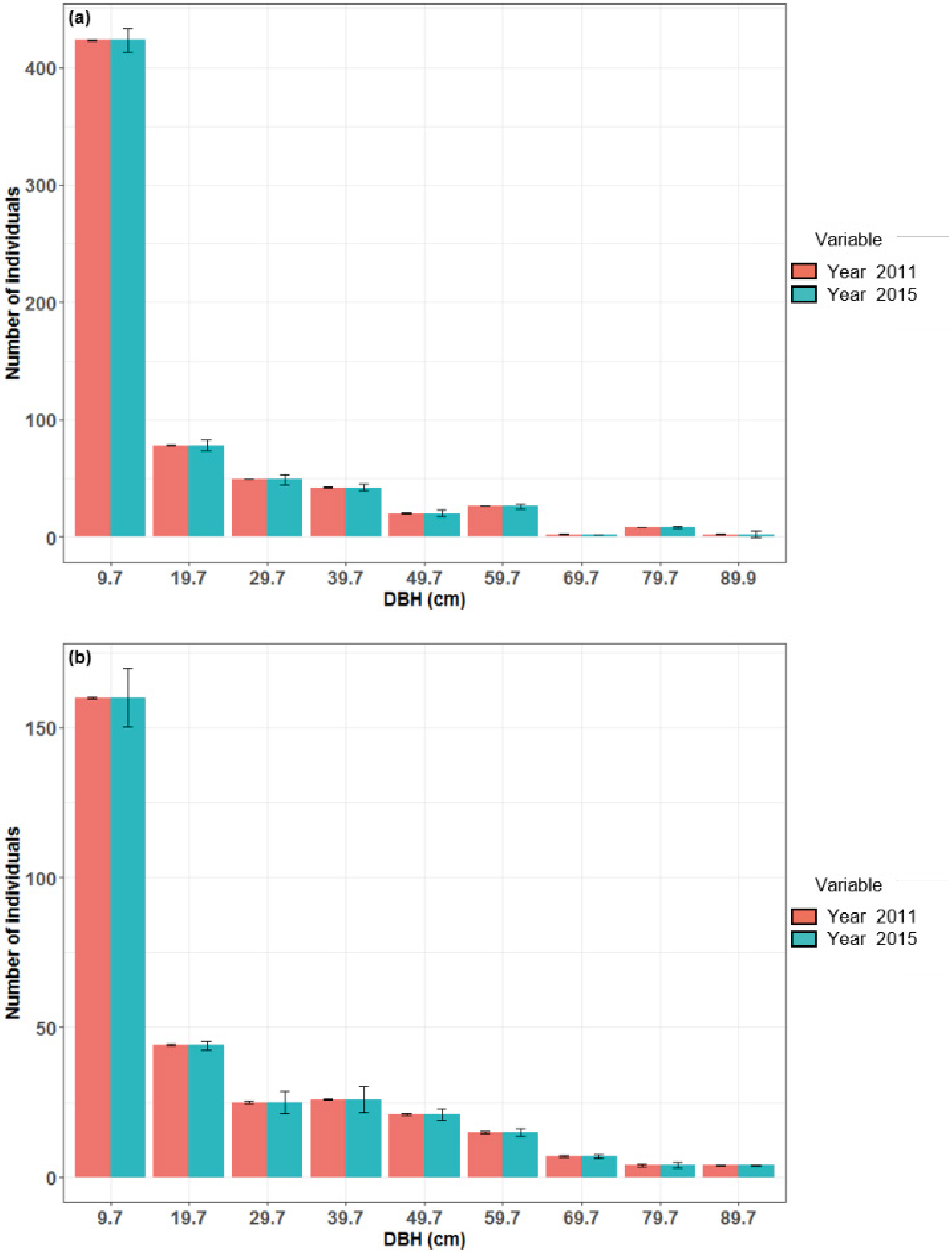

Figure 2. Population structure of *Mora paraensis* in 2011 and 2015 by the distribution percentage (calculated 5 in the last monitoring year) of the abundance of trees in diametric classes, in the close and far areas from the 6 north Amazon River channel. (a) Near, (b) Distant.

The survival of *M. paraensis* individuals demonstrated a strong dependence on size, indicating the importance of using a structured demographic model that considers this variable. In general, only individuals smaller than 50 cm in diameter died within one year. Mortality of individuals larger than 50 cm in diameter was only observed in the population located on the transects near the north Amazon River channel. The total number of dead pracuúba trees at the end of the monitoring in the near areas was 9 individuals, whereas 3 individuals were found dead at the end of the 4 years period in the more distant areas. For the population near the Amazon River, survival and growth were recorded in all individuals (sampling interval 1) and mostly in individuals with DBH ranging from 4.7 to 63 cm (≈ log10 1.8; sampling intervals 2, 3, and 4) (Figure 3). Above that DBH (63 cm; log10 1.8) individuals survived and remained in stasis (sampling intervals 2 and 3) or decreased their diameter (sampling interval 4) (Figure 3). In the population distant from the Amazon River, survival and growth were recorded for individuals with DBH ranging from 4.7 to 25 cm (≈ log10 1.4; sampling interval 1) and for all individuals (sampling interval 2) (Figure 4). In the population distant from the Amazon River, were also observed survival and stasis for individuals with DBH > 25 cm (≈ log10 1.4; sampling interval 1) and for all individuals (sampling interval 4) (Figure 4). In both populations (near and distant) fecundity was recorded only in individuals with DBH > 31 cm (≈ log10 1.5; Figure 3 and Figure 4). Due to the lower number of seedlings (N = 1) recorded in sampling interval 3 for the population distant from the Amazon River, it was not possible to perform the analysis for this interval.

According to IPM analysis, population growth rates (λ) ranged from 1.02 to 1.25 (Table 2). Both the population near and distant from the Amazon River exhibited increasing population growth rates in all sampling intervals (Figures 3 and Figure 4). The percentage of increase in the growth rates of the population near the Amazon River was 7 to 25%. On the other hand, the percentage of increase in the growth rates of the population distant to the Amazon River was 2 to 19%. None of the populations showed a decrease in their population size during the study years. The bootstrap estimates of population growth rates (λ_b) were similar to population growth rates (Table 2). Again, due to the lower number of seedlings (n = 1) recorded in sampling interval 3 for the population distant from the Amazon River, it was not possible to perform the analysis for this interval.

The vital rates that most impacted the population growth rates (λ) in both near and distant populations were the survival and growth of the smallest individuals (4.7 to 10 cm; Figure 3 and Figure 4). An exception was observed in the population distant from the Amazon River for the sampling interval 4. In this sampling interval, the elasticity was more evenly distributed by the survival and growth of all individuals (Figure 4).

DISCUSSION

Although the abundance of *pracuúba* trees has been greater in areas near the Amazon River, most parameters assessed were similar between populations. In general, mortality was only registered in individuals with DBH < 50 cm; whiles survival and growth were registered for all individuals in both near and distant populations. Also, in both populations (near and distant), fecundity was only recorded in individuals with DBH > 34 cm. In terms of population growth rates, none of the populations showed a decrease in their population size during the study years, with the population near the Amazon River showed greater increases in the percentage of growth. Population elasticity patterns were also very similar, with survival and growth of the smallest individuals the vital rates that more strongly impacted population growth rates.

The analysis of the population structure confirmed a high density of *pracuúba* trees, with higher concentrations in the initial classes in all populations. In a study carried out on lowland forests in the same municipality (Carim *et al.* 2008), an average of 73 ind.ha^{-1} of *M. paraensis* greater than 10 cm of DBH was found, and dominance of 17.65% of the total basal area of the forest by the *pracuúba* trees. Although considered high, this value is still much lower than those found in this study, whose inventory inclusion diameter was 5 cm. In another work that conducted a floristic survey of the arboreal stratum with DBH ≥ 10 cm in lowland forests in the states of Pará and Amapá, it was also found that *M. paraensis* is a dominant species, as well as the family Fabaceae to which this species belongs (Almeida & Jardim 2011).

Regarding the geographic question, it was detected that there is a greater density of *pracuúba* trees in areas close to the Amazon River than in the more distant areas. The same density pattern was also reported in Pinto (2014), where the author found more *pracuúba* trees in areas near the Amazon River. These density values could be related to the dominance of *M. paraensis* found in floodplain regions of the Amazon estuary,

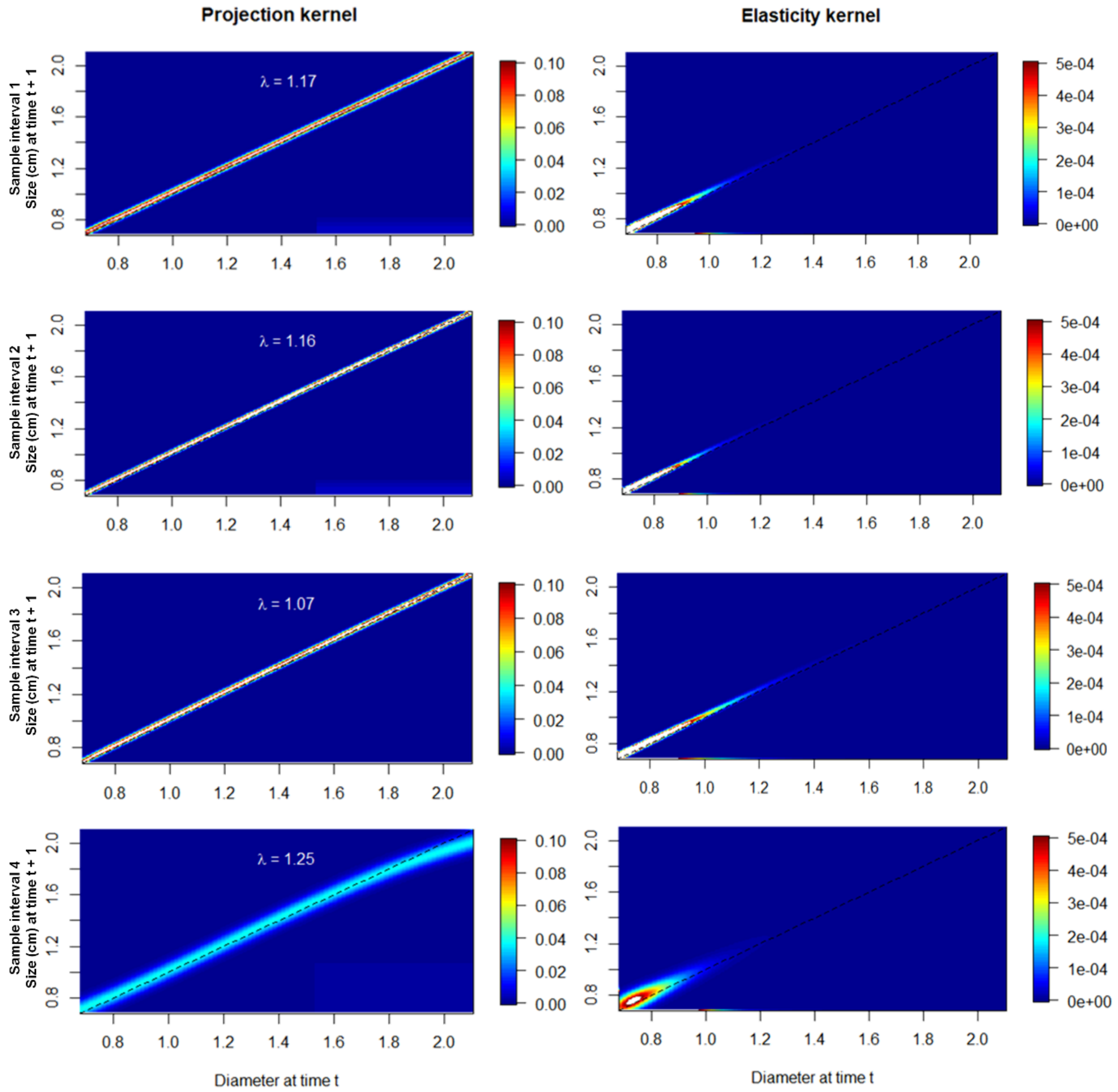

Figure 3. Demographic analyses using Integral Projection Models (IPM), for four sampling intervals (from 2015 to 2018), on the population near to the Amazon River of *Mora paraensis*, in the municipality of Mazagão, southern Amapá state, Brazil. Left: the projection kernels, built from a P function (which represents survival and growth, depicted on the main diagonal of each image) and an F function (which represents fecundity, depicted on the lower right of each image). The kernels represent all surviving individuals in the sampling interval. Right: the elasticity kernels, showing the vital rates (survival, growth, fecundity) that most impacted the population growth rates. The dashed line in the main diagonals (on both sides) is used as a reference for the probability of stasis. Individuals on the line did not change size (stasis), the ones above the line increased in size, and the ones below the line decreased in size. The warmest colors as well as the white color indicate higher probabilities of transition. The x and y axes are on logarithmic scale (1.0 = 10 cm; 2.0 = 100 cm).

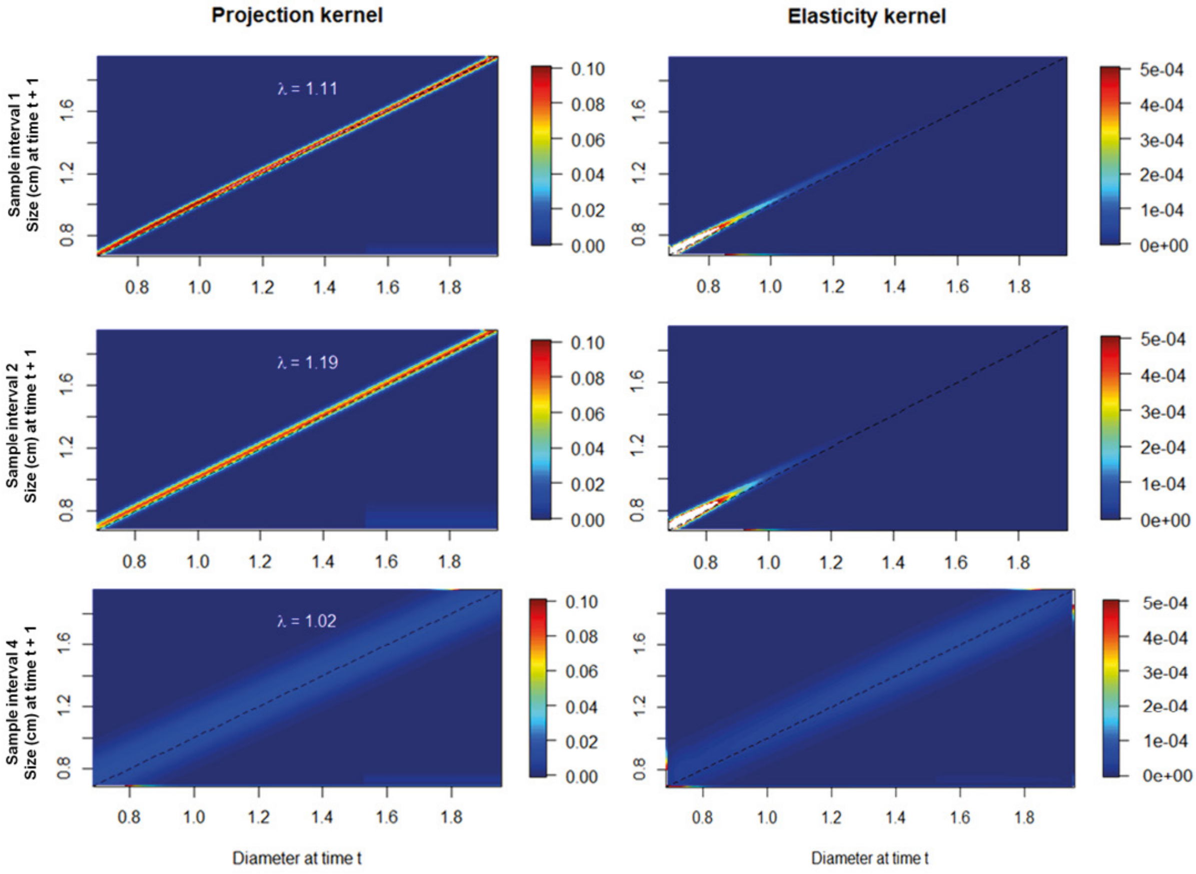

Figure 4. Demographic analyses using Integral Projection Models (IPM), for three sampling intervals (from 2015 to 2018), on the population distant from the Amazon River of *Mora paraensis*, in the municipality of Mazagão, southern Amapá state, Brazil. Left: the projection kernels, built from a P function (which represents survival and growth, depicted on the main diagonal of each image) and an F function (which represents fecundity, depicted on the lower right of each image). The kernels represent all surviving individuals in the sampling interval. Right: the elasticity kernels, showing the vital rates (survival, growth, fecundity) that most impacted the population growth rates. The dashed line in the main diagonals (on both sides) is used as a reference for the probability of stasis. Individuals on the line did not change size (stasis), the ones above the line increased in size, and the ones below the line decreased in size. The warmest colors as well as the white color indicate higher probabilities of transition. The x and y axes are on logarithmic scale (1.0 = 10 cm; 2.0 = 100 cm). Due to the lower number of seedlings (N = 1) recorded in sampling interval 3, it was not possible to perform the analysis for this interval.

as demonstrated in forest inventory studies conducted in these regions. *Mora paraensis* was the species that presented the highest values of relative dominance in relation to other tree species (Carim *et al.* 2008, Aparício 2011). Such dominance could be related to the morphological characteristics of the species, adapted for flooded environments, and soil characteristics such as organic matter and clay content (Souza 2011, Pinto 2014).

There is a predominance of young individuals in all areas near and far, regardless of the distance variations of the Amazon River. This tendency was also found for other lowland species which presented a distribution with a greater abundance of youngsters than adults; a situation that suggests the sustainability of forest systems (Magnusson *et al.* 1999). On the other hand, Virillo *et al.* (2011) recommend that managers should not use measures of size structure as a basis for management decisions without applying more appropriate demographic studies. The authors found in their study with five tree species that density histograms of size distributions are not good indicators of future trends in population number.

Table 2. Population growth rate (λ), bootstrap estimate of population growth rate (λ_b), and bootstrap 95% confidence interval (CI-, CI+) for two populations of *Mora paraensis* in the areas near and distant from the north of the Amazon River channel, municipality of Mazagão, southern Amapá state, Brazil. Bootstrap values were computed using 1,000 bootstrap samples.

Population	Sampling interval	λ	λ_b	CI-	CI+
Near	1	1.17	1.163	1.162	1.164
	2	1.16	1.162	1.162	1.163
	3	1.07	1.062	1.061	1.063
	4	1.25	1.252	1.251	1.252
Distant	1	1.11	1.101	1.099	1.103
	2	1.19	1.185	1.184	1.186
	4	1.02	1.023	1.022	1.025

However, in this work, it was found that the relative abundance proportion of *pracuúba* trees in the first class is different between areas near and far from the Amazon. In the nearest areas, the first class of younger individuals represents 61% of the abundance, while it represents 52% in the more distant areas. This difference is confirmed by the higher average diameter in the more distant areas, indicating that there is proportionally a larger amount of thicker trees established in these areas. This result indicates that the nearest areas, being subject to greater flooding, have a more adequate regenerative niche for the species than more distant areas, and these provide better settlement conditions for larger trees. The niche is considered a determining factor for establishing regenerating individuals, indicating their tolerance to physical-chemical and biotic factors (Grubb 1977). Another hypothesis is that individuals near the river grow slowly and consequently small individuals are in higher density. It was pointed out by Fortini & Zarin (2011) that found that flooding had at least a marginally significant negative effect on the growth of *M. paraensis.*

There was no year with higher mortality which could characterize some temporal effect of an atypical year on the dynamics of the trees. Higher mortality was expected in 2015, a year of strong nesting in the Amazon, as detected for regenerating individuals (< 5 cm of DBH) of the species in the same study areas (Miranda *et al.* 2018). Although there was no higher mortality of adult pracuúba trees in 2015, the population in the more distant areas, which had been showing positive rates of population growth in previous years, stopped growing in the period 2014-2015. This may be a reflection of the lower ingress of regenerants for the adult class in the last year of monitoring as a consequence of the higher mortality of the regeneration components.

The use of integral projection models (IPM) enables analyzing population demography as in matrix models (Easterling *et al.* 2000) but without the need to categorize individuals. This can be an advantage, especially for working with arboreal individuals (Lopes 2007, Metcalf *et al.* 2009, Zuidema *et al.* 2010), in which classes are always artificial. In addition, with a relatively small data set (up to 300 individuals), integral projection models may perform better than matrices due to lower bias and variance in determining vital rates (Ramula *et al.* 2009). This criterion was reached in our work in all the years of monitoring in both areas, with more than 300 trees to perform the modeling. The results of this analysis showed that the population growth rates of *M. paraensis* are increasing. This indicates that the influx of individuals into the population is at least enough to replace those who died. In one of the few studies that analyzed the dynamics of tree populations of the estuarine floodplain forest, it was also found that some species explored in the study region, among them *M. paraensis,* are in stable equilibrium (Fortini & Zarin 2011). These authors found a higher concentration of individuals in the initial classes and a balance in the vital rates, concluding on the stability of the populations of *M. paraensis.*

The population growth rate found near the Amazon River was higher than the population growth in distant populations. These high percentages in areas near the Amazon River could be related to increased seedling recruitment in these sites. As previously mentioned, 61% of the abundance of individuals in areas close to the river are in the smallest size classes. Such abundance could be related to the high germination rate of the seeds (*ca.* 73%; Miranda 2009), influenced by the environmental and physiological characteristics of the floodplain areas. Besides that, was reported that the density of regenerating individuals of *M. paraensis* was high in the study area (between 1543 and 2693 ind.ha^{-1}) (Miranda *et al.* 2018). Since regenerating individuals are in the smallest size classes and these individuals are the ones who most influence lambda values, this would explain the results found. The higher abundance and population growth rates presented by the population situated near the Amazon River indicate that this population has greater fitness than the population localized far from the river. *M. paraensis* seems to be more adapted for flooded environments, and soil characteristics such as less clay content and fertility (Souza 2011, Pinto 2014), even with timber harvesting being higher in these areas.

Elasticity, which is derived from the vital rate and size structure that most impact the population growth rate (lambda), was very similar between populations and between years. In most cases, the highest values of elasticity were related to the survival and growth of individuals and never related to fecundity. Long-life, slow-growing, and late-breeding species are expected to have the highest elasticity values that correspond to stasis, and more specifically that the highest elasticity values are relative to adult survival (Silvertown *et al.* 1993, Alvarez-Buylla *et al.* 1996, Horvitz *et al.* 1997, Bruna 2003, Fortini & Zarin 2011). Our work and others that used IPM with tree species (Lopes 2007, Zuidema *et al.* 2010) found higher elasticity values for growth. In addition, we find larger elasticities in the smaller classes, for survival and growth. This may be a reflection of the high natural regeneration capacity of *M. paraensis,* as demonstrated by Fortini & Zarin (2011) and Miranda *et al.* (2018).

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SUPPLEMENTARY MATERIAL

Table S1. Model structures for survival based on plant size (diameter) with corresponding Akaike Information Criterion (AIC) scores for two populations of the pracuuba tree *Mora paraensis* during four sampling intervals. The models selected are highlighted in bold with their respective coefficients.

Table S2. Model structures for growth based on plant size (diameter) with corresponding Akaike Information Criterion (AIC) scores for two populations of the *pracuúba* tree *Mora paraensis* during four sampling intervals. The models selected are highlighted in bold with their respective coefficients.

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