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Population structure and small-scale spatial pattern of *Mora paraensis* (Fabaceae) in a *várzea* forest in the Amazonian estuary

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ABSTRACT

Detailed knowledge about structural attributes and spatial patterns of tree species is fundamental to enable sustainable management of forest resouces. However, this knowledge remains poorly understood in the context of eastern Amazonian Floodplain forests, even of some economically important species such as *Mora paraensis*. In this paper, we focused on the structural parameters and spatial distribution pattern of *M. paraensis* in an 11.7 ha area of floodplain forest in eastern Amazonia. The structural analysis included quantitative and qualitative parameters, and the spatial distribution pattern was analyzed using the univariate Ripley's K function. A total of 48 trees of *M. paraensis* were measured, with a total density of 4.1 individuals ha^{-1}, a mean height of 7.1 m, and a basal area of 0.2324 m^2 ha^{-1}. *Mora paraensis* showed a relatively good density of trees, an inverse J-shaped diameter distribution pattern, and individuals in almost every diameter class. The population was predominantly young (75% of individuals), however, the qualitative parameters suggested unfavorable conditions regarding the health of *M. paraensis* trees, perhaps affecting their development in this environment. At the within diameter class level, the aggregate pattern dominated in smaller diameter classes, but shifted into a random pattern in the larger diameter classes. This study reinforces the importance of using methods that take into account different distance scales, allowing a better understanding of the relationships between the species attributes and their spatial distribution pattern, especially to scientifically manage and utilize forest resources in areas with conservation interest.

Keywords: Diameter distribution; Flooded forest; *Pracuúba*; Ripley's K function; Spatial analysis of trees.

Estrutura populacional e padrão espacial em pequena escala de *Mora paraensis* (Fabaceae) em uma floresta de várzea no estuário amazônico

RESUMO

O conhecimento detalhado sobre atributos estruturais e padrões espaciais de espécies arbóreas é fundamental para permitir um manejo sustentável dos recursos florestais. No entanto, esse conhecimento ainda permanece pouco compreendido no contexto das florestas de várzea do leste da Amazônia, mesmo para algumas espécies economicamente importantes como *Mora paraensis*. Neste artigo, focamos nos parâmetros estruturais e no padrão de distribuição espacial de *M. paraensis* em uma área de 11,7 ha de floresta de várzea no leste da Amazônia. A análise estrutural incluiu parâmetros quantitativos e qualitativos, e o padrão de distribuição espacial foi analisado usando a função K univariada de Ripley. Um total de 48 árvores de *M. paraensis* foi medido, com densidade total de 4,1 indivíduos ha^{-1}, altura média de 7,1 m e área basal de 0,2324 m^2 ha^{-1}. *Mora paraensis* apresentou uma densidade relativamente boa de árvores, um padrão de distribuição diamétrica em forma de J invertido e indivíduos em quase todas as classes de diâmetro. A população foi predominantemente jovem (75% dos indivíduos), porém, os parâmetros qualitativos sugeriram condições desfavoráveis quanto a sanidade das árvores de *M. paraensis*, o que pode estar afetando o seu desenvolvimento neste ambiente. No nível da classe de diâmetro, o padrão agregado dominou nas classes de menor diâmetro, mas mudou para o padrão aleatório nas classes de maior diâmetro. Este estudo reforça a importância do uso de métodos que levem em consideração diferentes escalas de distância, permitindo uma melhor compreensão das relações entre os atributos das espécies e seu padrão de distribuição espacial, especialmente para gerenciar e utilizar cientificamente os recursos florestais em áreas com interesse em conservação.

Palavras-chave: Distribuição diamétrica, Floresta inundável, Pracuúba, Função K de Ripley, Análise espacial de árvores.

Introduction

Amazonian *várzea* forest are areas periodically flooded by sediment-rich whitewater rivers (Amazon River is the largest) originating from the Andes and sub-Andean regions, covering an area of approximately 98,110 km^2 (MELACK; HESS, 2010). *Várzea* forests contain fewer species than their non-flooded counterparts in the same region (JUNK, 1989; WITTMANN et al., 2004). Many physical and ecological processes (mineral cycling, decomposition, and forest sucession) are affected by the flood pulse, which is generally regarded as the main driving force determining the patterns of tree species composition in these forests (JUNK, 1989; WITTMANN et al., 2004, 2006). The duration and height of the flooding modulate the morphoanatomy and ecophysiology of trees, which require special adaptations to cope with the periodically anoxic conditions (PAROLIN et al., 2004; WITTMANN et al., 2004; ASSIS et al., 2015).

In the Amazonian estuary, the *várzea* forests are subject to short, predictable, polymodal flood pulses, influenced (directly or indirectly) by the oceanic tide (JUNK et al., 2011). Most of this area is covered by secondary forests that served as the principal source of timber in this region for over three centuries (CATTANIO et al., 2002). Today, the Amazonian estuary is also a source of various non-timber forest resources such as Acai palm (*Euterpe oleracea* Mart.), rubber, fruits, and oilseeds [e.g. *Pentaclethra macroloba* (Willd.) Kuntze and *Carapa guianensis* Aubl.], as well as hunting and fishing for the local populations (CATTANIO et al., 2002; FORTINI et al., 2006; FORTINI; ZARIN, 2011). Timber exploitation in these forests focuses on local and regional markets, mainly for construction purposes (QUEIROZ; MACHADO, 2007; MIRANDA et al., 2018).

Among the locally exploited species, *Mora paraensis* (Ducke) Ducke (Fabaceae known as *pracuúba*) stands out as an endemic species in eastern Amazonia (WITTMANN et al., 2013). It is highly dominant in the region, especially in the Amazonian estuary (CARIM et al., 2008; 2017; QUEIROZ; MACHADO, 2008; FORTINI; ZARIN, 2011), and is characterized by the largest timber stocks and a high wood density (LIMA et al., 2014; FORTINI et al., 2015). *Pracuúba* is a large tree species (maximum 127.3 cm in diameter and 40 m in height) that occupies the canopy in estuarine floodplain forests. In the field, this species is characterized by composite leaves, cylindrical trunk with greenish and lenticellate bark, large tabular roots at trunk base, inflorescence in long spikelets, small white flowers, and sessile, strongly aromatic, large sickle-shaped fruits of legume type, with several embedded reniform seeds (DUCKE, 1949; LOUREIRO; SILVA, 1968).

Overall, the economic importance of floodplain forests in the Amazonian estuary indicates the need for sustained management of this ecosystem. The detailed knowledge about structural attributes and spatial patterns of tree species is fundamental to enable sustainable management of forest resources. However, this knowledge remains poorly understood in the context of eastern Amazonian floodplain forests, even of some economically important species. Determining the spatial distribution pattern of trees may help support forest management plans, conservation in forest communities, and sampling processes, in addition to improving the knowledge of autecology of species of interest in a variety of habitats (ANJOS et al., 1998; ARAÚJO et al., 2014; BRUZINGA et al., 2013; HIGUCHI et al., 2008; JOHN et al., 2007). Generally, there are three main tree spatial patterns in natural communities: aggregated; regular or uniform; and random (WONG; LEE, 2005).

Previous researches focused on floristic characteristics and forest community types in the region (e. g., RABELO et al., 2000; 2002; BENTES-GAMA et al., 2002; ALMEIDA et al., 2004; CARIM et al., 2008, 2017). However, few studies focused on population structures and characteristics of dominant tree species in forest communities (PINTO, 2014; DANTAS et al., 2017; MIRANDA et al., 2018). Methods of spatial point pattern analysis were ideally suited to analyze spatial association patterns in plant communities. These methods allowed the quantification of the spatial distribution of mapped positions of individual plants within a given study area. No study to date has tried to explore in detail the spatial clustering of *M. paraensis* at the local forest scale, taking into account diameter classes.

This study aimed to evaluate some structural parameters and the spatial distribution pattern of *M. paraensis* in a floodplain forest in the Amazonian estuary. Two main questions were addressed: (i) how structural parameters characterize the trees of *M. paraensis* and (ii) at the local distance scale, does the spatial pattern of *M. paraensis* population remains the same?

Material and Methods

Study area

The study was conducted at the Experimental Station of Universidade do Estado do Amapá (UEAP), in Macapá municipality, Amapá state, eastern Amazonia, Brazil (51°04'42.39" W, 0°01'55.02" S; Figure 1). The forest sampled has a total area of 11.7 ha, and corresponds to floodplain forest in the secondary succession stage, classified as Alluvial Ombrophilous Dense Forest (IBGE, 2012), with elevation ranging between 11 and 24 m. As for the floristic composition, a total of 20 families and 38 tree species have already been surveyed in the area (BATISTA et al., 2013; SILVA et al., 2013).

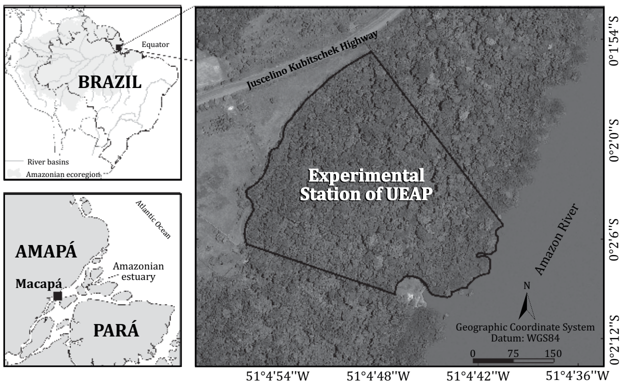

Figure 1. Location of study area in a *várzea* forest of the Amazon River, Amapá, eastern Amazonia, Brazil / **Figura 1.** Localização da área de estudo em uma floresta de várzea do Rio Amazonas, Amapá, leste da Amazônia, Brasil.

The climate type of the region is considered Am (tropical monsoon), according to Köppen-Geiger (ALVARES et al., 2013), with the following mean annual values: precipitation 2549.7 mm, temperature ranging from 23.8 to 31.5 °C, and relative humidity 82.2%. The highest rainfall occurs between January and June, and relatively fewer rains are observed in the other months of the year (INMET, 2018). The dominant soil type is Typical Eutrophic Ta Melanic Gleysol, shallow, silty, and fertile, which may show some level of acidity, toxicity, and deficiency of certain nutrients (PINTO, 2014).

Collection procedures

The study area was subdivided into five equidistant (72 m) transects, almost parallel to the Amazon River, which was used as a reference for the census of *M. paraensis* trees. All individuals with CBH (Circumference at Breast Height, at 1.30 m of soil) ≥ 10 cm were identified, georeferenced, and measured. Diameters at Breast Height (DBH) were calculated from the circumference values, measured with a tape graduated in centimeters. The total tree height was field-measured based on visual estimation, and the geographical coordinates were obtained with a GPS Garmin model 75CS-x.

We also evaluated the stem shape, tree crown position, and the presence of lianas (woody climbing plants) for each tree. As for the stem shape, we adopted the following classification: SS = straight stem, STS = slightly tortuous stem, VTS = very tortuous stem. For the crown position, we adopted the following categories: DO = dominant (upper stratum occupancy with high tree crown exposure to illumination), CDO = codominant (intermediate stratum occupancy with medium tree crown exposure to illumination), and DS = dominated or suppressed (lower stratum occupancy with low tree crown exposure to illumination) (COSTA et al., 2013).

Data analysis

The total number of individuals, total density, and sectional and basal areas (SOUZA; SOARES, 2013) were calculated using Equations 1 and 2 for structural analysis. Diameter data were represented using frequency histograms; the number of classes was determined using the Sturges' rule (STURGES, 1926) and the class interval was based on the total amplitude of diameter data, according to Equations 3, 4 and 5.

$$\mathbf{TD} = \frac{\mathbf{N}}{\mathbf{A}} \quad (1)$$

$$\mathbf{BA} = \sum \mathbf{g} = \frac{\pi * \mathbf{DBH}^2}{\mathbf{40{,}000}} \quad (2)$$

$$\mathbf{k = 1 + 3.33 * logN} \quad (3)$$

$$\mathbf{H = DBH_{max} - DBH_{min}} \quad (4)$$

$$\mathbf{CI} = \frac{\mathbf{H}}{\mathbf{k}} \quad (5)$$

where:
TD = Total density (individuals ha^{-1}).
N = total number of individuals sampled.
A = total sampling area (ha).
g = sectional area, with DBH in cm.
BA = basal area (m^2).
k = number of classes.
H = amplitude between the largest and smallest observed diameter.
CI = DBH class interval.

Regarding small-scale spatial aspects of the dynamics of *M. paraensis* trees, we used the univariate Ripley's K function (RIPLEY, 1977). The K-function considers the distance between all pairs of points (trees) in a two-dimensional space by using the number of points available in a circle of radius r centered on each tree. The univariate estimator of the K-function for a certain pattern of points is calculated using Equation 6.

$$\mathbf{Kr} = \frac{\overline{\mathbf{n}}_{\mathbf{(r)}}}{\mathbf{p}} \quad (6)$$

where:
$\overline{\mathbf{n}}_{(r)}$ = mean number of neighbors within a distance r from a subject tree, and p = stand density.

We used the linearized L-function (BESAG, 1977) that modifies the shape of the K-function, stabilizes its variance (CRESSIE, 1992), and is calculated using Equation 7.

$$\mathbf{L_r} = \sqrt{\frac{\mathbf{K_r}}{\pi}} \quad (7)$$

A value of Lr = 0 indicates a random spatial pattern, whereas values smaller and larger than 0 correspond to regular and aggregated spatial patterns, respectively. We applied Ripley's isotropic correction formula for edge correction (RIPLEY, 1991). To test the statistical significance of the deviation of L_r values from zero under the null hypothesis of complete spatial randomness, we used the Monte Carlo simulation method. We computed the 95% confidence intervals of L_r based on 1000 random permutations. In this study, the range of distances used to calculate the L-function ranged between 0 and 300 m, with a grain-size of 5 m. Georeferenced data were integrated into the ArcGIS 10.1 software (ESRI, Redlands, CA, USA) and analyzed with the R software (R CORE TEAM, 2019), using "maptools" and "splancs" packages for point pattern analysis.

Results

Structural parameters

A total of 48 trees of *M. paraensis* were sampled, with a total density of 4.1 individuals ha^{-1}, a mean height of 7.1 m, and a total basal area of 0.2324 m^2 ha^{-1}. An overview of the structural parameters is shown in Table 1 and Figure 2.

Table 1. Number of individuals (N), minimum (min), maximum (max), mean ($\bar{x}$), and standard deviation (sd) for each diameter class (including interval and center of class) and total population, with regard to structural parameters DBH (cm), total height (m), and basal area (m^2) of *Mora paraensis* trees in a *várzea* forest of the Amazon River, Amapá, eastern Amazonia, Brazil / **Tabela 1.** Número de indivíduos (N), mínimo (mín), máximo (máx), média ($\bar{x}$) e desvio-padrão (dp) para cada classe de diâmetro (incluindo intervalo e centro de classe) e para população total, em relação aos parâmetros estruturais DAP (cm), altura total (m) e área basal (m^2) de *Mora paraensis* em uma floresta de várzea do Rio Amazonas, Amapá, leste da Amazônia, Brasil.

DBH (cm)								Basal area (m^2)				Total height (m)			
class	interval	center	N	min	max	$\bar{x}$	sd	min	max	$\bar{x}$	sd	min	max	$\bar{x}$	sd
1	3.5 –| 17.1	10.3	36	3.5	15.9	3.5	3.6	0.001	0.0199	0.0055	0.005	2.5	13	5.6	3
2	17.1 –| 30.7	23.9	6	18.3	29	25.7	3.8	0.0263	0.0659	0.0526	0.0141	7.5	15	11	3
3	30.7 –| 44.3	37.5	1	35	35	35	-	0.0963	0.0963	0.0963	-	10	10	10	-
4	44.3 –| 57.9	51.1	0	-	-	-	-	-	-	-	-	-	-	-	-
5	57.9 –| 71.6	64.8	2	61.1	63.7	62.4	1.8	0.2934	0.3183	0.3058	0.0176	12	14	13	1
6	71.6 –| 85.2	78.4	2	79.6	82.8	81.2	2.3	0.4974	0.5379	0.5177	0.0287	14	16	15	2
7	≥ 85.2	86.7	1	98.7	98.7	98.7	-	0.7647	0.7647	0.7647	-	11	11	11	-
	Population		48	3.5	98.7	17.7	22.4	0.001	0.7647	0.063	0.1563	2.5	16	7.1	4

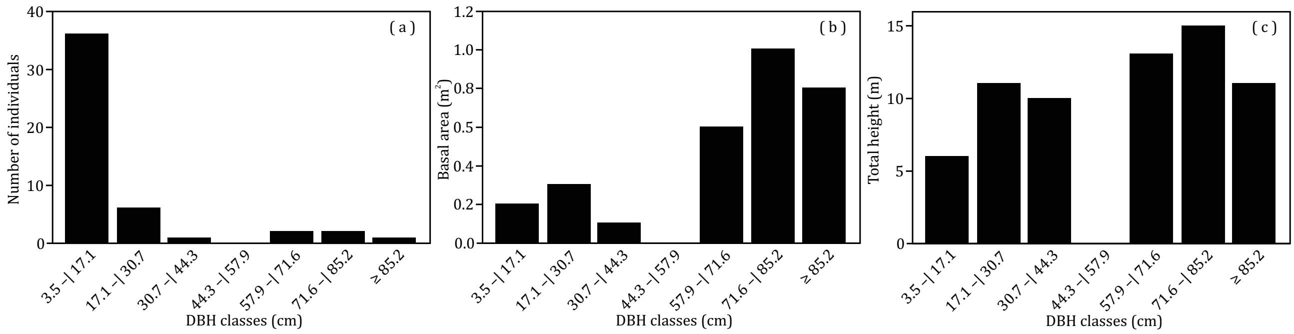

Figure 2. Frequency histograms per diameter class of *Mora paraensis* trees in a *várzea* forest of the Amazon River, Amapá, eastern Amazonia, Brazil. (a) Number of individuals, (b) Basal area (m^2), (c) Total height (m) / **Figura 2.** Histogramas de frequência por classe de diâmetro de *Mora paraensis* em uma floresta de várzea do Rio Amazonas, Amapá, leste da Amazônia, Brasil. (a) Número de indivíduos, (b) Área basal (m^2), (c) Altura total (m).

The population distribution showed an exponential curve of inverse J-shaped (a unimodal distribution with positive asymmetry), with a discontinuity observed in at least one of the diameter classes. Among all the sampled individuals, 75% (n = 36) were concentrated only in the first diameter class, with a sharp reduction observed in the number of individuals in subsequent classes (Figure 2a). The same pattern was observed for basal area, which presented an inversely proportional distribution pattern to the number of individuals (Figure 2b). Regarding height, the distribution showed a bimodal tendency with negative asymmetry (Figure 2c). Despite the presence of a greater number of individuals in classes 1 and 2 (DBH < 30.7 cm), classes 5, 6, and 7 (DBH > 57.9 cm) presented individuals with higher values of height and basal area (Table 1).

Qualitative data obtained from the sample of trees were also organized as per diameter classes (Table 2). About 73% of trees presented a slightly tortuous stem, 45.8% had a dominated or suppressed crown, while 75% of the trees showed the presence of lianas. Class 1, represented by young individuals, presented a high percentage of lianas, which might be directing trees toward the formation of tortuous stems and suppressed crowns (Table 2). In addition, these parameters suggested unfavorable conditions regarding the health of M. paraensis trees, which may be affecting their development in this environment.

Table 2. Qualitative characterization of the stem shape, tree crown position, and presence of lianas for each diameter class of *Mora paraensis* trees in a *várzea* forest of the Amazon River, Amapá, eastern Amazonia, Brazil / **Tabela 2.** Caracterização qualitativa quanto a forma do caule, posição da copa e presença de lianas para cada classe de diâmetro das árvores de *Mora paraensis* em uma floresta de várzea do Rio Amazonas, Amapá, leste da Amazônia, Brasil.

Diameter classes	Stem shape (%)			Tree crown position (%)			Presence of lianas (%)	
	SS	STS	VTS	DO	CDO	DS	AL	PL
1	12.5	52.1	10.4	6.3	22.9	45.8	14.6	60.4
2	2.1	10.4	0	8.3	4.2	0	2.1	10.4
3	0	2.1	0	2.1	0	0	0	2.1
4	0	0	0	0	0	0	0	0
5	2.1	2.1	0	4.2	0	0	2.1	2.1
6	0	4.2	0	4.2	0	0	4.2	0
7	0	2.1	0	2.1	0	0	2.1	0
Total	17	73	10	27	27	46	25	75
Mean	4	18	3	7	7	11	6	19

SS = straight stem; STS = slightly tortuous stem; VTS = very tortuous stem; DO = dominant; CDO = codominant; DS = dominated or suppressed; AL = absence of lianas; PL = presence of lianas / SS = caule reto; STS = caule levemente tortuoso; VTS = caule muito tortuoso; DO = copa dominante; CDO = copa codominante; DS = copa dominada ou suprimida; AL = ausência de lianas; PL = presença de lianas.

Spatial pattern

Transformed values of Ripley's K function indicated that the spatial distribution pattern of *M. paraensis* trees varied with the spatial scale as well as with diameter classes (Figure 3). The sampled population showed a predominant aggregate pattern at the local distance scale, as the L (r) function was above the confidence intervals up to 225 m, thus, rejecting the hypothesis of complete spatial randomness. After this distance, the population tended to show a regular pattern.

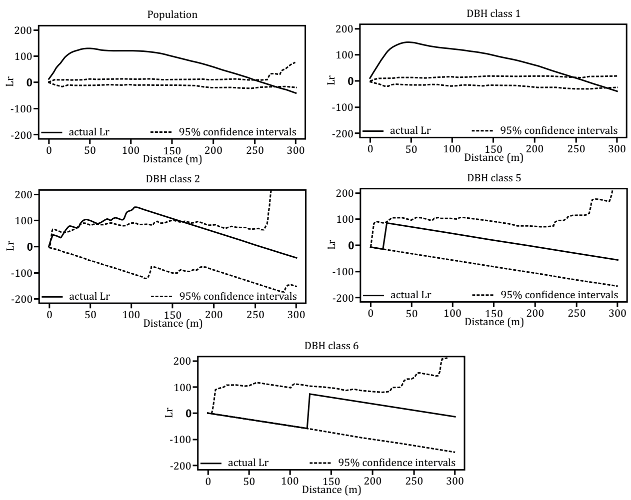

Figure 3. Univariate Ripley's K function (L estimated) at 0–300 m scale for the total population and per diameter class of *Mora paraensis* trees in a *várzea* forest of the Amazon River, Amapá, eastern Amazonia, Brazil / **Figura 3.** Função K de Ripley univariada (L estimado) na escala de 0–300 m para a população total e por classe de diâmetro das árvores de *Mora paraensis* em uma floresta de várzea do Rio Amazonas, Amapá, leste da Amazônia, Brasil.

When analyzing the spatial distribution per diameter classes (classes 3, 4, and 7 not included due to the insufficient number of individuals), different levels of aggregation were observed. The spatial pattern of trees belonging to diameter class 1 was predominantly aggregate, similar to the total population, as it included the largest number of individuals. This pattern reflects the high concentration of young trees near the mother trees or source of propagules (Figure 4). Individuals belonging to class 2 were aggregate until about 100 m when a small spatial scale was considered, and they were distributed randomly when a large spatial scale was considered. Individuals belonging to classes 5 and 6 had a predominantly random distribution in the study area (Figure 3). Young trees were mainly concentrated around the source of propagules, whereas adult trees (diameter classes 5, 6, and 7) were randomly distributed (Figure 4).

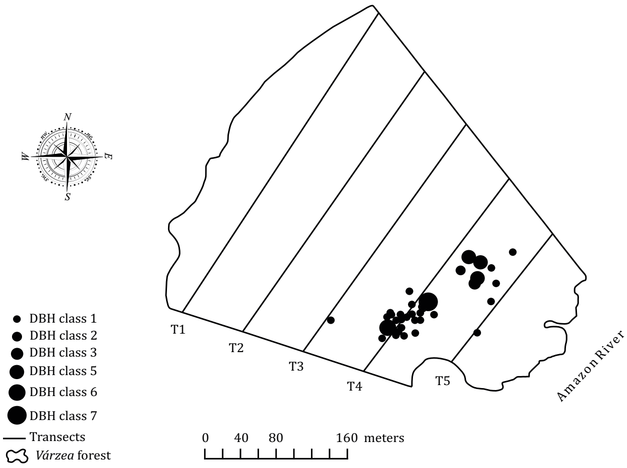

Figure 4. Spatial pattern per diameter class of the *Mora paraensis* population in a *várzea* forest of the Amazon River, Amapá, eastern Amazonia, Brazil / **Figura 4.** Padrão espacial por classe de diâmetro da população de *Mora paraensis* em uma floresta de várzea do Rio Amazonas, Amapá, leste da Amazônia, Brasil.

Discussion

Structural parameters

In the Amazonian estuary, many studies have shown that *M. paraensis* is a dominant species that accounts for about one-third of all estimated biomass in the region (CARIM et al., 2008), with the values of density and the basal area ranging from 1.5 to 219 individuals ha^{-1} and 4.4 to 43.1 m^2 ha^{-1}, respectively (RABELO et al., 2000, 2002; BENTES-GAMA et al., 2002; ALMEIDA et al., 2004; CARIM et al., 2008, 2017; FORTINI; ZARIN, 2011; PINTO, 2014). While the calculated total density (4.1 individuals ha^{-1}) in the present study was within the reported range for this region, our value of basal area was relatively lower (0.2324 m^2 ha^{-1}). Furthermore, in other studies, only a single height interval between 15.5 and 20 m accounted for the largest number of individuals (SANTOS; JARDIM, 2006; CARIM et al., 2008; 2017), whereas here, the observed height values ranged from 3.5 to 16 m for all diameter classes, indicating that the forest stand was mainly composed of young trees (Figure 2, Table 1).

The low values of height and basal area could be related to the dominance of young trees, likely due to anthropogenic disturbances (urban expansion and historical timber extraction activities in the region), which may have gradually affected the structure and dynamics of the area. One evidence for this is the high population density of *Calycophyllum spruceanum* (*Pau-mulato* tree) surveyed in the same area (SANTOS et al., 2016). This species has intrinsic ecological characteristics associated with disturbed *várzea* forests (natural or anthropogenic factors) (CARIM et al., 2008; SANTOS et al., 2016).

The diameter distribution of trees is an important tool for generating knowledge about the structure of native forests, as it is often used as a proxy of age, based on the assumption that young trees are small and adult trees are large. Inverse J-shaped pattern is a characteristic of the species from unequal tropical forests, which present a higher concentration of individuals in the lower classes, with a progressive reduction in frequency in higher classes (LAMPRECHT, 1990). This pattern has already been reported in *M. paraensis* (FORTINI; ZARIN, 2011), as well as in the *várzea* forests in the same region (RABELO et al., 2002; QUEIROZ et al., 2006; SANTOS; JARDIM, 2006; CARIM et al., 2008), which suggests that the population shows a good regeneration and stock of young population, given the high number of young trees that would replace the present-day adults in the future.

In spite of the above, *M. paraensis* regenerates extensively, and all the growth phases, from seedlings to adults are present in the region (RABELO et al., 2000; MIRANDA et al., 2018). The reproductive capacity of the species is high and the dynamics of individual establishment in regeneration and ingress into adult classes depend on the changes in biotic and abiotic factors over time (MIRANDA et al., 2018). Considering the results obtained here, although the predominantly young population of *M. paraensis* showed a relatively good density per hectare, the young trees may be facing difficulties during ingress into the adult classes, which generally showed a low number of individuals and a low basal area.

Spatial pattern

Studies in Amazonian estuary floodplain forests have reported an aggregated pattern for *M. paraensis* (BENTES-GAMA et al., 2002; QUEIROZ et al., 2005). These studies used dispersion indices, which only detect patterns at one scale (plots), and therefore, the result is strongly affected by the plot size. Ripley's K function identifies the pattern at different scales simultaneously, making it possible to detect the pattern at all analyzed scales.

Populations usually show a combination of patterns, with aggregation at large scales, and uniformity on smaller scales (DIXON, 2002). Although *M. paraensis* population showed a predominantly aggregate pattern, when we analyzed the spatial pattern by diameter classes, the species assumed a random pattern (Figure 3). The different patterns showed by the species change according to the maturation stage of trees, wherein young trees are densely clustered around the source of propagules (Figure 4), but when only the sources of propagules are considered, they assume a random pattern. For example, *Pentaclethra macroloba*, another dominant species in the Amazonian estuary (CARIM et al., 2017), also exhibited a pattern similar to that of *M. paraensis*, when the same method was used (DANTAS et al., 2017).

In contrast to what was observed in young trees, a random spatial distribution and a large space between individuals were observed in adult trees (diameter classes 5 and 6). This pattern is frequently found in rainforests and has been suggested as a key factor for the coexistence of tree species, leading to high diversity in these forests (JANZEN, 1970; CONNELL, 1971; GAVIN; PEART, 1997). Furthermore, the changes from aggregate to a random spatial pattern during tree lifespan could indicate the existence of a density-dependent factor playing an important role for seedlings (GAVIN; PEART, 1997), such as herbivory (JANZEN, 1970; CONNEL, 1971), competition, or predation (SOUSA; MITCHELL, 1999). According to the Janzen-Connell hypothesis (JANZEN, 1970; CONNELL, 1971), the greater distance from adults, the higher are the chances of survival of young trees. Seed dispersal, therefore, is a key issue in the success of the establishment and new plant growth, launching propagules to more favorable sites.

Seeds of *M. paraensis* have hypogeal germination (cotyledons at soil level) and a large amount of reserves, characteristics that allow diaspores to remain under the crowns of mother trees (KUBITZKI; ZIBURSKI, 1994; MOREIRA; MOREIRA, 1996; MIRANDA et al., 2018). This species forms a seedling bank, with a high density of individuals in regeneration (MIRANDA et al., 2018). These factors may directly modulate the spatial distribution of individuals (HUBBELL, 2001), explaining the predominantly aggregate pattern. Diaspores of many tree species have morphological structures that enhance their probability of being dispersed away from the mother tree (HUGHES et al., 1994; GRIZ; MACHADO, 2001). Fruit and seed morphology affect species distribution, for example, species with edible aril or pulp are less aggregated than those without (SEIDLER; PLOTKIN, 2006). In the case of *M. paraensis*, its propagules are not very attractive to frugivorous (e.g. propagules without bright color and fleshy pulp, and with large size; pers. obs.), making hydrochory probably the more effective dispersion syndrome, due to adaptations that have evolved impart buoyancy to the seeds (KUBITZKI; ZIBURSKI, 1994).

Conclusion

The evaluation of the qualitative parameters suggested unfavorable conditions regarding the health of *M. paraensis* trees, which may be affecting their development in this environment. At the within size-class level, the aggregate pattern dominated in smaller diameter classes, but shifted into a random pattern in the larger diameter classes. The large individuals of *M. paraensis* were found closer to the smaller individuals than to those of their class. Thus, this species may have present different spatial distribution patterns when considering different diameter classes and distance scales. This study reinforces the importance of using methods that take into account different distance scales, allowing a better understanding of the relationships between the species attributes and their spatial distribution pattern, especially to scientifically manage and utilize forest resources in areas with conservation interest.

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