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Diameter distributions and spatial distribution patterns of tree species are important for planning sustainable management in natural forests in the eastern Amazon

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Abstract

Background: Do tree species that have wood of high commercial value which are being extracted in the Saracá-Taquera National Forest have diameter and spatial distribution patterns that enable continuous production of timber to meet the criteria of ecological conservation and sustainable management of their populations? To answer this question, we evaluated diameter and spatial distributions of 15 commercial tree species of ecological and economic importance, in a concession area in the Saracá-Taquera National Forest, Eastern Amazon.

Methods: The data were obtained from a forest inventory carried out in 24 50 m × 50 m plots, considering a minimum diameter of 30 cm. The 15 species were selected based on three criteria: importance value index; volume stock; and commercial value of the wood. The trees were distributed into diameter classes with an interval of 10 cm between them to analyse the diameter distribution. The spatial distribution patterns of the species were analysed using the univariate Ripley's *K* function.

Results: The results showed that the presence of large trees and the aggregated spatial distribution in most of the tree species studied may determine the feasibility of continuous timber production to meet conservation and sustainable management criteria. The spatial distributions of stocks should guide planning of forest management activities, including pre-logging, logging and post-logging activities. However, the low population density of most species suggests that logging must be well planned to avoid population declines. Although forest management on a sustainable basis has advanced substantially in recent years in the Amazon, the factors that promote different diameter and spatial distributions of species are still considered complex and little studied.

Conclusions: The results point to a need to expand research on this topic in managed areas, including the same technological approach as the work described here. This type of analysis can constitute an important tool for defining population management strategies for each species, considering their ecological characteristics and environmental adaptation at a local level.

Keywords: Amazon rainforest; Saraca-Taquera; Amazon timber species; management of tropical natural forests; Ripley's *K* Function.

Introduction

The Amazon comprises a set of ecosystems containing the greatest biodiversity in the world, representing more than 50% of tropical forests, housing countless rare species, and is crucial for maintaining large carbon stocks (Malhado et al. 2013; Ter Steege et al. 2013; Van der Sande et al. 2017; Silva et al. 2018). Managing this biodiversity in numerous ecosystems is complex. One of the great challenges is to reconcile management of these forest resources with sustainable economic, environmental and social development (Lima et al. 2018; Castro et al. 2021). In this sense, Brazilian legislation has advanced, creating specific technical standards on the management of natural forests, which guide Sustainable Forest Management Plans (SFMP) applied in the Brazilian Amazon (Leite et al. 2018). One of the forest policy alternatives used especially in Brazil for territorial planning and management, was to allow sustainable forest management (SFM) in publicly owned areas through forest concession policies (Lima et al. 2006; Merry et al. 2009; Pinto et al. 2015; Lima et al. 2018; Sist et al. 2021).

According to the guidelines for SFM in concession forests, reduced impact logging (RIL) techniques must be adopted to maintain the structure and ecological functions of logged forests as close as possible to original conditions (Oliveira et al. 2023). Reduced impact logging is based on the planning and execution of operations with specialised labor in order to minimise damage to the environment and reduce operational costs and waste (Avila et al. 2017). However, the main variables that guide management activities in natural forests, such as harvesting intensity, minimum cutting diameter, cutting cycle and protected species, were established for the entire Brazilian Amazon without considering local specificities of each region or forest area (Capanema et al. 2022) or each species specifically (David et al. 2019; Castro et al. 2021).

Given this context, two important pieces of information for SFM that have been little studied are diameter distribution structures of tree species populations and spatial distribution patterns of these species (Herrero-Jáuregui et al. 2012; Cordero et al. 2016; Rockwell et al. 2017). Study of spatial distribution patterns can help us understand the dynamics of plant populations and the effects of selective logging on harvested species (Cordero et al. 2016). Legislation governing SFMP in the Amazon does not yet take into account patterns of diameter distributions and spatial distributions of species in a managed forest (Souza et al. 2021). Some studies have addressed this issue, mainly on diameter distributions, but there is still not enough information to serve as a basis for consistent legislation. Therefore, it is necessary to know the patterns of diameter distributions and spatial distributions of tree species in the Brazilian Amazon to implement legislation to properly regulate PMFS.

The diameter structure of a tree population reflects its demographic condition at a given moment, reflects its responses to past environmental variations (Condit et al. 1998), and may allow us to estimate its future state. Knowledge of spatial distribution patterns is fundamental to establishing long-term conservation and management strategies for forest resources (Myster & Malahy 2012; Ebert et al. 2016; Cysneiros et al. 2018). The distribution of individuals within the forest significantly influences various ecosystem functions and ecological processes (Borregaard et al. 2008; Gupta & Pinno 2018). In natural forests, trees can be spatially distributed in a random, uniform, or clustered manner, influenced by environmental factors and by particular characteristics of each species, such as their reproductive strategies, dispersal mechanisms, and growth habits. (Condit et al. 2000; Herrero-Jáuregui et al. 2012; Zhang et al. 2013; May et al. 2015; Clark et al. 2018; Miron et al. 2021).

In the study described here we sought to answer the question: do commercial tree species that are being harvested in the Saracá-Taquera National Forest (STNF), have diameter and spatial distribution patterns that enable continuous timber production that meets criteria for conservation and sustainable management of their populations? We considered the hypothesis that "if the species population has a reverse J-shaped diameter distribution or has adult trees in all diameter classes and grouped spatial distributions, then it may be suitable for continuous production and be included in SFMPs". The diameter and spatial distribution patterns of 15 commercial tree species were evaluated in the STNF, which was being logged under a forest concession regime.

Methods

Study area

The study was carried out in the Forest Management Unit II (UMF-II) in the Saracá-Taquera National Forest (STNF), located between the geographic coordinates 1°20'-1°55' South latitude and 56°00'-57 °15' West longitude, on the right bank of the Trombetas River, in the municipalities of Terra Santa, Oriximiná and Faro (Bevilacqua et al. 2020), in the Pará state, Brazilian Amazon (Fig. 1). The STNF area is about 441282.63 ha (MMA 2001), covered by natural forest, with annual rainfall ranging from 1900 to 2500 mm, a dry season from June to October with less than 100 mm monthly rainfall. The region's climate is hot and humid, annual average temperature is 26 °C. The most common soil found in the FNST is Dystrophic Yellow Oxisol (Brasil 2004).

The Forest Management Unit II (FMU-II) in the FNST has a productive area of 25,546.00 ha. In this FMU-II, Annual Production Unit number 06 (APU-06) was selected, with a total area of 1302.16 ha, being 1238.82 ha of effective management and 63.34 ha of permanent preservation area (PPA). APU-06 was divided into seven work units (UT), to facilitate the execution of activities in the field. The data for the present study were obtained from forest inventories carried out in six UTs (1, 2, 3, 4, 6 and 7), totaling 1021.83 ha (Fig. 1).

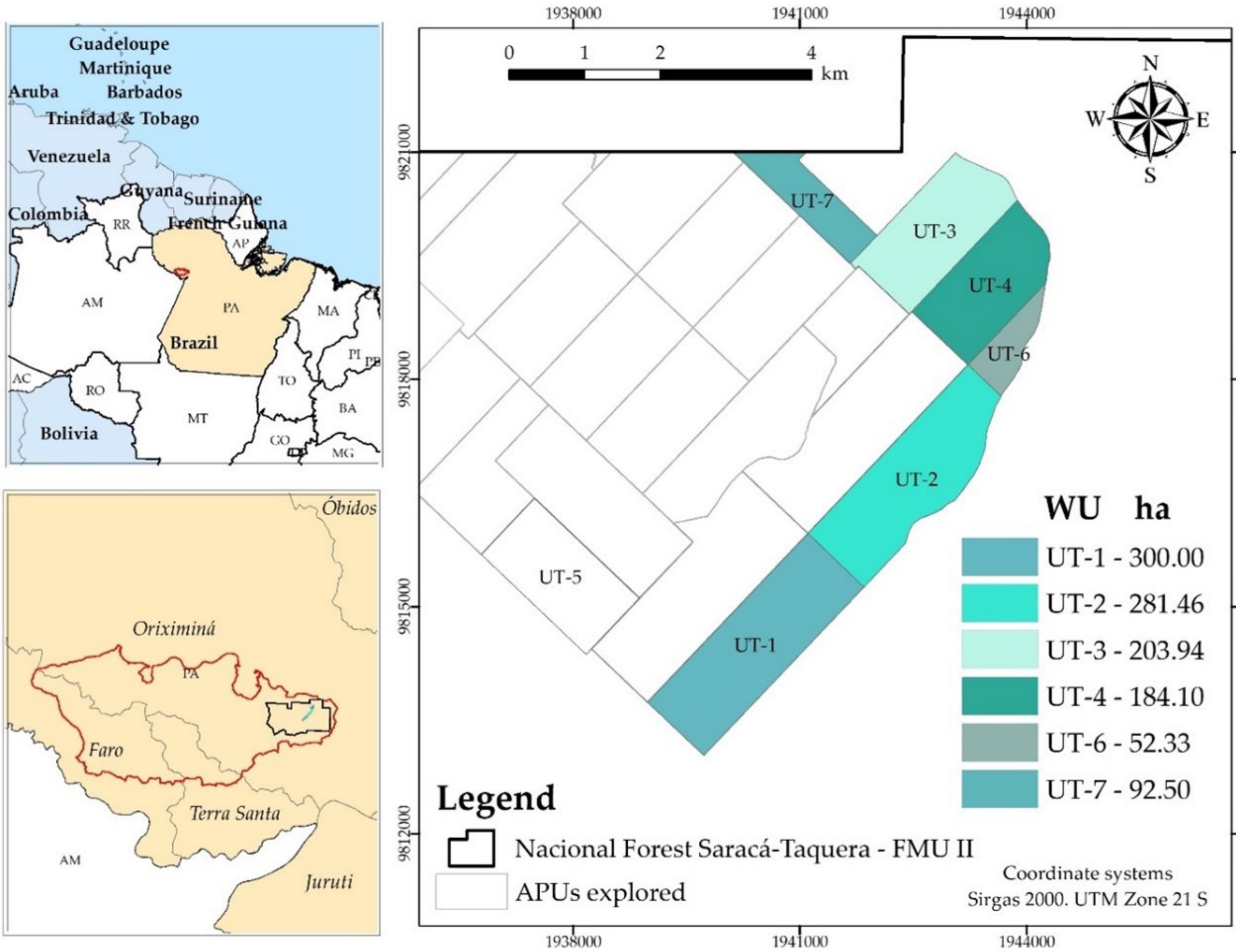

FIGURE 1: Location of the Saracá-Taquera National Forest, FMU-II and APU-06, a total of 1021.83 hectares.

Data and species selection criteria

The research was conducted with data collected before the start of forest exploitation in August 2017. In the forest inventory, trees were identified at the species level, DBH (diameter at 1.30 m from the ground) was measured, with a minimum diameter of 30 cm, and commercial height was recorded. The geographic location of the trees was determined using GPS devices. The UT areas were subsequently subdivided into 50 m × 50 m plots using a geographic information system (GIS). For an area of 1021.83 hectares, approximately 450 plots of 50 × 50 metres were distributed, with no sub-plots within those plots. The plots are evenly spaced 100 metres apart.

According to David et al. (2019), sustainable forest management plans in the Amazon involve around 80 tree species. In the inventory carried out at APU-06, 45 tree species whose wood has commercial value were identified. In the present study, 15 species were used, selected based on one ecological criterion and two economic criteria. The ecological criterion was the Importance Value Index – IVI (Cysneiros et al. 2018) and the economic criteria were the volume of timber and the export value of timber of each species (Table 1).

The IVI was calculated by the phytoR function (Dalagnol et al. 2019), using the statistical program R (R Core Team 2021); the timber volume of each species was calculated using a local equation adjusted by the concessionary company; and the export value timber was obtained through a consultation carried out by the concessionary company that holds the Forest Management Project (FMP) on the values practiced in the timber trade in the Pará state in 2017. The 15 species selected, according to these three criteria, represented 33.33% of the number of commercial species, 80.98% of the total number of trees inventoried, 79.96% of the IVI and 83.56% of the total volume available (Table 1).

Diameter structure of the studied species

The trees were placed in classes, 10 cm between classes, and a minimum diameter of 30 cm to analyse the diameter distribution. Information regarding the minimum DBH, maximum DBH, amplitude, average and coefficient of variation of forest inventory data can be seen in Table 2.

Ecological and dendrometric characteristics of the selected species

Some secondary information was obtained through literature consultations to enrich the discussion of the results. The 15 selected species were classified into two ecological groups (1 – shade-tolerant species; and

TABLE 1: Timber volume, Importance Value Index (IVI) and price in US dollars (US$), of sawn wood in 2017 of the species selected for the analysis of the spatial pattern in the Saracá-Taquera National Forest, Brazilian Amazon.

Species	**Family**	**Volume (m^3)**	**IVI (%)**	**Export value (US$ m^{-3})**
Caryocar villosum (Aubl.) Pers.	Caryocaraceae	1119.47	1.56	1,200
Clarisia racemosa Ruiz & Pav.	Moraceae	3051.35	1.52	800
Dipteryx odorata (Aubl.) Forsyth f.	Fabaceae	2129.19	4.35	1,200
Endopleura uchi (Huber) Cuatrec.	Humiriaceae	307.51	5.35	800
Enterolobium schomburgkii (Benth.) Benth.	Fabaceae	560.09	1.27	800
Goupia glabra Aubl.	Goupiaceae	1935.22	6.13	1,200
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Bignoniaceae	1974.21	0.55	2,100
Hymenaea courbaril L.	Fabaceae	1211.95	3.14	1,200
Hymenaea parvifolia Huber	Fabaceae	1995.95	3.43	1,200
Hymenolobium excelsum Ducke	Fabaceae	1093.19	2.43	1,200
Lecythis pisonis Cambess.	Lecythidaceae	675.63	3.63	800
Manilkara elata (Allemão ex Miq.) Monach.	Sapotaceae	26595.3	37.83	1,200
Mezilaurus itauba (Meisn.) Taub. ex Mez	Lauraceae	1450.1	4.77	1,200
Pseudopiptadenia suaveolens (Miq.) J.W. Grimes	Leguminosae	900.89	2.33	800
Ruizterania albiflora (Warm.) Marc.-Berti	Vochysiaceae	2833.58	1.66	800
Total		47833.6	79.95	

2 – light-demanding species), according to Pinheiro et al. (2007), Gualberto et al. (2014), Oliveira et al. (2017), Gomes et al. (2018) and Castro et al. (2021). Fruit and seed dispersal was based on Amaral et al. (2009). Information on average commercial height was obtained from inventory data carried out at APU-06, and information on apparent wood density was obtained from the website of the Institute of Technological Research (IPT 2022) (Table 3).

Spatial modeling - Univariate Ripley's *K* function

The spatial distribution pattern (aggregate, random or uniform) was determined using Ripley's univariate *K* function (Ripley 1977), which tests the hypothesis of complete spatial randomness (CSR) (Tang et al. 2015). This method is based on counting distances, using geographic coordinates of each tree.

Each tree was plotted on a map to be the centre of a circle, within which all neighbouring trees were

TABLE 2: Minimum, maximum and medium diameters, coefficient of variation and number of trees for each species studied in an area of 1302.16 ha in the Saracá-Taquera National Forest, Brazilian Amazon.

Species	**Diameter (cm)**			**Coefficient of variation**	**Number of trees**
	Minimum	**Maximum**	**Medium**		
Caryocar villosum	38.20	216.45	93.32	18.12	157
Clarisia racemosa	40.74	115.23	64.51	19.44	207
Dipteryx odorata	44.88	171.89	70.02	23.36	574
Endopleura uchi	31.83	95.49	58.04	32.17	783
Enterolobium schomburgkii	45.20	101.86	67.34	18.94	164
Goupia glabra	44.88	127.32	71.04	13.59	795
Handroanthus impetiginosus	45.20	159.15	73.59	22.37	66
Hymenaea courbaril	45.20	141.65	78.58	21.35	372
Hymenaea parvifolia	40.11	120.96	63.18	24.68	472
Hymenolobium excelsum	43.93	128.92	69.57	32.58	310
Lecythis pisonis	44.88	168.70	77.51	21.08	441
Manilkara elata	38.20	206.90	75.05	24.43	5,685
Mezilaurus itauba	44.88	159.16	77.22	17.29	580
Pseudopiptadenia suaveolens	45.20	101.86	68.16	21.85	307
Ruizterania albiflora	45.20	117.77	72.48	24.21	218

TABLE 3: Ecological group (EG), fruit/seed dispersion (SD), Average commercial height (Hc) and wood density (WD) of 15 tree species occurring in the Saracá-Taquera National Forest, Brazilian Amazon.

Species	EG	SD	Hc (m)	D (kg m^{-3})
Caryocar villosum	2[1]	Zoochory[6]	11.80	930
Clarisia racemosa	1[4]	Zoochory[6]	11.83	1,010
Dipteryx odorata	2[1]	Zoochory[6]	11.20	1,090
Endopleura uchi	2[2]	Zoochory[6]	11.32	780
Enterolobium schomburgkii	2[2]	Anemochory[6]	11.50	790
Goupia glabra	2[1]	Zoochory[6]	11.55	870
Handroanthus impetiginosus	2[1]	Anemochory[6]	12.44	1,010
Hymenaea courbaril	1[1]	Zoochory[6]	13.23	960
Hymenaea parvifolia	1[1]	Barochory and Zoochory[6]	11.81	960
Hymenolobium excelsum	1[3]	Anemochory[6]	12.18	710
Lecythis pisonis	1[1]	Barochory[6]	11.19	880
Manilkara elata	1[1]	Zoochory[6]	12.59	1,000
Mezilaurus itauba	1[1]	Zoochory[6]	12.41	960
Pseudopiptadenia suaveolens	2[1]	Anemochory[6]	11.97	900
Ruizterania albiflora	2[5]	Anemochory[6]	11.71	650

Ecological Group: 1- Shade-tolerant; 2- Light-demanding.
[1] Pinheiro et al. (2007); [2] Gualberto et al. (2014); [3] Gomes et al. (2018); [4] Castro et al. (2021); [5] Oliveira et al. (2017); [6] Amaral et al. (2009).

recorded. Distances between trees were determined by the univariate *K* function (Ripley 1977; 1979). A circle with a radius of 5 m was adopted, with a maximum search radius of 1,680 m, in accordance with Bruzinga et al. (2014).

Confidence envelopes were constructed to test the hypothesis of Complete Spatial Randomness (CSR) using the Monte Carlo method, which is a statistical method that is based on massive random sampling to obtain numerical results for problems that are a priori deterministic (Halton 1970). Analyses were reproduced for a number of random replications (Vieira et al. 2017).

One thousand Monte Carlo simulations were carried out to construct confidence envelopes, with 99%$(1/(1 + m)) \times 100\%$ probability (Ebert et al. 2016; Dantas et al. 2018). According to Goreaud and Pélissier (2003), 1000 Monte Carlo simulations are sufficient in most situations to test spatial patterns. In this way, random spatial patterns were simulated, so that all trees were randomly redistributed in the study area, according to the number of simulations determined. The confidence envelopes were created considering the largest and the smallest values calculated by the *K* function.

Subsequently, the *K* function was calculated for the real data, comparing the observed pattern and the confidence envelopes produced. To make easier the analysis, the values obtained from the function $K(s)$ (estimator of the Ripley function in the univariate case and s a vector of distances) were transformed to $L(s)$ (value of the transformed function $K(s)$) (Ripley 1979). This transformation is indicated to stabilise the variance of the results. The transformed values were distributed graphically in which the abscissa and ordinate axes represent, respectively, the accumulated distances and the transformed values of the *K* function, according to Equation 1:

$$\hat{L}(s) = ((\sqrt{k(s)})/\pi) - s, s > 0 \quad (1)$$

Where $\hat{L}(s)$ is the function $\hat{K}(s)$ transformed.

To interpret the results of the function, $\hat{L}(s)$ <0 indicates that there are few neighbouring events within radius r, showing a tendency of inhibition between events, representing a uniform spatial distribution, $\hat{L}(s)$ >0 indicates a tendency for interaction between events, causing an aggregated spatial distribution for distance r.

The CSR analysis was done graphically to facilitate the visualisation of deviations in relation to the null hypothesis (Ripley 1977). For interpretation of the method, values above the upper line of the confidence envelope indicate a clustered (aggregated) spatial distribution and values below the lower line indicate a uniform (regular) spatial distribution (Ebert et al. 2016; Vieira et al. 2017). Ripley's $k(s)$ function was estimated using the Splancs package (Bivand et al. 2008), in the R software, version 4.1 (R Core Team 2021).

Results

Diameter distribution of the tree species

In the analysis of the diameter distribution of the group of 15 species, it was observed that 61.94% of the trees had a DBH of (50-80] cm, 23.99% had a DBH of (80-100] cm, 7.32% of [30-50 cm] and only 6.75% with DBH>100 cm (Fig. 2).

In the diameter distribution by species, the majority had a greater number of trees in the (70-80] cm DBH class, except for the species *Hymenolobium excelsum*, *Hymenaea parvifolia* and *Caryocar villosum*, which had a greater number of trees in the (80-90] cm class, and *D. odorata* and *Enterolobium schomburgkii* in the (60-70] cm class. Only *Caryocar villosum*, *Endopleura*

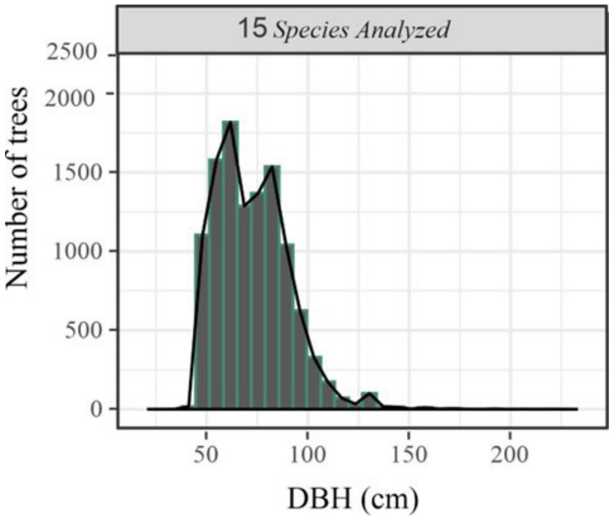

FIGURE 2: Tree diameter distribution of 15 commercial species in the Saracá-Taquera National Forest, Brazilian Amazon.

uchi and *Manilkara elata* had individuals in the smallest diameter class ([30-40] cm). The majority of species show a tendency towards normality, that is, a low number of trees in the smaller diameter classes, a high number of trees in the intermediate classes and a sharp reduction in the higher DBH classes (Fig. 3).

Location and population density of the tree species

In the analysis of location (distance) and density (number of trees ha^{-1}), it was observed that 14 (93.3%) of the 15 species studied have less than one individual per hectare, being *Caryocar villosum* (0.16 tree ha^{-1}) and *Handroanthus impetiginosus* (0.07 tree ha^{-1}) the least abundant species (Fig. 4). Only *Manilkara elata* showed high density (6 tree ha^{-1}).

Spatial distribution patterns of species using univariate Ripley's *K* function

The spatial distribution pattern of most species at the analysed distance scales (0-1680 m) was aggregated, mainly at the three smallest radii (distances of 0-1110 m) (Table 4). The random distribution pattern was observed in 12 species in the smallest radius (distance 0-370 m). Only one species showed a regular distribution pattern and only in the largest distance interval ((1490-1680] m).

Only *Hymenolobium excelsum*, *Manilkara elata* and *R. albiflora* did not present more than one spatial distribution pattern. *Hymenolobium excelsum* was the only species with a completely random spatial distribution, with *K* observed within the confidence intervals. *Manilkara elata* and *R. albilflora* occurred in aggregates at all distance scales, as it was demonstrated by the observed *K* being higher than the confidence envelope. These two species were the only ones for which the hypothesis of complete spatial randomness (CSR) was not accepted, considering that the other species presented points of spatial randomness, depending on the distance radius. *Hymenaea parvifolia* was the species that showed the greatest fluctuation in the spatial distribution pattern (random up to 30 m and from 940-1485 m; aggregate from 35-935 m; and uniform from 1490-1680 m) (Fig. 5).

Discussion

Diameter distribution and density of species

The 15 species studied showed a diameter distribution with a predominance of trees in the intermediate or large classes (Figs. 2 & 3), which is fundamental for planning sustainable forest management (Braz et al. 2014).

Considering the minimum measurement diameter (30 cm) used in the inventory, it was observed that the largest number of trees had DBH of 50-100 cm, which can be a positive factor for forest management, considering that Brazilian legislation determines that the minimum cutting diameter (MCD) for natural forests in the Brazilian Amazon is 50 cm (Brasil 2006). Other studies carried out in dense forests in the Brazilian Amazon (e.g. Francez et al. 2009; Reis et al. 2014), which measured trees from 10 cm DBH, found that most species presented a reverse J-shaped diameter distribution. It is known that this is the pattern of dense forests in the Amazon, but analyses carried out on specific populations, separately, have shown curves different from the reverse J-shaped diameter distribution pattern. Schulze et al. (2008), also in the Brazilian Amazon, studied trees with DBH > 20 cm and reported that 37% of the 70 commercial species studied had a greater number of individuals with DBH > 50 cm. This information about the low number of individuals in the smallest diameter classes (20 cm; 30 cm; 40 cm) is worrying, as it may indicate that there will not have trees enough for the next harvests (Reis et al. 2014), suggesting that younger individuals (DBH < 20 cm) as well as natural regeneration (DBH <10 cm) should also be inventoried.

It is likely that in the more recent history of the natural regeneration dynamics of these species, mechanisms occurred in the forest that made it difficult for individuals to grow from seedlings or saplings to adults (Felfili 1997; Condit et al. 1998; Herrero-Jáuregui et al. 2012) influenced by factors such as, for example, fruiting (Herrero-Jáuregui et al. 2012), as many species do not produce fruits and seeds regularly. Other factors that influence the establishment of natural regeneration of young individuals are: the amount of solar radiation, light requirement (Condit et al. 1998); limited seed dispersal (Machado et al. 2012); and high mortality rates of juveniles due to competition (Janzen 1970). To be sustainable, the forest management plan must contain information about the diameter distribution pattern of tree species and their autoecology in the area to be managed, as well as the population density of each species, especially those selected to be harvested (Castro et al. 2021).

The evaluation of the number of trees of the 15 species showed a high occurrence of species with low population density (<1 tree ha^{-1}) (Fig. 4), except *Manilkara elata*, whose population showed greater abundance and higher IVI. In studies by Pitman et al. (1999) in the Peruvian

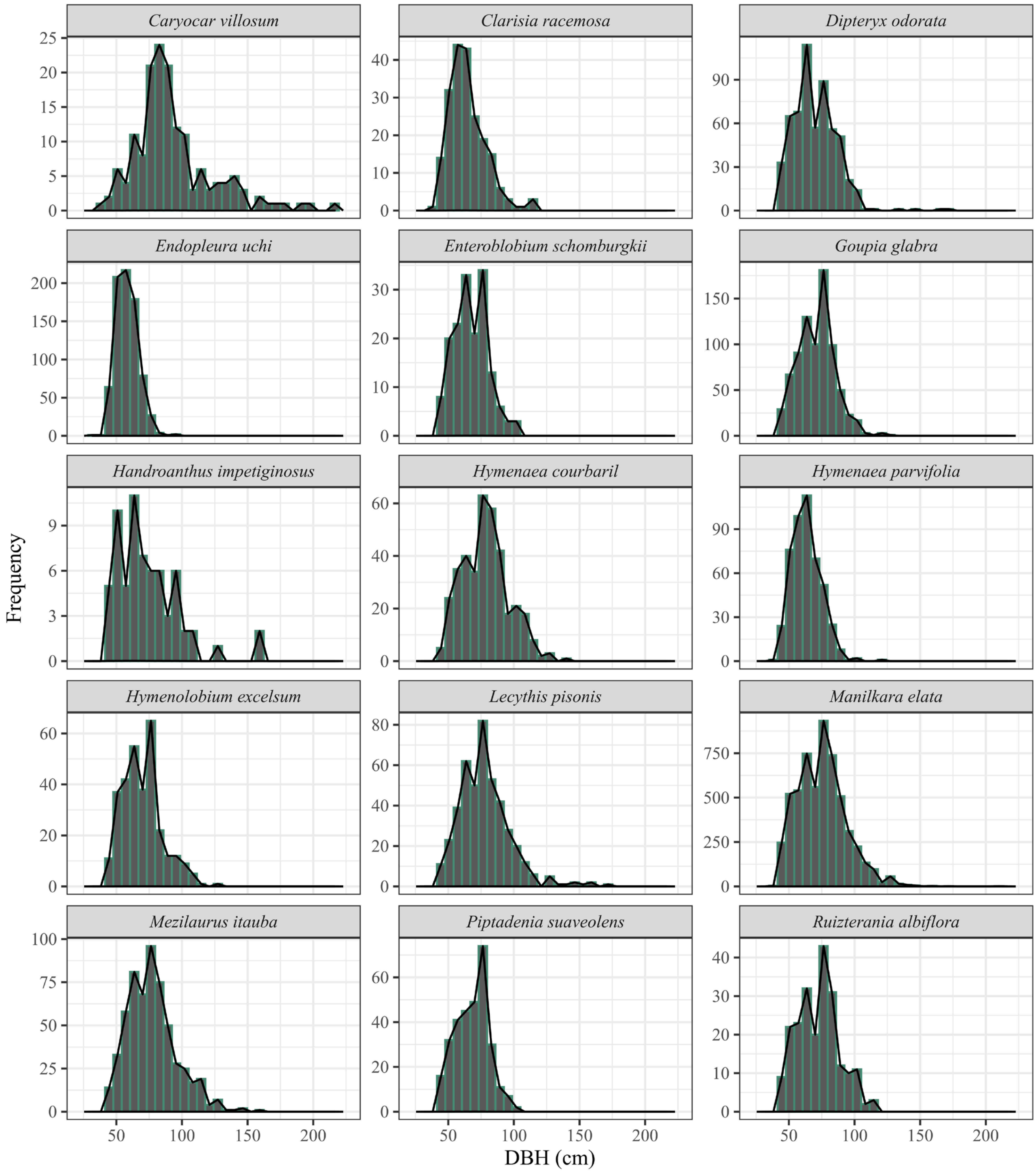

FIGURE 3: Diameter distribution of commercial tree species in the Saracá-Taquera National Forest, Brazilian Amazon.

Amazon and by Ter Steege et al. (2013) throughout the Amazon, most tree species also had a population density of less than 1 tree ha^{-1}.

Of the 15 species, *Hymenolobium excelsum*, *Hymenaea parvifolia* and *Mezilaurus itauba* are on the Official National List of Flora Species Threatened with Extinction in the vulnerable category (Brasil 2014). *Manilkara elata*, although not on this national list, is on the list of species threatened with extinction in the state of Pará, Amazon, in the vulnerable category. According to Brazilian legislation, species in the vulnerable category can have timber harvested following the criteria: i) maintenance of four trees per species per 100 ha, in each Work Unit (UT); and ii) maintenance of all trees of species whose abundance of individuals with DBH greater than the minimum cutting diameter (MCD) is equal to or less than four trees per 100 ha (Brasil 2015). In this sense, the 15 species evaluated in the present study can be logged, at least in the first cut.

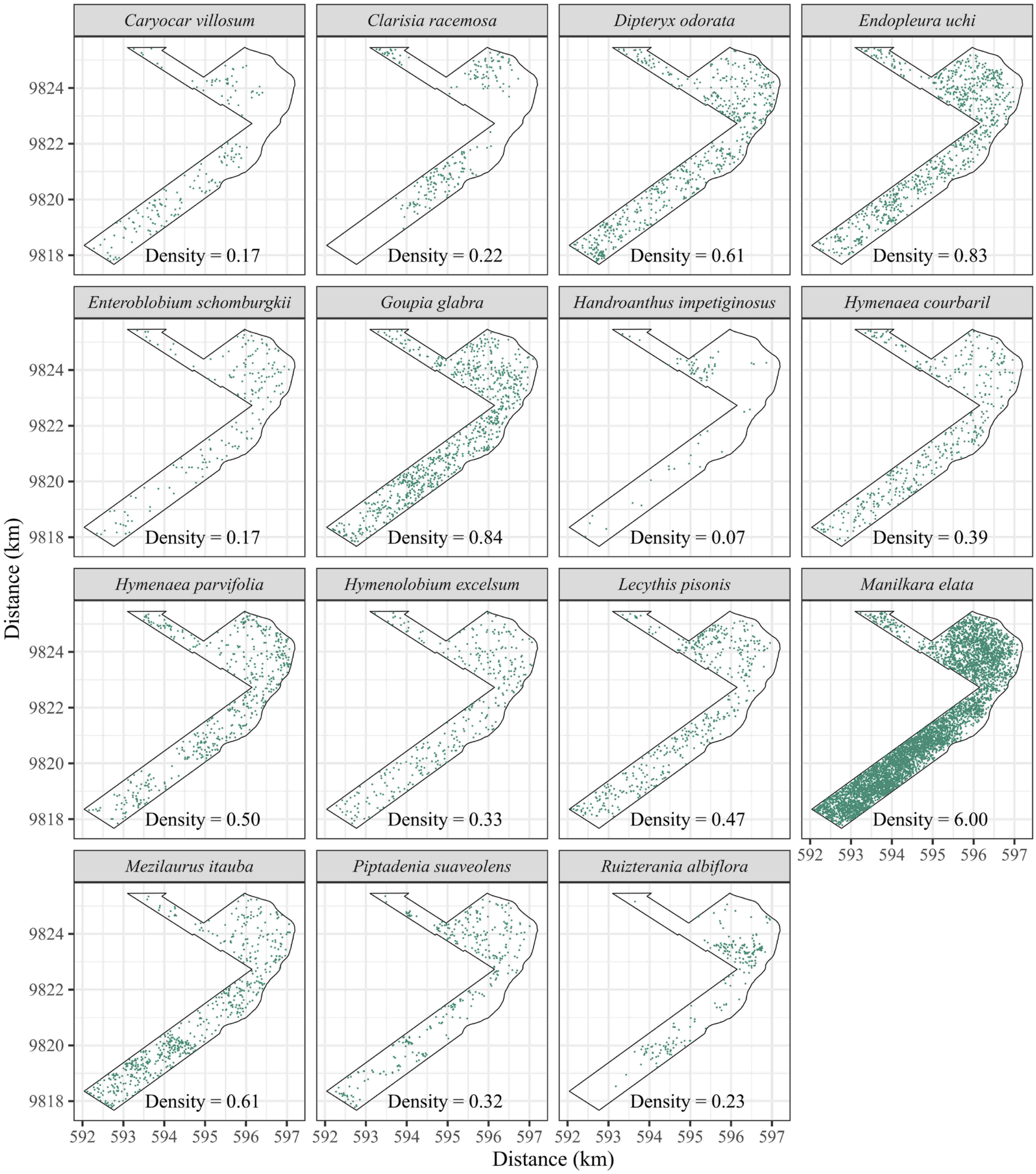

FIGURE 4: Location and population density of trees of 15 commercial species in 1,302.16 ha in the Saracá-Taquera National Forest, Brazilian Amazon.

TABLE 4: Number of timber species for each spatial distribution pattern in the Saracá-Taquera National Forest, Brazilian Amazon.

Radius (m)	**Distribution**		
	Aggregate	**Random**	**Uniform**
[0-370]	13	12	0
(370-740]	14	2	0
(740-1,110]	13	3	0
(1,110-1,480]	8	7	0
(1,480-1,680]	8	7	1

Manilkara elata has been the most commercialised timber species in the state of Pará, Brazilian Amazon. Its production in 2017 corresponded to around 19% of the entire volume produced in the state of Pará (Ibama 2017), demonstrating that despite the high diversity of tree species occurring in the Amazon, the logging focuses on only around 80 species of known commercial value (David et al. 2019), which are not always of high population density, as it was observed in this study. For example, *Handroanthus impetiginosus*, which in 2017 had the highest export value of sawn wood from the Amazon (US$2,100 m^{-3}) (Table 1), second only to *Handroanthus serratifolia*, was the species with the lowest occurrence in the study area (0.07 tree ha^{-1}) (Fig. 4).

Spatial distribution patterns using univariate Ripley's K

The predominant spatial distribution pattern for the 15 species studied (Fig. 5) was strongly aggregated, with some species tending towards randomness and with a rare uniform distribution, as has also been reported in studies carried out in other tropical forests, with different methodological approaches (e.g. Condit et al. 2000; Réjou-Méchain et al. 2011; Zhang et al. 2013; Araújo et al. 2016; Cysneiros et al. 2018; Miron et al. 2021). An aggregated spatial pattern can be indicative of species with similar ecological requirements (Rüger et al. 2009) and this spatial aggregation can be attributed to several important mechanisms and processes (Li et al. 2009), such as: way of dispersal of seeds (Condit et al. 2000; Lai et al. 2009; Réjou-Méchain et al. 2011; Ai et al. 2013; McFadden et al. 2019); shade tolerance (Réjou-Méchain et al. 2011; Zhang et al. 2013; Araújo et al. 2016); environmental heterogeneity (John et al. 2007; Borregaard et al. 2008; Lai et al. 2009; Li et al. 2009; Ai et al. 2013; Zhang et al. 2013; Miron et al. 2021); rarity of species in the environment (Fangliang et al. 1997; Condit et al. 2000); tree height (Fibich et al. 2016); and wood density (Réjou-Méchain et al. 2011).

Seed dispersal greatly influenced the pattern of spatial distribution of species, especially those whose dispersion is carried out by animals (53%) such as, *Manilkara elata*, whose dispersing agents are large birds of the genus *Ramphastos* and mainly primates of the genera *Alouatta*, *Ateles* and *Pithecia* (Simmen & Sabatier 1996; Van Roosmalen & Garcia 2000). Dispersal by primates is more aggregated, especially for species with high seed production (Vieira et al. 2003). But there are also species that are dispersed by animals, such as *Hymenaea courbaril*, which presented a random spatial pattern in 62% of the distance intervals observed.

Primates and parrots, such as those of the genus *Anodorhynchus*, are the main dispersing agents of *G. glabra* (Van Roosmalen 1985), the second highest IVI species. This species presented a random spatial distribution in the initial 30 m of distance and an aggregated distribution in the remaining radii (> 30 m). One of the possible explanations is that birds are responsible for a more random dispersion pattern (Vieira et al. 2003).

Caryocar villosum seeds are dispersed in the Amazon region by rodent mammals, such as *Cuniculus paca* and *Dasyprocta azarae* and other mammals, such as those from the Dasypodidae family (Moraes 2011). The adaptation of the species is intrinsically conditioned by the behavior and changes in the density of its dispersers (James et al. 1998).

Some anemochorous dispersal species had aggregated spatial distribution (64% of distance intervals for *Enterolobium schomburgkii*, 100% for *R. albiflora*, 74% for *P. suaveolens* and 88% for *Handroanthus impetiginosus*). *Hymenolobium excelsum* was the only species with a completely random occurrence. *Lecythis pisonis* had only barochoric dispersion and was completely aggregated up to 1425 m, from this distance the species showed a tendency towards spatial randomness. *Hymenaea parvifolia* presented two types of dispersing agents (zoochoric and barochoric) and had the spatial distribution pattern with the greatest oscillation: aggregate of 35-935 m (53.57% of distance intervals); random from 0-30 m; 930, 940-1485 (35% of distance radii), and uniform at distance radii of 1,490 to 1,680 m (11.61%).

The spatial aggregation patterns obtained in all distance intervals evaluated for most species by Li et al. (2009) in subtropical China and by Condit et al. (2000) in Central America and Asia were greater than 90%. The results of the present study confirm the change in the spatial distribution pattern for the same species, according to the distance radius.

It could then be said that spatial aggregation in tropical forests can be explained by dispersal limitation by animals, according to studies carried out in Africa by Hardy and Sonké (2004) and Obiang et al. (2019). However, in studies by Condit et al. (2000) in six tropical forests in Panama, Malaysia, Thailand, India and Sri Lanka, it was observed that species dispersed by zoochory had a more random distribution than species dispersed by anemochory or barochory, because the animals have a high capacity to move over long distances.

In the present study, the aggregate distribution pattern was predominant, mainly in species with seed dispersal carried out by animals, with the exception of *Hymenolobium excelsum* which was random in all distance intervals. Regarding the capture of solar radiation by trees, shade-tolerant species with higher levels of spatial aggregation (above 95% of distance intervals) were represented by *Clarisia racemosa*, *Mezilaurus itauba* and *Manilkara elata*, while those with higher levels of spatial randomness were represented by *Hymenolobium excelsum* (100% of distance intervals) and *Hymenaea courbaril* (62% of distance intervals). In the group of light-demanding species, only *Enterolobium schomburgkii* presented the random pattern as predominant (63% of the distance intervals), while 88% of the species in this group occurred aggregated: *P. suaveolens* and *D. odorata* (above 70% of the analysed intervals); *Handroanthus impetiginosus* (above 80%); and *Caryocar villosum*, *Endopleura uchi*, *G. glabra* and *R. albiflora* (above 90%). Therefore, there were more light-

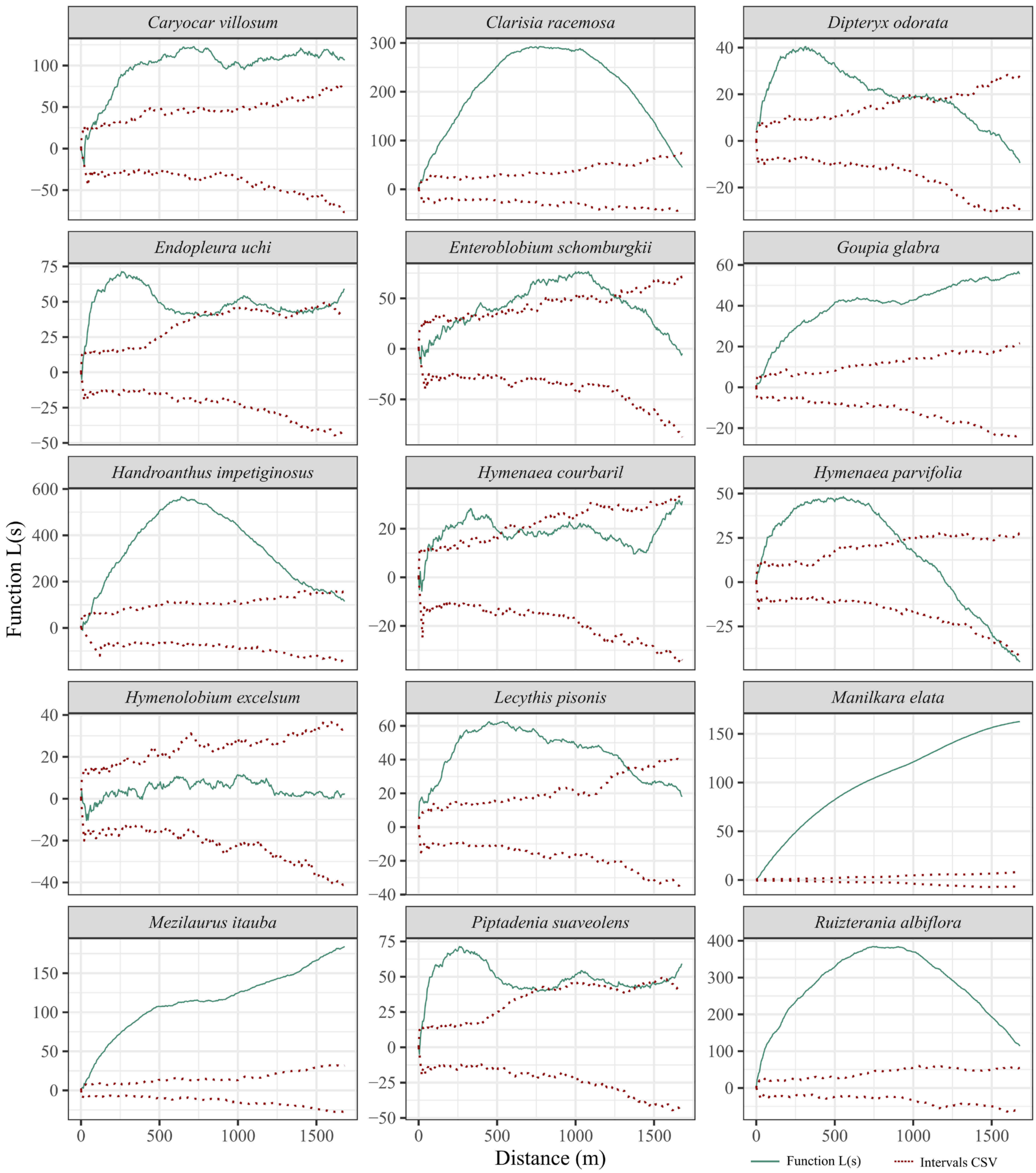

FIGURE 5: Spatial distribution pattern obtained with the univariate *K* function for commercial tree species in the Saracá-Taquera National Forest, Brazilian Amazon. The solid line is the univariate Ripley's *K* function and the dotted lines are the confidence intervals of the simulations with 99% probability.

demanding species with aggregate distribution than shade-tolerant species, confirming that solar radiation had an influence on the spatial distribution pattern of tree species in the study area.

There are studies that found a greater number of shade-tolerant species occurring in aggregates. One of the possible causes for this difference between studies may be the minimum diameter used in the inventory, as in the present study this diameter was 30 cm, while in studies that used smaller diameters, most species with an aggregated distribution pattern were shade-tolerant.

In relation to wood density (kg m^{-3}), species with wood density equal to or greater than 1.0 kg m^{-3} (*D. odorata*, *Clarisia racemosa*, *Handroanthus impetiginosus*, and *Manilkara elata* (Table 3) presented a predominantly aggregated spatial distribution pattern

(Fig. 5). Some wood species with a density lower than 1.0 kg m m^{-3}, such as *R. albiflora* (650 kg m^{-3}), and *Endopleura uchi* (780 kg m^{-3}), showed aggregated distribution, but *Hymenolobium excelsum* and *Enterolobium schomburgkii* presented a random distribution pattern. The results analysed differed from those obtained by Réjou-Méchain et al. (2011) in Central Africa forests, and Clark et al. (2018) in Central American forests, that softwood species occurred more aggregated in the environment.

In addition to the mode of dispersal, the influence of solar radiation, the rarity of the species and the density of the wood (kg m^{-3}), the species may have a preference for a certain habitat (Zhang et al. 2010), which may be another factor influence its spatial distribution pattern (Zhang et al. 2013; Zuleta et al. 2020; Miron et al. 2021), mainly considering topography, edaphoclimatic conditions, environmental gradients, inter and intraspecific competition and biotic interactions (Ter Steege et al. 2013). When associating these factors with the spatial distribution of the species in the present study, *Manilkara elata* was considered a habitat generalist while *Handroanthus impetiginosus* was considered a specialist, according to Hubbell and Foster (1986). Generalist species are normally favoured by environmental heterogeneity, while specialists are kept below their maintenance potential in the habitat, due to low tolerance to environmental changes (Brown 1996).

In the study carried out by Miron et al. (2021) for six species of commercial interest in the Central Amazon, including *Manilkara elata* and *G. glabra*, common to this study, the species also presented the aggregate spatial distribution pattern as dominant. *Manilkara elata* presented the same characteristic observed here, aggregation at 100% of distance scales. These authors associated the strong spatial aggregation with the elevation and slope of the terrain and distance from watercourses. Characteristics such as seed dispersal, for example, were not analysed. According to them, topographic variables influence species density, as well as spatial distribution, as these can be locally sensitive to habitat variability, that is, the environmental conditions of each forest distinguish its characteristics in terms of diameter and spatial distribution.

Implications for forest management

Many species of high commercial value have been successively logged, due to local demands, physical access, land tenure systems and market prices (Richardson & Peres 2016), also because they have large trees (Tritsch et al. 2016), for example, the 15 species analysed in the present study.

Some alternatives are proposed to guarantee the ecological sustainability of the most commercialised tree species in the Amazon, such as the logging of some dominant species, which, although they do not have wood of high commercial value, can supply regional markets (Ter Steege et al. 2013), based on the fact that species with a wide distribution in different habitats and high population abundance are ecologically less vulnerable (Caiafa & Martins 2010). Another alternative to maintaining sustainable wood production is to replace some harvested commercial species with new ones that were not harvested in the first logging (Castro et al. 2021). Dominant species of high commercial value have been intensively logged and have slow growth, such as *Manilkara elata* (Ferreira et al. 2020) also considered at risk of extinction and can therefore be replaced in the management plan by others species with high quality wood, but not marketable yet (Castro et al. 2021).

In addition to encouraging the logging of dominant species, it is important to adopt other strategies to maintain species diversity, such as: drawing up a list of priority species for regional conservation, considering criteria of rarity and vulnerability (Gauthier et al. 2010; Maciel et al. 2016); assessment of species in relation to rarity in certain locations and in relation to abundance in others, within the same APU, which can lead to the preservation of trees of a species in different locations within the management area (Alves & Miranda 2008); and assessment of population densities and diameter distribution of trees aiming at species-specific management, with silvicultural treatments aimed at stimulating natural regeneration rates and the growth of younger trees (Condé et al. 2016; David et al. 2019 ; Castro et al. 2021).

The high occurrence of seed dispersal by animals and, consequently, the formation of aggregate spatial distribution patterns suggests that measures to mitigate impacts on local fauna be included in sustainable forest management plans. The availability of nests, the structural complexity of the vegetation and the presence of attractive food resources, mainly fruits, must be maintained to attract fruit and seed dispersing animals (Wunderle 1997).

Environmental heterogeneity in the study area appears to have influenced the spatial distribution pattern of the studied species (Zhang et al. 2013), as species more tolerant to the effects of the environment produced a greater number of descendants, resulting in more aggregated populations. The strong tendency towards grouping of most of the studied species is desirable for a reduced impact logging plan, considering forest management in large areas. In the management plan, the spatial distribution of trees must be considered to make the right decisions about logging activities, especially since some species are more aggregated on smaller scales, causing changes in spatial distribution and density. The commercial volume stock can vary spatially in the same area, causing implications for planning the intensity of logging, infrastructure and operations in the forest (Miron et al. 2021).

Conclusions

The presence of large trees and the aggregated spatial distribution in most of the tree species studied may indicate the possibility of continuous timber production to meet conservation and sustainable management criteria. The spatial distribution of stocks should guide the planning of forest management activities, including pre-logging, logging, and post-logging activities.

However, the low population density of most species suggests that logging must be carefully planned to avoid population declines. We highlight the need to consider the diameter distribution and spatial distribution patterns of species when planning forest management.

Although forest management on a sustainable basis has advanced in recent years in the Amazon, the factors that promote the different diameter and spatial distributions of species are still considered complex and little studied. Therefore, the results obtained point to the need to expand research on this topic in managed areas, including with the same technological approach as the present study. The inclusion of this type of analysis can constitute an important tool for defining population management strategies for each species, considering their ecological characteristics and environmental adaptation at the local level.

Additionally, we suggest that forest management planning in other locations carefully consider the diameter and spatial distribution of species, integrating these parameters into management practices to ensure sustainability. The application of these criteria can assist in the formulation of forest management recommendations that are adaptable to different regional contexts in the Amazon and other tropical forest regions around the world.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

QSB: Conceptualization, Investigation, Methodology, Formal analysis, Writing - Original Draft, Supervision. EFS: Conceptualization, Methodology, Formal analysis, Writing - Original Draft. NMMR: Writing - Review & Editing, Visualization. BLR: Methodology, Writing - Review & Editing. ARM: Writing - Review, Visualization. GFS: Writing - Review & Editing, Visualization. JOPC: Writing - Review & Editing, Visualization. TCC: Writing - Review & Editing. MVNO: Writing - Review & Editing, Visualization; EKBO: Writing - Review, Visualization, JPMS: Methodology, Visualization. QSR: Investigation.

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