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Neighbour's identity of commercial tropical tree species in a tropical rainforest near Manaus, Brazil

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ABSTRACT

The use of spatially explicit neighbourhood approach helps to understand the processes which structure and guide tree communities over space and time, contributing for the conservation and forest management. We investigated the neighbours of *Brosimum* spp., *Eschweilera coriacea*, *Ocotea cernua* and *Protium hebetatum*, hypothesizing that there is a taxonomic pattern around these focal species, been important information for the maintenance of the forest's structure submitted to the management actions. We used a 2-ha plot in a tropical rainforest in Brazil where all trees with diameter at breast height (DBH) ≥ 10 cm were stem-mapped in 2005. First, we determined how focal species were spatially structured by using Ripley's *K* function. For the neighbourhood analysis, the nearest 20 trees around focal trees were identified to compute the mean richness, mean proportion of conspecifics, relative frequency distribution and the number of neighbour species by distance from focal trees. Our findings demonstrate that conspecific neighbours are occurring associated with focal trees, mainly at shorter distances for all focal species with possible more intra-specific interactions as a very few heterospecific neighbours were associated with focal trees. The spatial structure, more than abundance of focal species, may have contributed for the conspecific encounters, mainly for *Brosimum* spp. and *Ocotea cernua*. Rare species were found frequently associated with focal species, calling our attention for the effects of the forest management of commercial trees on community structure in order to prevent local extinctions.

Keywords: Neighbourhood Analysis, Tropical Tree Species, Central Amazonian, *Terra Firme* Forest.

INTRODUCTION

Recent decades have seen an increasing decline in species' biodiversity as a result of human interference leading to a growing concern about the future survival of ecosystems and their functioning (ILLIAN & BURSLEM, 2007; ELLWANGER *et al.*, 2020; HABIBULLAH *et al.*, 2022). Understanding the impact of biodiversity loss on ecosystems requires an understanding of the processes that structure communities and the mechanisms that sustain biodiversity (CASTILHO *et al.,* 2010L; IMA *et al.*, 2018; TROGISCH *et al.*, 2021).

Insights on biodiversity can be obtained by analysing the spatial patterns of plants in natural communities as the patterns provide information about the processes which operated in the past, which form the template on which processes will take place in the future, thus reflecting complex historical and environmental differences, climate and sunlight factors, competing vegetation, and the chance of success of different species over time depending on their individual life history characteristics (CAPRETZ *et al.*, 2012; GIMOND, 2020; MOTA *et al.*, 2020; TURNER, 2020).

Tropical forests, one of the world's most species-rich terrestrial ecosystems, are the focus of ongoing attempts to describe, interpret, mensure and understand the importance of such mechanisms for community-level properties and that characterized as a fundamental question in ecology (LAW ET AL., 2009; ALVES, 2019; LIMA *et al.*, 2018; MOTA *et al.*, 2020; MOURÃO, 2021) where the locations of plants are likely to have been determined, at least in part, by the neighbourhood in which they disperse and share with other plants (ROCKWELL *et al.*, 2017; SANTOS *et al.*, 2018; TROGISCH *et al.*, 2021).

The way trees are arranged in horizontal space in a forest, that is, the pattern of spatial distribution of species, represents the result of several ecological processes that act over time. It has been recognised that coexistence is in part determined by the inter- and intra-specific interactions in a community, competition, predation, herbivory among other phenomena (SANTOS *et al.*, 2018; TROGISCH *et al.*, 2021), where processes are predominantly local and need to be modelled from the point of view of every individual, taking local growing conditions as well as local competition into account, because plants compete with their immediate neighbours for limited resources above or below ground, or for both (SANTOS *et al.*, 2018). Then, the use of the spatially explicit neighbourhood approach can help to understand the process structuring and driving the community along space and time, offering insights into the underlying competitive inter-tree interactions, mainly on a small spatial scale (FICHTNER *et al,* 2018; SANTOS *et al.*, 2018).

Although overall densities of most species in very diverse tropical communities are low, local densities can nevertheless vary among species in response to crowding or to the identity of neighbouring species, which is likely to contribute to the maintenance of species diversity in tropical forests (MOTA *et al,* 2020; WIEGAND *et al.*, 2021). Also, the rarity of the majority of species in tropical forests demands the grouping of species, using some criteria that capture their potentially different effects on target species. Historically, forest modellers have chosen from one of several grouping criteria, including taxonomic affinity, ecological guilds, similar growth dynamics, among others. The knowledge about the interactions between target species and their neighbours is very important for the forest management, which helps in the maintenance of forest structure and the ecosystems function (PACHECO *et al,* 2021; TROGISCH *et al.*, 2021; SANTOS *et al.*, 2018).

In the present study, we hypothesized that there is a taxonomic pattern in the occurrence of neighbours of four commercial tree species in the Brazilian Amazon "terra firme" tropical rainforest, characterized mainly by the occurrence of conspecific neighbour species, which are important features to help forest management in the maintenance of forest's structure and interactions among species. To address this issue, we used the nearest neighbour analysis to investigate the identity of 20 k-nearest neighbours around each focal tree and the Ripley's K function, to identify how species are locally spatially structured.

METHODS

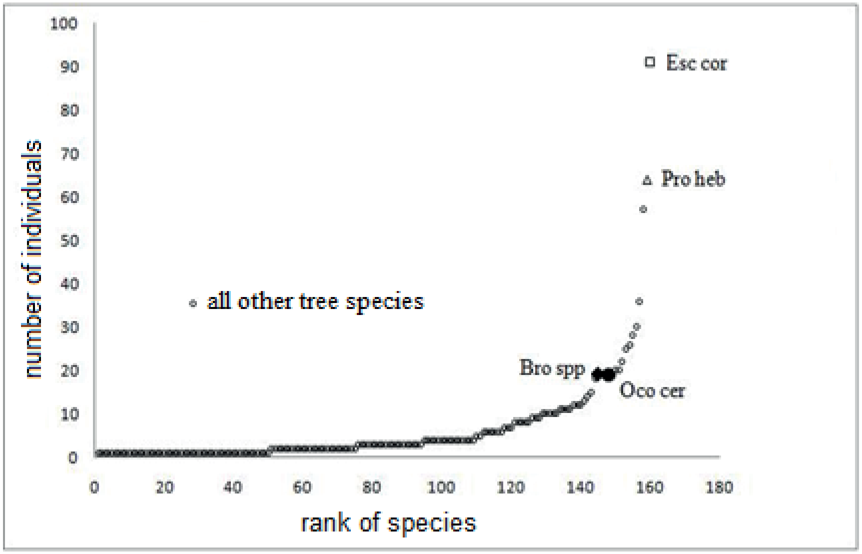
Study area

The study area is located in a Western Amazon upland ("terra firme") dense forest, at the Embrapa Experimental site, in Manaus, state of Amazonas, Brazil, with an area of 2ha, entirely located at the top position according to the local topography, at the coordinates 60° 2.4'W and 2° 31' 58.8" S. The climate is tropical, type "Am" (Koppen classification), with a mean annual rainfall from 1355 to 2839 mm. The mean annual temperature ranges from 25.6°C to 27.6 °C, with relative humidity from 84 to 90% (RADAM, 1978). On a broad scale, soils are fairly homogeneous throughout the stands; heavy-textured dystrophic yellow latosol predominates, covered mainly by dense forest with emergent trees (IBGE 2006). The upland areas are plateaus formed by Tertiary sediments that cover the largest portion of the Amazon sedimentary basin, shaped by landforms dissected in extensive interfluvial plateaus and hills (PUPIM, 2019). Rainforests in the area are evergreen and terra firme (not seasonally flooded), with forest canopy typically 30-40 m tall, with emergents to 55 m.

Field sampling and species information

At the 2 ha study area (100x200m), all trees with DBH ≥ 10 cm were stem-mapped (x-y coordinates) in 2005 and botanically classified at species level. A total of 1,055 individuals, classified into 163 species and 42 families were identified, with about 30 percent of species having only one (01) individual and about 68 percent from 1 to 5 individuals (Fig. 1).

Fig. 1. Number of individuals per species at the 2 ha study area, highlighting the four commercial species studied.



Source: authors.

From the list of species identified at the 2-ha plot, four commercial tree species largely used in the lumber industries in Amazonas state were selected (Lima Filho *et al.*, 2005). The species studied were: Brosimum spp. (Bro spp), Eschweilera coriacea (DC.) S.A. Mori (Esc cor), Ocotea cernua (Nees) Mez (Oco cer) and Protium hebetatum D.C. Daly (Pro heb), which, from now, are referenced as focal species and their individuals, as focal trees. The number of individuals per focal specie is: 19 for (Bro spp), 91 (Esc cor), 19 (Oco cer) and 64 (Pro heb). The focal species "Bros spp", combined four species because, according to Lima Filho *et al.* (2005), this genus is used by lumber industries without a specific species preference. The species in this genus and its respective number of individuals are: (1) Brosimum lactescens (S.Moore) C.C.Berg. (1 individual); (2) Brosimum acutifolium Huber ssp. Interjectum C.C.Berg (2 individuals); (3) Brosimum utile (H.B.K.) Pittier ssp. ovatifolium (Ducke) C.C.Berg. (5 individuals) and (4) Brosimum rubescens Taub. (11 individuals).

The species in the genus "Brosimum", Moraceae family, is generally 20 to 30 meters tall, presents high density wood and small seeds. According to studies of Lorenzi (2016) they behave like secondary species, with low growth under shade environments and faster growth in gaps.

Eschweilera coriacea (Esc cor), Lecythidaceae family, is a common canopy tree up to 37 m tall, widely distributed in the Amazon basin, with high densities (Heuertz, 2020). The pyxidium fruits are medium size and contain one to several large seeds that may attract some frugivorous animals, such as large birds and bats. Gravity plays a role in their dispersal and vertebrate consumers, such as rodents and primates may also disperse seeds (Prance e Mori, 1978).

Ocotea cernua-lauraceae family, produces small fruits and trees occupy the midstorey and canopy position (Vásquez & González, 2018). There is little information available in literature about this species.

Protium hebetatum belongs to the Burseraceae family, which is one of the most dominant families in the Central Amazon, it is typical understory species, medium tall and has medium size fruits and seeds, with mainly endozoocoric dispersal (Silva *et al.*, 2021).

Nearest neighbour analysis

Twenty nearest neighbour trees of the four focal species were analysed with the intent of identifying and describing a compositional pattern around focal species and how conspecifics are distributed over them. The analysis was carried out using the Spatstat software system in R (BADDELEY; RUBAK; TURNER, 2020), based on the following measures at each species, separately:

(1) mean distance to each of the 20 nearest neighbours from focal trees, aiming to know the range of occurrence of the neighbours; (2) Ripley's K point pattern analyses, univariate function, with the result presented as "L(r) – r" instead of K, which is a transformation of the Poisson K function to the straight line, making it easier to assess the deviation from the theoretical function*(3)* the mean species richness and mean number of conspecifics, considering all 20 nearest neighbours at each focal tree; (4) the mean proportion of conspecifics, calculated over all focal trees; (5) the most frequent species occurring along the 20 nearest neighbours measured over all focal trees; (6) the number of species registered within each k-nearest neighbour investigated, plotted against the mean distance from the focal tree to the *k*th-nearest neighbour, and (7) the frequency calculated within each *k*-nearest neighbour, which might present a pattern in the occurrence of the neighbour species.

■ RESULTS AND DISCUSSION

Resultts

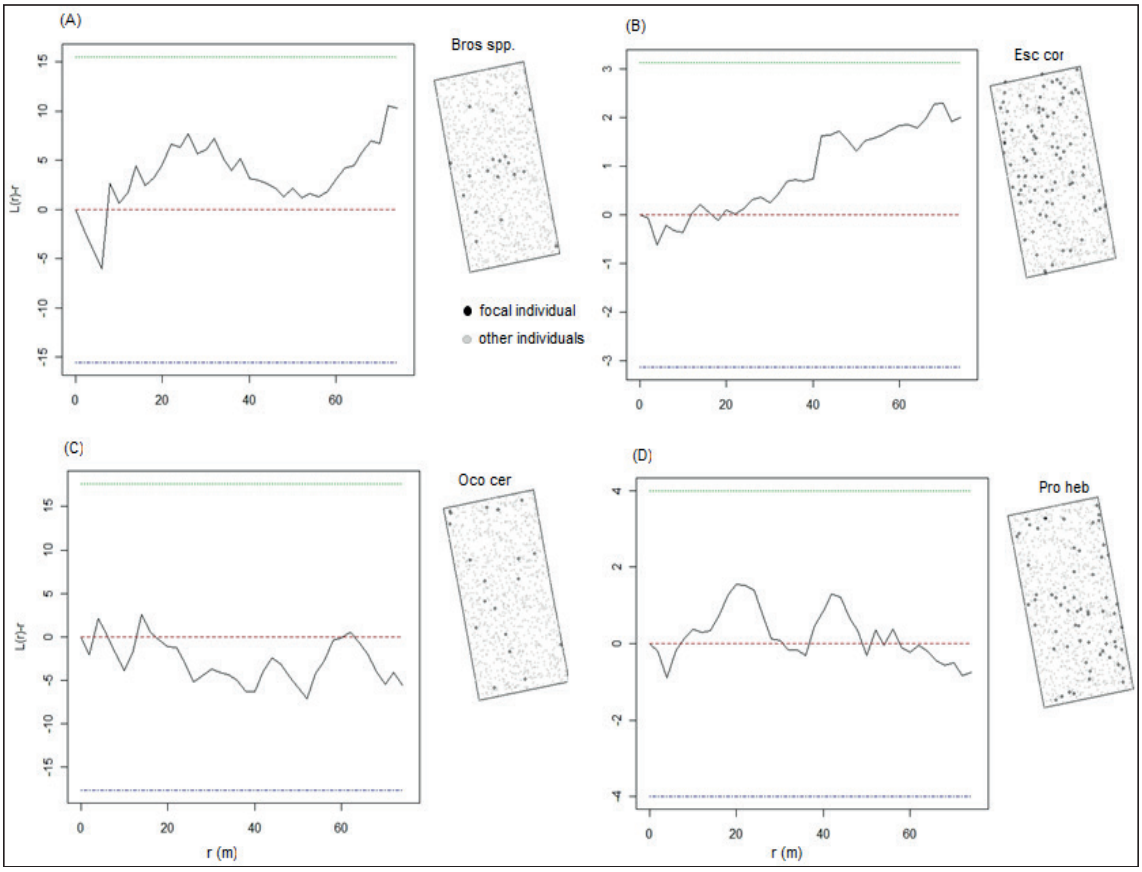
The observed spatial pattern for each of the four species revealed different behaviours, but no significant differences from the random pattern (Fig.2). There was a tendency to an aggregated pattern for "Bro spp" and "Esc cor", and a regular pattern for "Oco cer". Protium hebetatum (Pro heb) oscillated between the aggregated and regular pattern, with tendency to aggregation for intermediate distances.

Composition variation along the focal trees

The four species investigated (Bro spp, Esc cor, Oco cer and Pro heb) have similar curves (Fig. 3) related to the mean distance to the 20 nearest neighbours from the focal trees analyzed. Such distances ranged from 2 to 11 meters, on average with "Oco cer" presenting the highest values and "Bro spp" the lowest.

Rare species, occurring with one individual at the study area appeared mainly as neighbour species of "Pro heb", "Esc cor", "Oco cer" and "Bro spp", in decreasing order, ranging from 28 and 19 percent of the number of species registered occurring as neighbours of the focal species. If we consider species with up to five individuals, the values vary from 57 to 60 percent, with low variation among the four focal species.

Fig. 2. Função de Ripley " *L(r)-r"* para as quatro espécies estudadas. (A) *Brosimum* spp.; (B) *Eschweilera coriacea* , (C) *Ocotea cernua* e (D) *Protium hebetatum*. As linhas superiores e inferiores pontilhadas são os envelopes críticos simultâneos de 95% com base na aleatoriedade espacial completa.



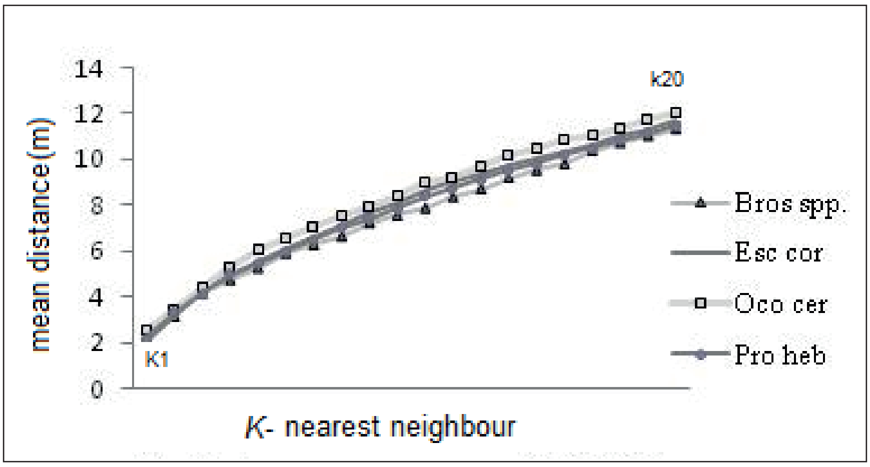
Source: Authors.

The analyses aiming to investigate the taxonomic pattern in the occurrence of neighbours of focal species are presented below for each focal species individually.

(1) Brosimum spp. (Bro spp) - Forty seven species were registered up to 20 th nearest neighbour of 19 focal trees of "Bro spp". The species with the higher relative frequencies, measured at each focal tree and along all k-nearest neighbours investigated (20-k multiplied

by 19 focal trees) were “Esc cor”, Eschweilera collina Eyma (Esc col) and “Bros spp”, with 18, 10 and 7 percent, respectively (Fig.4). On average, the richness measured at each focal tree was 12 species and the mean proportion of conspecifics accounted for seven percent with 1.26 standard deviation (SD) measured at the number of conspecific trees.

Fig. 3. Mean distance from focal trees of the four commercial tree species up to the 20th nearest neighbour at 2-ha study area.



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In spite of the low mean proportion of conspecific trees along the 20-k-nearest neighbours, the relative frequency of their occurrence analysed within each k-nearest neighbour measured along 19 focal trees, showed that the conspecifics are mainly concentrated on the first three nearest neighbours with average of 26 percent of the occurrences of all species, up to third nearest neighbour. It indicates a conspecifics’ pattern at shorter distances (Fig.4).

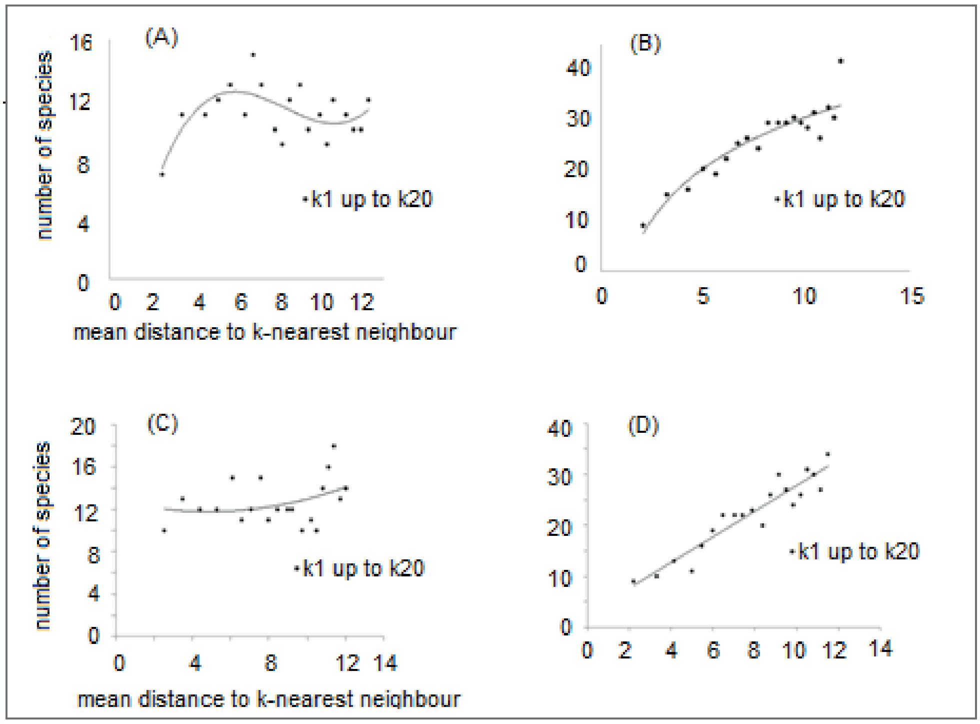
Fig. 4. Frequency of occurrence of neighbour species of *Brosimum* spp. up to the 20-k nearest neighbour.

K_nearest_neighbour of *Brosimum* spp.																				
neighbour species	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20
Amb duc	1	1		3	2	2			1				1							
Car pal	1		1																	
Buc gra	2		1									1								
Boc vir	3	2	1	2	3		1	2	2	2	2	1		2	1					
Asp mar	3	2	3		1	2	1				1	1	2							
Boc mul	3				1		2	2			1	1		1	1		1			1
Bro spp	6		4	2	2	2	1	2	1				1							1
Dis bra		1	1	1	1		1		1	3	1	2	1	1		1	1	1	1	
Ape ech		1		1							1								1	
Ann amb		1			1	1		1											1	
Cas gra		1			1		1				1									
Chi sp.		1																		
Cla rac		2	1	1	2	1	2	1			1					1				
Cou alt		2	2	4	1	2				3			1		1		1	2	1	1
Cou ste			1	1		4	2	2		2	1	1		1	2		3		1	1
Ani can			1										1							
Chi duc			3	1																
Ani meg				1				1						1	1		1	1		
Ago bra				1									1							
Asp alb				1																
Dur fus					1		1		1											
Dip odo					1				1			1								
Con gui					2			1				1								1
Duc ces						1	1		3	1										
Cou gui						1														
Dip mag						1														
Emm aff						2	1	2								1	1			
Eri bic							1					1						1		1
Ani hos							1							1						
Ani ros							1									1				
Esc col							2		4	1	3	3	2	4	6	1	2	5	3	3
Esc atr								1	1	1	1	2		1	1	1	1			2
Epe gla								1								1			1	
Din exc								1												
Esc cor								2	4	5	5	3	8	5	5	7	6	5	7	5
Dip rod										1								1		
Ast lec											1									
Ent sch												1								
End uch													1							
Gei arg														1	1	1		1		1
Cor rim														1		1		1	2	
Fer ell																1	1			
Gou gla																2				1
Gua poe																	1			
Hel sca																		1		
Gus ell																			1	
Gua oli																				1
sum	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20

Source: Authors.

The total number of species registered at the first k-nearest neighbour (k1) increased to the second quickly, around 57 percent (Fig. 5A). After the second k-nearest neighbours, the increment decreases, with values oscilating slightly up to the latest k-nearest neighbours, with species presenting low relative frequencies, less than 16 percent measured at 19 focal trees (Fig. 4 and 5A). The exception is the neighbour species "Esc cor", which presented the highest frequency of occurrence from the 10-k-nearest neighbours (ranging from 26% to 42%), Fig. 4, which might mean a pattern of co-occurrence with "Bros spp" at distances larger than 8m, on average. For the other neighbour species, these low frequencies might indicate that they are occurring in a randomly way at each k-nearest position after the first k-nearest neighbours. Eschweilera collina showed similar behaviour as “Esc cor”, but with small frequency values.

Fig. 5. Number of species by the mean distance registered up to the 20-knearest neighbours of four focal species at the study area. (A) Brosimum spp. (Bro spp), (B) Eschweilera coriacea (Esc cor), (C) Ocotea cernua (Oco cer), and (D) Protium hebetatum (Pro heb).



Source: Prepared by the authors.

(2) Eschweilera coriacea (Esc cor) - Along with the 20 nearest neighbours of 91 trees of Esc cor, 64 neighbour species were registered. Eschweilera coriacea (“Esc cor) and Eschweilera collina Eyma (Esc col) were the neighbour species with higher relative frequency of all k-nearest neighbours investigated, with 25 and 13 percent, respectively (Fig. 6). The mean richness measured at each focal tree was 11 species and the mean proportion of conspecifics, 25 percent, with SD equals to 1.9 presenting great variability on the occurrence of conspecifics.

The conspecifics found along the 20-k-nearest neighbours are concentrated mainly on the first five k-nearest neighbours, presenting on average 41 percent of frequency measured within each one of the five k-nearest neighbours, which might reveal a pattern on the distribution of conspecifics, mainly at shorter distances, ranging from 2 to 5.6 meters, on average. After the fifth k-nearest neighbours up to the 20th, the frequency of conspecifics decrease to 20 percent, oscillating around this value. Another neighbour species that seems to exhibit a pattern is Esc col, which was registered at the whole 20-k-nearest investigated. This species showed higher relative frequencies of occurrence within the first seven k-nearest with value around 20 percent on average. After the seventh k-nearest position, the value drops to 13 percent and below. Other species, such as Couratari stellata A.C.Sm. (Cou ste) and Inga obidensis Ducke (Ing obi) presented some association at distances around 8 meters from the focal trees, but with lower relative frequencies when compared with “Esc cor” and “Esc col”.

Considering the other species, there is no visible pattern in their occurrence due to the low frequency values (below 4 %) for both short and high distances. This could be ratified by the tendency of fast increase in the number of species from the first k-nearest neighbour, with the highest value to the second one (66%), and after increasing on average seven percent, with SD value equal to 6.0 species, presenting large variability (Fig. 5B).

Fig. 6. Frequency of occurrence of neighbour species of *Eschweilera coriacea* along the 20 nearest neighbours.

K-nearest neighbour of *Eschweilera coriacea*																				
neighbour species	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20
Dis bra	1	1		2	4	9	4	2	2	1	1	2	1	2	4	2	2	1	2	3
Ent sch	1	2	2	1				1		1	1	1		5				1	2	2
Epe gla	1	2		1	1	1	2		2	2				1			1			1
End uch	1		1		1	1	1	1		1				1	1				1	1
Eri bic	3	1	1			1	1	1	1		1				1	1		2		2
Gei arg	4	6	6	6		1	2		1	6	1	3	1	1		1	3	1		2
Esc atr	11	8		9	7	3	2	2	1	3	4	4	1		3	3	1	1	4	4
Esc col	24	17	24	14	15	23	20	12	10	10	13	11	9	5	7	8	10	7	4	5
Esc cor	45	39	39	31	31	18	19	22	18	15	17	12	15	18	17	22	25	18	15	20
Gly ped		1	1	1	2	3			1	1	1		1		1				2	
Ing alb		1	1	1	5	2	4	6	8	3	2		2	3	2	1	1	2	1	
Fer ell		1	3							2										
Hel spr		1		3	3	4	2	1		2	2	1	1	2				1	1	3
Gua oli		2		2		5				2		2	2					1		1
Gus ell		2			1	1		1			2	2	1			1	1			
Gou gla		7	3	1	7		2	6	2	1	3	3		2	1	1				
Esc rho			1	1				1		1								2		
Ecc gui			1	1																
Emm aff			1	4	2	2	3	1	3	1	3		1	1	2	1	1	1	2	1
Duc ces			1				1	1	2			2	1	1						1
Hev gui			2	3	2	2	4	4	7	2	2	5	3	3	2	1		3	2	1
Hel sca			4	6	1	3	5	2		3	2	2	4	1	2	4		2	3	
Cou alt				1	1		3	3	13	7	5	9	7	11	12	3	4	7	11	4
Dur fus				1	2	1	1	1		1		1	2			2				1
Dip odo				2					1			1		1			1			1
Gua poe					1	1	1	1	2				1	1		2		1		1
Cou ste					2	6	5	9	4	8	5	4	8	6	5	5	3	1	4	1
Ing obi					3	2	2	7	2	9	12	3	10	2	3	5	8	7	5	3
Dip mag						1	1							1					1	
Dip rod						1	3	1		1	1	1				1				
Cro caj							1	1	1		1				1			1		
Iry cor							1		2	3	1	5	3	3	5	4	4	1	5	1
Lec gra							1				1		2	3	3	4	4	2	3	2
Hym par								1	1			3								
Ing sub								1	2			1		2	1	2	1			1
Hym suc								2		1	1									1
Jac cop									2		1							1		1
Ing cor									3	1				1						
Cor rim										1	1	1								
Cla rac										1	4	3	2	8	3	2	2	3		2
Lic ape										1				1	5	5	7	8	6	2
Con gui											1	1	1			1		1	4	
Lec bar											1	4	4	2	2		2	2	2	3
Ing gra											1		2		1		1			
Din exc												1	2							
Chi sp.												1		1						
Lic ado												2	1							
Ing sti													1			1				
Bro spp													1					2	1	2
Cec sci													1						1	1
Lec usi														2		2	2	4	1	1
Lic het															1	1	1	1		
Cou gui															1	1				1
Cec pur															1		1			
Lic mic															2	2			2	2
Cas gra															2		1		1	2
Car pal																1	1	1	2	3
Lec pra																1				
Boc mul																	3		1	1
Boc vir																		2	1	2
Lic obl																		3	1	2
Asp mar																				1
Buc gra																				1
Lic gui																				1
sum	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91
	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20

Source: Authors.

Fig. 7. Frequency of occurrence of neighbour species of *Ocotea cernua* along the 20 nearest neigbours.

K-nearest neighbour of *Ocotea cernua*																				
neighbour species	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20
Mic sip	1	1	1	1								1				1				
Par nit	1	1																		
Nau cal	1	2		1	1		1			1			1					1		
Man bid	1		1	3	1	1	1	1			2	1					1			1
Mou ang	1			1																
Oco cer	2	2		2	1	3	1	1	1	1	2	1			1					
Mou cal	2	3			1						1	2			1				1	
Pal cor	2			1																
Nee opp	3	1	1	1		1														
Min gui	5	1	2			2				1		1	1			1	1		1	
Pou lau		1	1	2	1	4	1	1	1	4	2	1	1	2			2	2	2	2
Par orm		1	2																	
Pla duc		1		1																
Mic tru		1			1							1	2							
Pou cai		1					1				1							1		1
Pou min		3	3	2	3	3	5	1	3	1			3	1	4	1	1		1	
Lic mic			1			1											1			1
Par pen			1				1													
Lic obl			2	3	2	1	2	2	3		1			1		2				
Pip sua			2		1	1	2	1												
Pou myr			2					1		1				1						1
Pla ins				1				1												
Lic ape					1	1		1	1	2			1			1	1	1		1
Mez ita					1				1								1			
Mab sp.					1													1		
Lic gui					1															
Mic guy					1															
Pro heb					2		2	4	3	4	4	6	7	6	4	3	1	1	4	
Pau mac						1			1											
Pou ret							1						1						2	
Lic ado							1													
Lec bar								1	1						1	1				
Pou ven								1	2	1		2			2	2	1	1	1	
Ing obi								1	2	1				1			1	1		4
Par mul								1						1						
Oco cym								1							1			1		
Psi ara										1	1			2	2	1	2	1	1	
Pro hep										1				1				1	1	
Lic het											1	1						1		
Lue ros											1									
Man ama											1									
Jac cop											2	1								
Ing sti												1								
Rin gui													1			1				
Pra coc													1							
Mic reg														1		1				
Ing alb														2	2					
Qua alb															1					1
Lec usi																1		1		1
Pyt ola																1		1		
Scl hel																2		1		1
Pse mun																	1	1	1	
Hel sca																	1			
Lec gra																	1			
Qua acu																	1			
Slo exc																	2			
Pse cor																		1	1	
Iry cor																		1		2
Qua par																			1	
Hev gui																			2	
Hym suc																				1
Ing gra																				1
Scl mic																				1
sum	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19
	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20

Source: Authors.

(3) Ocotea cernua (Oco cer) - Sixty-three neighbour species were found along the 20 nearest neighbours of 19 focal trees belonging of this species (Fig. 7). The species with higher relative frequencies were “Pro heb”, Pouteria minima T.D.Penn. (Pou min) and Pouteria laurifolia (Gomes) Radlk (Pou lau), with 13, 9 and 6 percent, respectively, with other 60 species presenting less than five percent of relative frequency.

The mean richness at each focal tree is 14 species and the mean proportion of conspecifics 5 percent, with SD equal to 0.90 individuals. At shorter distances, within the first four nearest, the relative frequency of species is in general below 15 percent, with no tendency of association among species and the focal one, even for conspecific trees; excepting Minquartia guianensis Aubl. (Min gui) with around 26 percent of occurrence at the first k-nearest (k1).

At the intermediate k-nearest neighbour (6 to 15), which corresponds to 10 meters on average, only “Pro heb” seem to have some tendency to be associated with focal specie with 26 percent of the occurrences at these positions, on average (Fig. 7). In general, the number of species, measured within each k-nearest neighbour tends to increase with the distance, with increases of 30 percent from the first to the second k-nearest neighbour, and then oscilating in a very low or even negative range, with species showing low relative frequencies. (Fig. 5C). This indicates, again, the occurrence by chance for most neighbour species at specific kth nearest neighbour position.

(4) Protium hebetatum (Pro heb) - Sixty-seven neighbour species were found within the 20 nearest neighbours over all 64 focal trees. The richness around each focal tree was equal to 12 species, and the mean conspecific proportion equal to 22 percent with the highest variability on the number of conspecifics at each focal tree, which presented SD equal to 2.3 individuals.

Protium hebetatum (Pro heb), Pouteria minima (Pou min) and Psidium araca Raddi (Psi ara), at this order, presented the highest values of relative frequency when we added up all occurrences along the 20 nearest neighbours investigated, that represented 22, 12 and 8 percent, respectively (Fig. 8). Yet, the conspecific trees of “Pro heb” are concentrated mainly at the first four k-nearest with the highest frequency at the first one (67%). After these four k-nearest neighbour, the frequency decreased to 15 percent on average, but is still the highest, when compared with other species. “Pou min” and “Psi ara” were found at all 20ks-nearest, but with low values of frequency when compared with “Pro heb”, concentrating at shorter distances. Overall, there is no strong evidence of pattern in the distribution of the other neighbour species, except for “Oco cer”, Pouteria laurifolia (Pou lau), at the intermediate position and Minquartia guianensis (Min gui) at the latest k-nearest position (Fig. 8).

The number of species registered within each k-nearest neighbour at each focal tree presented a positive linear relationship with the distances from the focal trees (Fig.6d). This positive relation is then followed by the decrease in the conspecific trees with new species occurring with very low frequency along the 64 focal trees of “Pro heb” (Fig. 5D).

Fig. 8. Frequency of occurrence of neighbour species of Protium hebetatum along the 20 nearest neighbours.

K-Nearest neighbour of *Protium hebetatum*																				
neighbour species	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20
Pou lau	1	5	8	9	11	1	4	2	5	4	5	4	3		3	3	1	3	2	3
Pou myr	1		1	4		1				1	1	2	1	1	1	1	1			1
Pra coc	1												1	1						
Pro hep	2	1			1				2	1	1		1	2		2				
Pse mun	2					1				1	2	2				1			1	
Pou min	4	6	15	15	17	8	3	10	8	13	8	8	4	9	6	6	5	4	6	3
Pou ven	5	3	1		1	1	4	1	1		3	1	2	2		1	1	2		1
Psi ara	5	15	7	6	4	9	7	6	7	3	9	7	2	3	3	5	5	1	4	2
Pro heb	43	29	23	21	7	14	5	15	15	12	7	14	9	15	13	10	6	6	11	6
Scl hel		1	1	2	5	7	7	4	5	4	2	1	1			3	1	1	3	2
Pse cor		1	1				1					1	1					2		
Pyt ola		1		1	2		2	1		2		1		1	1					1
Qua alb		2	2	2	1	2	2	2	1	2	3	2	2	1	1	3	2	2	2	
Pou cai			1		1	1	1			1				1			1	1	1	1
Pou ret			1					1			1	1	3		1				1	
Rin rac			1					1			1				2		1			2
Rin gui			2		1				1		1			1				1		
Pla duc				1	1		1					1			2					1
Pip sua				1	2	3	7	1	1		1	1	1		1					
Qua par				2				1				1				1			2	
Par orm					1			2	2											
Slo exc					2	2	2	2	2	4	2		4	2				3	3	2
Scl mic					7	4	7	3	1	1	5	1		3	2	1	2	3	1	3
Swa rec						1	1	1				2	2		2					
Ste pru						1	1	3	2	2			2			1	2	1	1	1
Swa tes						1														
Pou amb						2	1	1	1	1	1	1								1
Pal cor						2	1		2	1		1		1	1	1			2	
Pau mac						3	4	2	1	1		1	1	1		1	1			1
Oco cer							1	2		4	7	6	7	4	7	3	4	3	2	3
Swa sch							1		3	1			1	1				1		1
Par mul							1								1		1			
Oco sp.								1			2			1						
Str sp.								2	1		2	1	3	1		1	1			
Par nit									1	2										
Sim ced									1			1						1		
Pou obl									1											1
Nau cal										1		1	2	3	7	4	2			2
Par pen										1			1	1			1			1
Str gui										1							1		1	
Pla ins												1	1							1
Orm gro												1	2							
Tac cf.													1	1	1	1	3	2		2
Mou cal													1	1	1	2	4	1	1	4
Nee opp													1	3			1		1	1
Tra bur													1		1		2	2	1	
Mou ang													1				1			
Min gui													2	2	4	5	8	8	7	5
Mic sip														1	1	2		2	3	2
Qua acu														1	1		1			
Tal cf.															1	2	1	1		1
Mic guy																1		1		
Vir mic																1				
Toc gui																2	1			
Tab ser																	1	1	1	
Mic tru																	1	4		1
Man bid																	1		3	2
Tou gui																		1	1	
Uno duc																		1		2
Sip sp.																		1		
Tri sep																		2		
Van gui																		2		
Tri mic																			1	2
Lic obl																			1	
sim ama																			1	
Pou per																				1
The sub																				1
sum	64	64	64	64	64	64	64	64	64	64	64	64	64	64	64	64	64	64	64	64
	k1	k2	k3	k4	k5	k6	k7	k8	k9	k10	k11	k12	k13	k14	k15	k16	k17	k18	k19	k20

Source: Authors.

DISCUSSION

In our study, the focal species analyzed presented patterns tending to aggregation (Bro spp and Esc cor), and to a regular one (Oco cer), although non-significant, (Fig. 2). However, it could be attributed more to the spatial pattern rather than the abundance, the slight differences in the proprotion of conspecifics observed for focal species over all k-nearest neighbours, where the tendencies of a more aggregated pattern might have contributed for more conspecific encounters. The focal species “Bro spp” has the same number of individuals as “Oco cer”, but presented higher conspecific value with clearer tendency of spatial aggregation, which could be due to the configuration of the trees in the field.

In a study conducted by Pottker *et al.* (2016) with the species *Ocotea odorifera* (Vell.) Rohwer, the aggregated spatial pattern was observed, which, according to the authors, occurs because of the irregular and discontinuous dispersion of the species, with the formation of dense stands in certain areas being natural, being rare and non-existent elsewhere. When species exhibit aggregated patterns, it is believed that intraspecific encounters may be much more frequent than interspecific ones, which can be explained, in most cases, by the species dispersion syndrome being mainly zoochoric (CONDÉ *et al.*, 2016; ROCKWELL *et al.*, 2017; VARELLA *et al.*, 2018). Alves *et al.* (2019) obtained similar results for the species *Bertholletia excelsa* Bonpl. (Family Lecythidaceae) in the state of Amazonas and in a study conducted by Pacheco *et al.* (2021) on the plant diversity associated with productive Brazil nut trees (*B. excelsa* Bonpl.) in 6 localities in Amazonas, the authors observed significant floristic differences between the areas that is due to the location in rivers of different structures and concluded that the floristic composition associated with the selected species did not vary significantly when considering the association by classes of fruit production.

All focal species but “Oco cer” had their conspecifics as one of the most frequent species measured along the 20 nearest neighbours investigated. Regardless of the value of occurrence of conspecifics for all four focal species, the conspecifics have been mainly concentrated near the focal trees, which could be a result of biological process, such as dispersal at short distances, leading to more intra-specific interactions.

The focal trees of “Esc cor” and “Pro heb” seem to be currently experiencing more intra-specific relationships at shorter distances ranging from 2 to 5 meters due to the more conspecific encounters, (Fig. 6 and 8). However, the above cited species were also found in the whole range of the 20 nearest neighbours investigated, still with high frequencies values, showing great plasticity in the occurrence of conspecifics at larger distances. This could be explained by the fact that “Esc cor” is a canopy species whose seeds are dispersed by large birds and bats, rodents and primates, where the secondary dispersal seems to contribute to this behaviour (HEUERTZ, 2020).

Leal *et al.* (2021) evaluated whether the presence of bamboo affects the spatial structure of native forest species in a tropical forest in Acre, finding that the studied area does not suffer interference in the spatial pattern of native forest species, because the occurrence of the bamboo can be related to the existence of the species. The fact that the focal species “Pro heb” and “Esc cor” were found in the whole range of the neighbours investigated with relative high frequency might be the result of early weaker intra-specific interactions due to larger distances among conspecifics, favouring the actual occurrence of a higher number of individuals of these two species.

The similar number of neighbour species registered for the focal species “Esc cor”, “Oco cer” and “Pro heb”, around 64 species, highlights the high local diversity at the study area. “Oco cer” presents the highest richness, also being the species with the lowest proportion of conspecific neighbours. The fact that two focal species with the same number of individuals (Bros spp and Oco cer) have a different number of species around them (63 and 47 species, respectively) demonstrates that focal trees are affected differently by their neighbour species, due to the biological and/or environmental differences at the study area. These differences lead to the necessity of different management strategies aiming to keep the ecosystem’s functionality. So, it is expected, in general, that a high species-richness of neighbours might lead to complementary resource use, which could increase the amount of resources consumed by the neighbours, and thus decrease the amount left available to the target species. Target performance would therefore decrease as the species-richness of the neighbours community increases (Milbau *et al.*, 2007). Further studies could ratify this assumption with the use of repeated measures through time and small diameter classes.

In a more detailed view of the distribution of neighbour species around focal trees, within each kth-nearest neighbour as a function of the distance, we found that the number of species increased with distance, but with different shapes of the curves (Fig. 5), again highlighting the influence of the high diversity and the rare species, which probably contributed for the values of richness observed. This could explain the positive linear tendency of richness and distances for all species, specially for “Pro heb”, which is the focal species with the highest number of neighbouring rare species followed by “Esc cor”, “Oco cer” and “Bros spp” at this order. Due to the occurrence of a large percentage of rare species at the study area, distributed along the focal species, it is necessary to care about the areas affected by logging in order to prevent local extinctions of rare species.

Overall, some species appeared more frequently at a specific k-nearest position, revealing a taxonomic pattern around focal trees. The focal trees of “Bro spp” and “Esc cor” had trees of “Esc cor” and Eschweilera collina (Esc col), at this order, as their main neighbours, where, for “Bro spp”, these occurrences happened mainly at the intermediate distances, about 8 meters, and for “Esc cor” over all range of the 20 nearest neighbours. Despite the low frequency of the neighbour species of “Oco cer”, the frequency distribution along the 20 nearest neighbours, suggests that “Pro heb” and Pouteria minima (Pou min), at intermediate distances (up to 8m), and Minquartia guianensis (Min gui) at short ones (2 m) are the species with a pattern in their occurrence around the focal trees of “Oco cer”. Protium hebetatum (Pro heb) had trees of “Pro heb” and “Pou min” as its main neighbours, with concentration of “Pro heb” at shorter distances and “Pou min” at intermediate distances.

CONCLUSION

Our findings provide important contributions for the development of tropical forest models aiming to study the ecology and dynamics of “terra firme” tropical rainforests. Our hypothesis of taxonomic pattern in the neighbour species around focal species, based on their frequency distribution, was confirmed with different co-occurrence strength for each focal species, which depended on the position of the neighbour investigated along the 20 nearest neighbours.

The conspecific trees were found occurring in a low frequency when all 20 k-nearest neighbours were considered, but with expressive values, mainly at shorter distances for all focal species, when we looked into each k-nearest investigated, excepting “Ocotea cernua”, suggesting that focal species might be currently experiencing more intra-specific interactions. Only three heterospecific neighbours had higher values of frequency around our focal trees, such as Pouteria minima, Minquartia guianensis and Eschweilera collina.

The spatial pattern of focal species seems to be more important than the abundance for the conspecific encounters, mainly for species with lower number of individuals, like Brosimum spp. and Ocotea cernua, highlighting the importance of spatial structure in the ecological interactions.

The rarity of the majority of species at the study area contributed for the high richness measured along the focal trees, calling our attention to the effects of the forest management on the rare species and other associated species, and for the necessity of further studies that contribute for the understanding of such complex interactions in order to better protect and manage highly diverse tropical rainforests.

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