KÁTIA EMÍDIO DA SILVA

FLORÍSTICA E ESTRUTURA ESPACIAL: 15 HECTARES DE PARCELAS PERMANENTES NA FLORESTA DENSA DE TERRA FIRME NA AMAZÔNIA CENTRAL

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ciência Florestal, para obtenção do título de *Doctor Scientiae*.

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Prof. Dr. Carlos Antônio A. S. Ribeiro
(Coorientador)

Prof. Dr. Nerilson Terra Santos
(Coorientador)

Dr.Celso Paulo Azevedo

Prof. Dr. José Marinaldo Gleriani

Prof. Dr. Sebastião Venâncio Martins
(Orientador)

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RESUMO

Silva, Kátia Emídio da, DSc., Universidade Federal de Viçosa, setembro de 2010. **Florística e estrutura espacial: 15 hectares de parcelas permanentes na Floresta Densa de Terra Firme na Amazônia Central.** Orientador: Sebastião Venâncio Martins. Coorientadores: Carlos Antônio Alvares S. Ribeiro e Nerilson Terra Santos.

Entender os mecanismos responsáveis pela manutenção da alta diversidade biológica nos trópicos, resultante das interações das espécies com o ambiente natural e entre si, é fundamental para minimizar a escassez de informações no setor florestal, e contribuir para a restauração, conservação e uso múltiplo sustentável das florestas. Esta tese objetivou descrever e analisar a composição florística e estrutura de 15 hectares de uma floresta densa de terra firme, localizada no campo experimental da Embrapa Amazônia Ocidental, Manaus, AM, Brasil. Dois principais tópicos foram desenvolvidos: i. Composição florística, e similaridade comparada a outras nove áreas inventariadas no estado do Amazonas; ii. Estrutura horizontal, incluindo análises espaciais explícitas da comunidade arbórea empregando a função *K* de Ripley, e, análises de vizinhança de quatro espécies arbóreas de interesse comercial no estado do Amazonas. Foram identificados 8771 indivíduos, distribuídos em 264 espécies e 53 famílias. As famílias com maior riqueza de espécies foram: Fabaceae-Faboideae (22sps.), Fabaceae-Mimosoideae (22), Sapotaceae (22) e Lecythidaceae (15). A família Burseraceae, com a menor diversidade de espécies (07), dentre as 10 primeiras famílias, é a que possui maior número de indivíduos registrados. As dez espécies mais abundantes, as quais possuem 40% do número de indivíduos indentificados foram *Protium hebetatum* (1037 individuals), *Eschweilera coriacea* (471), *Licania oblongifolia* (310), *Pouteria minima* (293), *Ocotea cernua* (258), *Scleronema micranthum* (197), *Eschweilera collina* (176), *Licania apelata* (172), *Naucleopsis caloneura* (170) e *Psidium araca* (152). Há uma grande ocorrência de espécies raras na área, com aproximadamente 36% ocorrendo com apenas um (01) indivíduo por hectare, bem como de espécies com baixa abundância e de ocorrência restrita a algumas parcelas, especialmente aquelas ocorrendo nas menores classes de IVI. A estrutura diamétrica é similar à encontrada em outros estudos, apresentando distribuição dos diâmetros na forma de J-invertido, com 80% dos indivíduos concentrados nas classes de DAP de 10-30 cm. Observou-se alta similaridade florística (> 60%) entre as parcelas da área de estudo, e de modo geral, a comparação com outras áreas no estado do Amazonas observou-se que quanto maior a distância geográfica, menor a similaridade florística entre as mesmas. As variáveis de solo (fertilidade, umidade e textura) e topografia exerceram forte influencia no arranjo espacial da comunidade de espécies arbóreas, observando-se dependência espacial entre as espécies e as variáveis ambientais. Entretanto, os padrões espaciais somente foram visualizados em parcelas com tamanho mínimo de 10.000 m^2, sendo mais evidente a partir de 14.000 m^2, sugerindo que a heterogeneidade ambiental e área mínima de estudo devem ser consideradas nos estudos de dinâmica das florestas de terra firme na Amazônia. Os resultados da análise das relações de vizinhança das quatro espécies arbóreas de interesse comercial no estado do Amazonas, *Brosimum* spp., *Eschweilera coriacea*, *Ocotea cernua* e *Protium hebetatum*, demonstraram grande ocorrência de vizinhos conspecíficos das espécies focais, principalmente a curtas distancias, mostrando que as espécies focais estão mais sob interações intra-específicas, apresentando um padrão taxonômico associado às espécies focais. A estrutura espacial, mais do que a abundância das espécies focais *Brosimum* spp. e *Ocotea cernua* contribuiu para os encontros de conspecíficos nas duas espécies, evidenciando a importância da estrutura espacial nas interações ecológicas. Espécies raras ocorreram associadas às espécies focais, principalmente a *Protium hebetatum*, ressaltando mais uma vez a importância da definição de estratégias de manejo que evitem extinções locais de espécies raras. Esta tese contribuiu para o conhecimento sobre a composição florística e estrutura espacial das espécies arbóreas da floresta densa de terra firme na Amazônia, subsidiando, assim, as ações de manejo, conservação e restauração das florestas tropicais.

ABSTRACT

Silva, Kátia Emídio da, DSc., Universidade Federal de Viçosa, September, 2010. **Floristic and spatial structure: 15 hectares of permanent plots in a Terra Firme Dense Forest in Central Amazonia.** Advisor: Sebastião Venâncio Martins. Coadvisors: Carlos Antônio Alvares S. Ribeiro and Nerilson Terra Santos.

In order to understand the mechanisms responsible for maintaining the high biological diversity in the tropics, resulting from the interactions between the species and the natural environment and among each other, it is essential to minimize the shortage of information in the forestry sector, and to contribute to the restoration, conservation, and sustainable multiple use of the forests. This thesis aimed to describe and analyze the floristic composition and structure of 15 hectares of a dense terra firme forest, located in the experimental site of Embrapa Western Amazonia, Manaus, Amazonas, Brazil. Two main topics were developed: i. Floristic composition and similarity compared to nine other areas inventoried in the state of Amazonas; ii. Horizontal structure, including explicit spatial analyses of the tree community, using the Ripley *K* function, and neighbor analyses of four tree species of commercial interest in the state of Amazonas. A total of 8771 individuals were identified, representing 264 species and 53 families. The families with the highest species richness were: Fabaceae-Faboideae (22 species), Fabaceae-Mimosoideae (22), Sapotaceae (22), and Lecythidaceae (15). The family Burseraceae, with the lowest species diversity (7), had the highest number of individuals. The ten most abundant species, which comprised 40% of the number of individuals identified, were *Protium hebetatum* (1037 individuals), *Eschweilera coriacea* (471), *Licania oblongifolia* (310), *Pouteria minima* (293), *Ocotea cernua* (258), *Scleronema micranthum* (197), *Eschweilera collina* (176), *Licania apelata* (172), *Naucleopsis caloneura* (170), and *Psidium araca* (152). There was a high incidence of rare species in the area, with approximately 36% having only 1 individual per hectare; as well as of species with low abundance and occurrence that were limited to some parcels, especially those occurring in the smallest Importance Value Index- IVI classes. The structure of trunk diameters is similar to that found in other studies, with the distribution of diameters having an inverted-J-shaped profile, and 80% of the individuals concentrated in the 10-30 cm DBH classes. The floristic similarity was high (> 60%) among the parcels of the study area, and in general, considering all the plots analyzed, the greater the geographical distance, the lower was the floristic similarity among them. The variables of soil (fertility, moisture, and texture) and topography exerted a strong influence on the spatial arrangement of the tree community, and a spatial dependence was observed between the species and the environmental variables. However, the spatial patterns were only perceived in parcels with a minimum size of 10,000 m^2, and were most evident at parcel sizes above 14,000 m^2, suggesting that environmental heterogeneity and minimum size of the study area should be taken into account in studies of the dynamics of the terra firme forest in Amazonia. The results of the analysis of the neighbor relationships of the four tree species of commercial interest in the state of Amazonas, *Brosimum* spp., *Eschweilera coriacea*, *Ocotea cernua*, and *Protium hebetatum*, demonstrated a high occurrence of conspecific neighbors of the focal species, principally at short distances, showing that the focal species are more subject to intraspecific interactions, showing a taxonomic pattern associated with the focal species. The spatial structure, more than the abundance of the focal species *Brosimum* spp. and *Ocotea cernua,* contributed to the encounters of conspecifics of the two species, evidencing the importance of spatial structure for ecological interactions. Rare species occurred associated with the focal species, principally with *Protium hebetatum*, once more emphasizing the importance of defining management strategies to prevent local extinctions of rare species. This thesis contributed to knowledge of the floristic composition and spatial structure of the tree species of the terra firme dense forest in Amazonia, thus supporting actions for the management, conservation, and restoration of tropical forests.

INTRODUÇÃO GERAL

A floresta tropical é um dos ambientes naturais mais complexos da Terra, sendo sua composição e estrutura determinadas, principalmente, pelo clima, solo, estado sucessional da vegetação e a história natural de cada sítio (Lamprecht 1990; Whitmore 1990). A floresta amazônica é o maior reservatório natural da diversidade vegetal do planeta, apresentando múltiplas interrelações entre seus componentes bióticos e abióticos, os quais formam um conjunto de ecossistemas altamente complexos e de equilíbrio ecológico extremamente frágil (Oliveira e Amaral 2004). Os desmatamentos de extensas áreas de cobertura vegetal na Amazônia, têm provocado perdas imensuráveis de recursos genéticos (Nobre *et al.* 1991; Houghton *et al.* 2000), onde espécies raras têm sido dizimadas e diversos habitats modificados pelas ações antrópicas, afetando a resistência e resiliência dos ecossistemas. Neste contexto, quanto maior o conhecimento da riqueza biológica amazônica, mais eficientes serão as ações de manejo, conservação e restauração deste bioma.

A região amazônica ocupa aproximadamente 60% do território brasileiro, sendo constituída por diferentes tipos de vegetação. A floresta densa de terra firme é a tipologia vegetal mais representativa dessa região, caracterizada pela elevada riqueza e diversidade de espécies (Prance *et al.* 1976; Lima Filho *et al.* 2001). Ocorre nas partes mais altas do relevo, dividindo-se em florestas ombrófilas densas e abertas. As florestas ombrófilas densas, objeto deste trabalho, são florestas não aluviais, Veloso *et al.*(1991) e caracterizam-se pela presença de fanerófitos, além de lianas lenhosas e epífitas em abundância. O dossel é geralmente composto por indivíduos adultos de 25 a 35 metros de altura, com emergentes de até 55 metros. Sua principal característica ecológica é a presença de ambientes ombrófilos com elevadas temperaturas (médias de 25ºC) e alta precipitação bem distribuída ao longo do ano. Apresentam os Latossolos como solos dominantes, sendo os mesmos de caráter distrófico. Diversas áreas são formadas por mosaicos de habitats, com diferentes conjuntos de espécies vegetais ocorrendo em áreas adjacentes sobre diferentes substratos, onde se observa, de modo geral, que a distribuição das espécies arbóreas tropicais pode se dar devido a preferências de habitats e/ou à variações na história evolutiva das mesmas (Pitman *et al.* 2001).

A influência de variáveis ambientais na composição florística e estrutura de comunidades vegetais tem sido objeto de vários estudos, onde a estrutura, dinâmica e distribuição das espécies são relacionadas às características dos ambientes, as quais determinam o sucesso do estabelecimento e exclusão de determinadas espécies (Campos e Souza 2002). A dinâmica e estrutura das florestas têm sido relatadas de variar através da bacia Amazônica em um gradiente leste-oeste, seguindo um padrão que coincide com variações na fertilidade do solo e geologia (Quesada *et al.* 2009). Descrever estes padrões de variações, utilizando grandes conjuntos de dados, que contemplem os diferentes gradientes ambientais amazônicos, é de suma importância para o entendimento dos mecanismos que determinam a distribuição das espécies, contribuindo, assim, para a definição de estratégias de manejo e conservação das florestas em face dos desmatamentos e das mudanças climáticas (Coronado *et al.* 2009).

Estudos desenvolvidos na Amazônia têm demonstrado que os ambientes florestais de terra firme apresentam alta diversidade, representada por poucos indivíduos de cada espécie (Prance *et al.* 1976; Lima Filho *et al.* 2001) e alta dissimilaridade florística entre parcelas adjacentes (Ferreira e Prance 1998). Oliveira e Amaral (2004), em um estudo desenvolvido em 1 ha de floresta de terra firme (vertente), na Amazônia Central, Manaus, Amazonas, Brasil, com nível de inclusão de 10 cm de DAP, encontraram alta diversidade florística, com índice de Shannon de 5,01, um dois maiores para a região, uma vez que este índice normalmente varia de 3,83 a 5,85 para esta tipologia vegetal. Os autores citam que a heterogeneidade edáfica e topográfica da área, as taxas de recrutamento de novos indivíduos e de espécies "localmente raras" podem ter contribuído para as altas dissimilaridades e diversidade florística documentadas no estudo.

Indivíduos de várias espécies e tamanhos podem estar associados entre si, apresentando estruturas que resultam de dinâmicas florestais complexas, tais como dispersão, crescimento, mortalidade, uso da terra e clima, com um grande número de potenciais interações inter e intra-específicas (Legendre e Fortin 1998; Comas e Mateu 2007). Neste contexto, identificar a estrutura espacial das espécies e/ou comunidades vegetais é de suma importância para o entendimento dos processos ecológicos que atuam estruturando a distribuição das plantas na natureza, os quais contribuem para a manutenção da alta diversidade biológica (Illian *et al.* 2008). O crescente interesse em estudar padrões espaciais em comunidades vegetais baseia-se no pressuposto de que para entendê-las deve-se descrever e quantificar características espaciais e temporais e relacioná-las a processos subjacentes como crescimento, competição, reprodução e mortalidade. Em geral, o que se procura em uma primeira abordagem é responder à pergunta relativa ao padrão exibido pela(s) espécie(s) ou comunidade em estudo, o qual pode ser completamente aleatório, agrupado ou regular e depois avaliar qual a importância ecológica desse padrão (Pereira *et al.* 2006). Assim, conhecer o padrão espacial de espécies-chave é vital para entender como dada espécie usa os recursos disponíveis, de que forma este recurso é importante, e sua função no sucesso do estabelecimento e reprodução da espécie (Condit *et al.* 2000). Entretanto, o nível de organização espacial das árvores no ambiente depende de diversos processos ecológicos e características do próprio ambiente, de modo que uma melhor compreensão destes processos fornece subsídios para o manejo e conservação das formações vegetais (Capretz, 2004).

Dentre os diversos métodos disponíveis para análise do padrão espacial (Fortin e Dale, 2005; Silva *et al.*, 2009), destaca-se a função *K* de Ripley, que é uma estatística descritiva do padrão espacial, sendo uma das ferramentas mais apropriadas para análises do padrão espacial de florestas, sobretudo quando os dados são apresentados sob a forma de mapas de vegetação, sendo conhecidas as coordenadas de suas árvores (Capretz, 2004). As principais vantagens do método são ele permitir a detecção do padrão espacial em diferentes escalas de distâncias simultaneamente, permitindo que o padrão espacial observado seja comparado a modelos conhecidos e investigar o padrão segundo altura, diâmetro e identificar o nível de independência espacial entre grupos de quaisquer árvores, como espécies diferentes ou árvores de diferentes tamanhos.

A função *K* de Ripley computa todas as distâncias entre todas as árvores em um mapa para investigar o seu padrão. De modo simplificado, o procedimento consiste em um círculo de raio S centrado em cada árvore, onde o número de vizinhos presentes dentro da área deste círculo é contado (Haase, 1995). Variando o raio S é possível detectar o padrão espacial em diferentes escalas. Esta flexibilidade em relação à escala de distâncias é o que difere substancialmente a função *K* de outras ferramentas mais utilizadas.

É grande a demanda por estudos ecológicos que possam embasar trabalhos de restauração, manejo e conservação da biodiversidade, e apoio à legislação ambiental, onde o conhecimento sobre a composição florística e estrutura da flora são essenciais para o atendimento desta demanda. Esta tese objetivou contribuir com o atendimento desta demanda, sendo estruturada na forma de 4 artigos, onde a partir de um conjunto de dados de 15 parcelas de 1-ha, analisou-se a composição florística e estrutura horizontal, incluindo análises espaciais explícitas dos dados. A área de estudo está localizada no Campo Experimental da Embrapa Amazônia Ocidental, a qual está inserida no âmbito do projeto "Manejo Florestal na Amazônia", coordenado pela Embrapa, com plano de ação-PA "Caracterização da vegetação e solo para manejo florestal na Amazônia" e "Atividade" intitulada" Influência das variáveis ambientais na distribuição de espécies arbóreas em floresta densa na Amazônia Ocidental".

A tese foi estruturada na forma de artigos, sendo os mesmos organizados da seguinte forma:

(1) Artigo 1. **Floristic composition and similarity of 15 hectares plots of a terra firme dense forest in Central Amazon, State of Amazonas, Brazil.**

1.1. Objetivos: descrever e analisar a composição florística de 15 ha de parcelas permanentes localizadas no Campo experimental da Embrapa Amazônia Ocidental, Manaus,AM, com nível de inclusão de 10 cm DAP, e comparar estas parcelas a outros nove inventários realizados no estado do Amazonas sob a hipótese de que quanto maior a distância geográfica entre as parcelas, menor a similaridade florística entre as mesmas;

(2) Artigo 2. **Estrutura do componente arboreo em 15 ha de parcelas permanentes de floresta densa de terra firme na Amazônia Central**

2.1. Objetivo: analisar a estrutura horizontal de 15 hectares de floresta densa de terra firme na Amazônia Central, Manaus, Amazonas, Brasil, a fim de contribuir para ampliar os conhecimentos sobre a organização das espécies na comunidade, auxiliando, assim, nas ações de restauração, conservação e manejo florestal na Amazônia;

(3) Artigo 3. **Spatial structure of tree species community in a "terra firme" Amazon forest near Manaus, Brazil**

3.1. Objetivo: avaliar a influência das variáveis ambientais na distribuição das espécies, sob a hipótese de que a distribuição das espécies arbóreas se dá de maneira diferenciada em relação à heterogeneidade ambiental da área de estudo, apresentando dependência espacial em relação a variáveis de solos, e que a deteccção desta estrutura espacial é dependente do tamanho da unidade de amostra analisada;

(4) Artigo 4. **Neighbour`s Identity of Commercial Tree Species in a Tropical Rainforest Near Manaus, Brazil.**

4.1. Objetivo: analisar as relações de vizinhança de quatro espécies arbóreas de interesse comercial no estado do Amazonas (*Brosimum* spp., *Eschweilera coriacea*, *Ocotea cernua* e *Protium hebetatum*), sob a hipótese de que há um padrão taxonômico na ocorrência dos 20 vizinhos mais próximos destas espécies focais, caracterizado principalmente pela ocorrência de vizinhos conspecíficos, onde o conhecimento deste padrão contribui para o manejo e manutenção da estrutura dos ecossistemas e das interações entre as espécies.

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Artigo 1

Floristic composition and similarity of 15 hectares plots of a terra firme dense forest in Central Amazon, state of Amazonas, Brazil.

Abstract: Investigating the high diversity in tropical forests brings up relevant contributions to the understanding of mechanisms that allow and maintain such diversity. In the present study we described the species composition and diversity of 15 1-ha plots in the Amazonian “terra firme” dense forest in Brazil, and compared the floristic similarity of this plots with nine others 1ha size, hypothesizing that the smaller the geographic distance the more similar they are. The 15 plots were randomly selected in 2005 from permanent plots at the Embrapa Experimental site, State of Amazonas. The floristic composition and diversity were analysed by using species/area curve and Shannon’s index, and the similarity analysis was done by applying the Sorensen’s index for similarity and Unweighted pair-group average (UPGMA) as clustering method. Mantel test was performed to study if the differences in species composition between sites could be explained by the geographic distance among them. Overall, we identified 8,771 individuals distributed into 264 species and 53 families. The majority of species were concentrated in few families and few species have large number of individuals. The families with more species richness were: Fabaceae-Faboideae (22sps.), Fabaceae-Mimosoideae (22), Sapotaceae (22), Lecythidaceae (15) and Lauraceae (13), but Burseraceae was the one with more number of individuals, with 11.8% of the total. The ten most abundant species were: *Protium hebetatum* Daly (1037 individuals), *Eschweilera coriacea* (DC.) S.A. Mori (471), *Licania oblongifolia* Standl. (310), *Pouteria minima* T.D.Penn. (293), *Ocotea cernua* (Nees) Mez s.l. (258), *Scleronema micranthum* Ducke (197), *Eschweilera collina* Eyma (176), *Licania apelata* (E.Mey.) Fritsch (172), *Naucleopsis caloneura* (Huber) Ducke (170) and *Psidium araca* Raddi (152), which represented 36.5% of the total number of individuals. Approximately 49% of species had up to ten individuals and 13% appeared only once at the whole sampled plots, showing a large occurrence of rare species. Our study area is a high tree diversity forest with Shannon's diversity index of 4.49, and the species/area curve showed that the diversity was fully represented in the sampled plots. The dendrogram showed two groups of plots with low similarity between them (less than 25%) and the closer the plots the more similar in species composition they were (Mantel R=0.3627, $p< 0.01$). The 15 plots in our study area shared more than 60% of their species composition and represent the group of plots that have the smallest pairs of distance between each other. Overall, our results highlight the high local and regional heterogeneity of environments in terra firme forests and the high occurrence of rare species, which should be considered in the management and conservation programs in the Amazon rainforest in order to maintain its structure over time.

Key words: Central Amazonian, tree species, floristic similarity, diversity, terra firme, upland dense forest.

Brazil has approximately one third of the remaining world's tropical forests being the most important biodiversity areas (PAS 2008), and has the most complex natural environments in the Earth. In the Amazon region several landscapes are formed by the mosaic of areas with different occurrences of a group of plant species in different environments (Pitman *et al.* 2001), where the differences in tree species distribution can be attributed to environmental differences and/or species' habitat preferences. In this context, an increased interest has aroused among scientists and society around the world, specially related to biodiversity loss due to deforestation, regional and global climate changes, and how species and communities behave under such changes (Houghton *et al*. 2000).

The Brazilian Amazon region occupy about 60% of Brazil's territory where approximately 65% of this region is classified as "terra firme" forests, which is characterized by high diversity with tree species having low number of individuals and high floristic dissimilarity among adjacent plots (Prance *et al.* 1976, Lima Filho *et al*. 2001). The state of

Amazonas has 1.5 million square kilometers in extension and large heterogeneity in natural ecosystems. Oliveira and Amaral (2004), studying a terra firme forest near Manaus, Amazon State, found in 1-ha plot with minimum diameter of 10 cm, 239 species and Shannon's diversity index of 5.01, revealing a high diversity in such forests.

Edaphic and climate factors, such as precipitation and drought regimes are regarded as the most important factors responsible for high plant diversity in Amazon, resulting in high dissimilarity between plant communities, which in some cases has also been associated to topographic variations (Gentry 1988, Tuomisto *et al.*1995, Coronado *et al.* 2009). Then, it has been documented that, even in closer plots, low similarity in terra firme forests can be observed (Ferreira and Prance 1998). Other authors associated the increased species richness to the natural dynamics of mortality and recruitment (Phillips *et al.* 1994).

There is an increased demand for ecological studies, specially about the floristic composition and structure of tropical rainforests, which can base actions for restoration, conservation and management of natural resources, that can prevent the extinction of rare and low- abundant species and could contribute to the maintenance of the high diversity of species and habitat in the several areas around this vast and complex Amazon region.

The aim of this paper is to describe and analyse the floristic composition and diversity in the large survey of 15 1-ha plots in terra firme tropical rainforest at the Embrapa Experimental site, situated in Western Amazon, Manaus, state of Amazonas, Brazil and compare the floristic composition of these 15 plots with other nine plots spread over the Amazonas State, hypothesizing that higher similarities are observed in geographically closer plots.

MATERIALS AND METHODS

Study site: The study area is located in a terra firme dense forest of Central Amazon, at the Embrapa Experimental site, Western Amazon, Manaus, state of Amazonas, Brazil, measuring 15-ha. The study area was randomly selected from 400 permanent 1-ha plots, belonging to the forest management project, which is being developed at Amazon region in Brazil.

The climate is tropical, type “Am” (Koppen classification), with a mean annual rainfall ranging 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 1999), but with a degree of local variation in topographic and edaphic conditions. 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 (Regis 1993).

Field sampling: From the area of 400 1-ha sized plots, 15 plots were randomly chosen in order to investigate the diversity, floristic composition, and similarity among nine other terra firme forests in the same Amazonas state. The 15 plots measure 100 x100m and had their topographic position recorded as top, slope and base. All trees ≥ 10 cm dbh (diameter at breast height) were tagged in 2005 and botanically classified according to species level. The botanical material was identified by specialist at the herbarium of the Instituto Nacional de Pesquisas da Amazonia, Manaus (INPA) and by experts and specialized literature (Ribeiro *et al.* 1999). The names were checked with the database from the Missouri Botanical Garden.

For the floristic similarity analysis, 24 plots were used (Table 1), consisting of 15 plots from our present study, called “EMB” plus the plot number and nine other plots coming from different surveys at the Amazonas State, located in the same forest typology, i.e., terra firme tropical rainforests, measuring . All plots are1ha sized (100 x 100 m) and had trees with dbh ≥ 10 cm inventoried. Of the nine plots used, all are positioned at the top position (plateaus) according to topography, excepting “ZF2B and ZF2V”, located in the base and slope position, respectively. The list of species from the nine plots was obtained from published and unpublished surveys done by INPA’s researchers and others. The coordinates of the all plots were defined by their centroid.

TABLE 1

*Information source for inventories in 100*m *x 100*m *plots with a minimum of 10 cm DAP, carried out in state of Amazonas, Brazil.*

Site	Lat.	Long.	Source
EEST	-2º 35’ 53.77”	-60º 02’ 52.69”	(Matos 2006)
IPIR	-2º 58’ 09.8”	-59º 54’ 18.0”	(Matos 2006)
ITAP	-2° 33' 30"	-58° 23'	(Amaral *et al.* 2000)
JURUA	-6º 36’	-67º 19’ 30”	Not published-INPA/CPBO[*]
ZFkm14	-2º 35’ 32,2”	-60º 06’ 40”	(Sposito *et al.* 2007)
ZF2B	-2° 35' 45"	-60° 12' 40"	(Formiga 2004)
ZF2P	-2° 35' 45"	-60° 12' 40"	(Oliveira *et al.* 2008)
ZF2V	-2° 35' 45"	-60° 12' 40"	(Oliveira and Amaral 2004)
ZFkm37	-2º 26’ 22.6”	-59º 47’ 48.5”	(Sposito *et al.* 2007)
EMB14	-2° 31.99'	-60° 0.25'	This paper
EMB15	-2° 31.94'	-60° 0.26'	This paper
EMB24	-2° 32.52'	-60° 0.09'	This paper
EMB39	-2° 31.71'	-60° 0.25'	This paper
EMB76	-2° 31.85'	-60° 0.11'	This paper
EMB103	-2° 32.53'	-59° 59.86'	This paper
EMB106	-2° 32.37'	-59° 59.9'	This paper
EMB107	-2° 32.31'	-59° 59.91'	This paper
EMB144	-2° 32.45'	-59° 59.77'	This paper
EMB149	-2° 32.18'	-59° 59.82'	This paper
EMB150	-2° 32.13'	-59° 59.83'	This paper
EMB165	-2° 32.39'	-59° 59.73'	This paper
EMB272	-2° 31.96'	-59° 59.53'	This paper
EMB273	-2° 31.91'	-59° 59.54'	This paper
EMB274	-2° 31.85'	-59° 59.55'	This paper

[*] INPA/CPBO(Instituto Nacional de Pesquisas da Amazonia/Coordenação de Pesquisas em Botânica)

Data analyses: The floristic diversity was estimated by the species richness and by the Shannon-Wiener’s index (Magurran 1988). The data diversity and floristic composition was analysed by using Mata Nativa software (Cientec 2006). The species/area curve was drawn by crossing the cumulative number of species by area size, and the floristic similarity analyses was done by using the Sorensen’s similarity index, clustered by the Unweighted pair-group average (UPGMA) method (Legendre and Legendre 1998). The PAST 1.94 software was used for these analyses (Hammer *et al.* 2009). To measure the influence of geographical distance on floristic composition among 24 sites, and within 15 EMB plots and within the nine plots alone, Mantel test (r) (Fortin and Dale 2005) was applied. The test was based on two matrixes; one of geographical distance (Euclidean distance) and another generated by converting the similarity matrix previously cited, on distance (dissimilarity), where the values were subtracted from one. Permutation test was applied to verify the significance of Mantel coefficients. The Mantel test was performed by using Passage 1 software (Rosenberg 2005).

RESULTS

A total of 8,771 individuals distributed into 264 species and 53 families were identified in 15 1-ha sized plots, at Embrapa Experimental site (Annex 1). The majority number of plots (66%) was completely positioned in top position according to topography.Three of them presented a gradient in top and slope, another one of them is completely in a base position and other is in the slope and base (Fig.1).

The ten families that presented more species richness, in decreasing order were: Fabaceae-Faboideae (22sps.), Fabaceae-Mimosoideae (22), Sapotaceae (22), Lecythidaceae (15), Lauraceae (13), Euphorbiaceae (11), Moraceae (11), Annonaceae (10), Fabaceae-Caesalpinioideae (10) and Chrysobalanaceae (9), Fig. 2a. The first three families contributed to twenty five percent of the species richness at the sampled plots. However, the five families with more number of individuals did not follow the same above order, being Burseraceae, Sapotaceae , Lecythidaceae, Chrysobalanaceae, and Moraceae the most abundant ones , which clustered 46% of the individual’s total number, Fig. 2b.

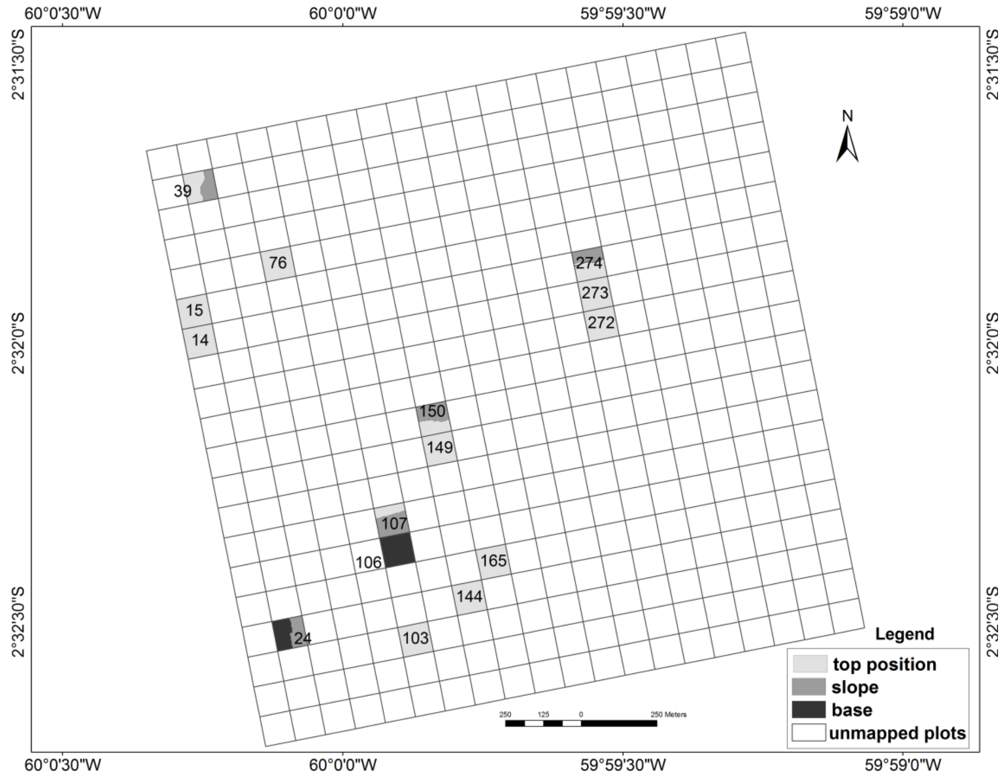

Fig. 1.Topographic position of 15 1ha sized plots at Embrapa Experimental site, Manaus, state of Amazonas, Brazil.

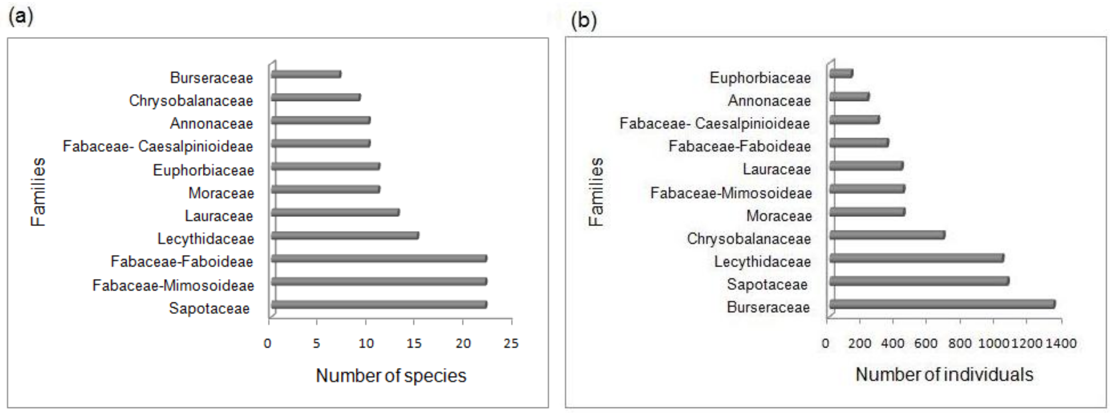

Fig. 2. Families with more number of species (a) and individuals (b) identified at 15 1ha sized plots at Embrapa Experimental site, Manaus, state of Amazonas, Brazil.

Out of 264 species recorded, the ten most abundant were: *Protium hebetatum* Daly (1037 individuals), *Eschweilera coriacea* (DC.) S.A. Mori (471), *Licania oblongifolia* Standl. (310), *Pouteria minima* T.D.Penn. (293), *Ocotea cernua* (Nees) Mez s.l. (258), *Scleronema micranthum* Ducke (197), *Eschweilera collina* Eyma (176), *Licania apelata* (E.Mey.) Fritsch (172), *Naucleopsis caloneura* (Huber) Ducke (170) and *Psidium araca* Raddi (152), Fig. 3.

These species represent 36.5% of the total number of individuals, and only *Protium hebetatum,* Burseraceae family has 11.8% of the relative abundance.

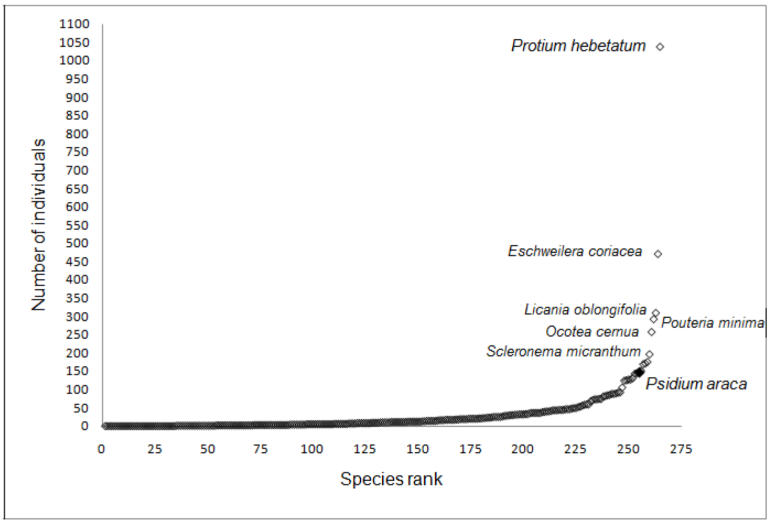

Fig.3. Species ranked by the number of individuals, highlighting the most abundant ones among *Pisidium araca* and *Protium hebetatum* at Embrapa Experimental site, Manaus, state of Amazonas, Brazil.

The number of individuals by plot varied from 497 to 688, with SD equals to 56.4, Table 2, showing a great variability in the abundance of species measured in all the 15 plots of the study area (Fig. 4). This figure shows the species distribution by class of number of individuals within each sampled plot. Thirty-four species (13%) appeared only one once when we summed the abundances over all 15 plots, showing the large occurrence of rare species in the study area. The 39 and 165 plots had no occurrence of species presenting only 1 individual.

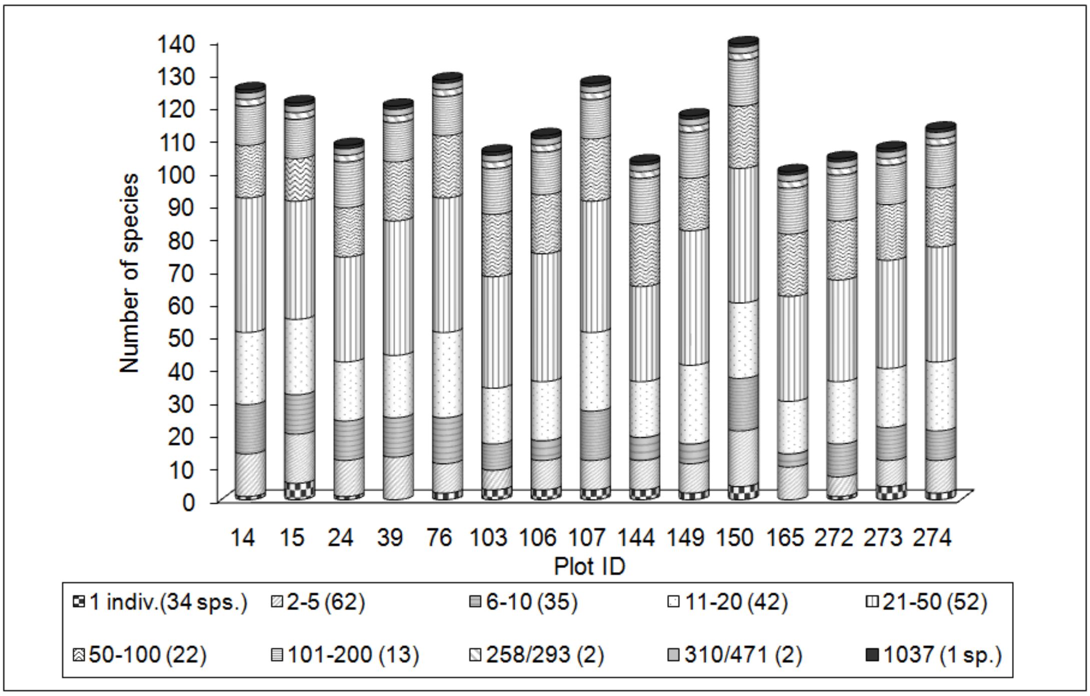

Fig. 4. Occurrence of species by class of number of individuals at each inventoried plots, summed in all 15 plots at the Embrapa Experimental site, Manaus, Amazonas state, Brazil.

The Shannon's diversity index ranged between 3.8 and 4.22 among 15 plots and showed the value of 4.49 as the general index (Table 2). The cumulative species-area curve (Fig. 5), shows that the diversity in the study area was fully represented by the sampled plots.

Our floristic similarity comparison between the 15 sampled plots used in this paper and the other nine plots (Table 1), all terra firme tropical rainforests are presented in Fig. 6. We can see two major groups formed by our 15 plots identified as "EMB" (group-1) and the other plots, (group-2), excepting the "ZF2B" and "JURUA" plots that were very different from the two groups, probably because they can have a particular environmental condition. The two groups shared low percentages of species, about 25%. The 15 "EMB" plots were grouped in higher values of similarity (higher than 60%) compared to the other group, which had approximately half of the plots (5) grouping in a level close to 40 percent.

TABLE 2

Abundance, diversity measures and proportion of specie/abundance at each sampled plot in the Embrapa Experimental site, Manaus, Amazonas State, Brazil.

Plots ID	N	S	H'	QM
14	538	126	4.22	1 : 4.31
15	519	122	4.19	1 : 4.29
24	528	109	3.99	1 : 4.90
39	583	121	4.14	1 : 4.85
76	620	129	4.21	1 : 4.84
103	530	107	3.9	1 : 5.01
106	495	112	4.07	1 : 4.44
107	626	128	4.2	1 : 4.91
144	607	104	3.8	1 : 5.93
149	628	118	3.87	1 : 5.37
150	682	140	4.26	1 : 4.91
165	649	101	3.99	1 : 6.55
272	571	105	3.99	1 : 5.55
273	560	108	3.97	1 : 5.26
274	635	114	3.92	1 : 5.61
general	8771	264	4.49	1:33.45

N= total number of individuals; S= number of species; H' = Shannon-Wiener index, QM= mixture coefficient (proportion species/abundance)

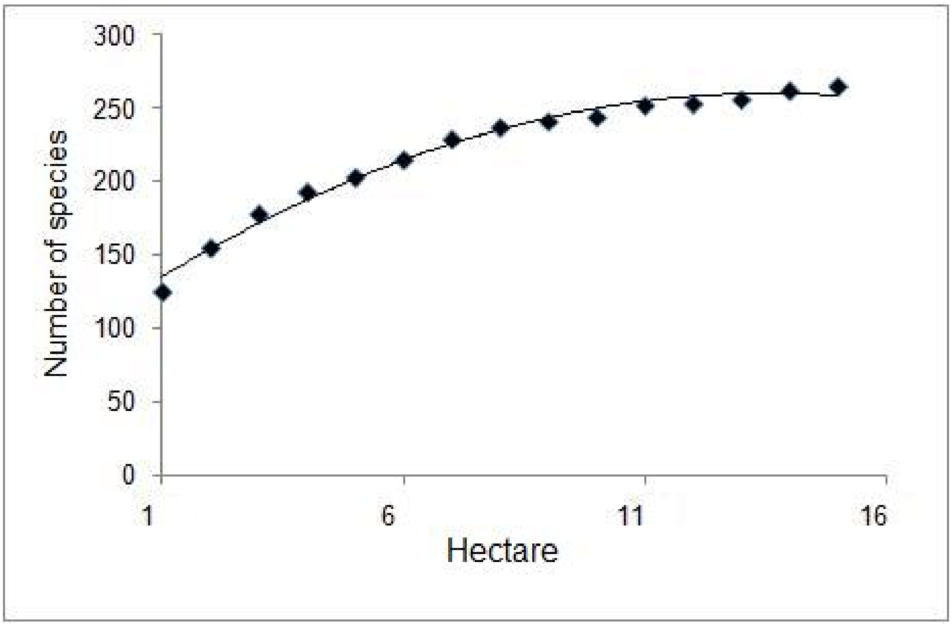

Fig. 5. Cumulative species-area curve for individuals with DAP ≥ 10 cm, considering 15 1ha sized plots at the Embrapa Experimental site, Manaus, state of Amazonas, Brazil.

For the 15 EMB plots the distances between pair of plots varied from a minimum of 100 m to a maximum of 1657 m (from “EMB39” to “EMB103” plot, Fig. 1). The other nine plots had larger distances between pairs, such as varying from a minimum of 100 m to a maximum of 918,000m (from “JURUA” to “ITAP” plot).The Mantel test, carried out to study the association between differences in species composition and geographic distances among plots, showed for all the 24 sites positive and significant correlation (R=0.3627, p< 0.01). For our 15 EMB plots we also found a significant correlation (R=0.4012, p< 0.001). However, the nine plots used to compare with our 15plots, showed, when analysed alone no significant correlation with geographical distances (R=0.3049, p>0.05).

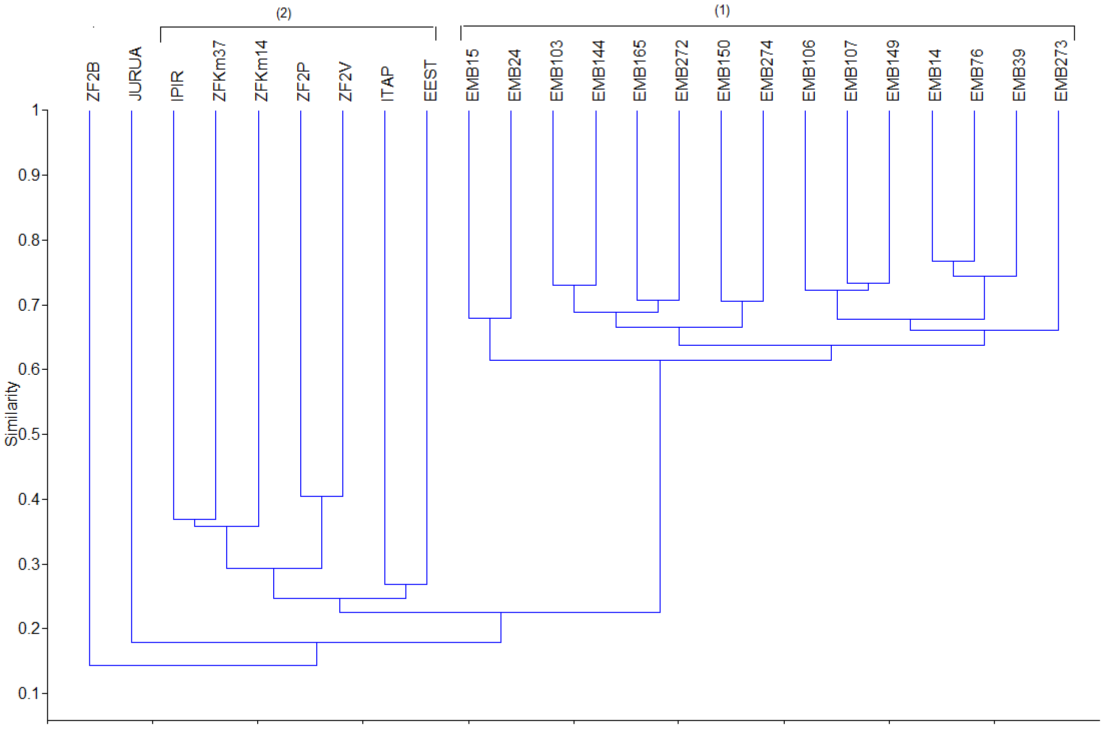

Fig. 6. Dendrogram of 24 1ha sized plots in tropical rainforests in the state of Amazonas, Brazil, using Sorensen’s similarity index, clustered by the Unweighted pair-group average (UPGMA) method. The numbers (1) and (2) represent two major groups and numbers in the branches stand for the plots identification.

DISCUSSION

Floristic composition and diversity: As many studies recorded for Amazonian terra firme forests, our study area has the majority of species concentrated in few families. Also, the larger number of individuals was concentrated in a few number of species, Fig.2 and Fig.3 (Rankin-de-Merona 1987, Milliken 1998, Amaral *et al.* 2000; Lima Filho *et al.* 2001, Oliveira and Amaral, 2004, Oliveira *et al.* 2008). This could be confirmed for the ten most abundant species, which had 36.5% of the total number of individuals identified and were found along the 15 sampled plots, with 100% of frequency (Fig. 4). Approximately 49% of species had up to ten individuals at the whole area (Fig.3 and 4), which is expected for the Amazonian region. Also, the families with the largest species richness were not the ones which had the greatest number of individuals, Amaral *et al.* (2000). Burseraceae family had small specie richness, not have been included among the species richest families, and had the largest number of individuals. However, we have found other studies showing that there might be a relation between richness and abundance in families (Tello 1995, Oliveira *et al.* 2008). It is noteworthy that there is a predominant group of families in terra firme tropical rainforests; a fact that was also observed in our present study, and has been proved helpful in dynamic studies aiming to measure the changes in composition and structure in forest communities by several sources of changes.

It is also important to highlight the occurrence of 36% of the species having up to five individuals considering the whole 15 sampled plots. If this occurrence is measured within each plot, this value could increase. The occurrence of rare species has been recorded by several studies (Prance *et al.* 1976, Oliveira and Amaral 2004, Caiafa *et al.* 2009). Hubbell *et al.* (2001) cite that one possible reason for the rarity in tropical forests may be that rare tree species suffer stronger density-dependent effects than common species do, resulting in a low number of individuals. Also, in the presence of a resources gradient, species can evolve in order to occupy different positions in these gradients, resulting in variations on the abundance distribution (Alves *et al.* 2008). In the present paper, we saw some degree of variability amongst plots, (Fig. 4), when we analysed the species distribution by their classes of number of individuals, especially when comparing the plots 150, 24, 103 and 165 to the other ones in small abundance classes. The fact that we have great local variability in topography may have contributed for the large occurrence of rare species due to environmental heterogeneity and probable specie's adaptation to such variability. Future studies could confirm these statements, once we did not test for these relations in the present study.

The 264 tree species (53 families) can be considered to reflect the overall tree diversity of the area, as demonstrated by the species/area curve (Fig. 5), which approaches an asymptote. The Shannon's diversity index for Amazonian forests generally ranges from 3.83 to 5.85, which are considered high values (Knight 1975). Our value for the whole area of 4.49 falls in the range of high diversity forest. From the previous knowledge of the study area we perceived a gradient of diversity in decreasing order, ranging from the clayey plots (150, 14, 15, 76) to the sandy ones (24, 106, 272, 273, 274). Edaphic heterogeneity seems to have important role in the maintenance of the high diversity in tropical forests with tree species distribution influenced by soil characteristics (Torres *et al.* 1997, Tuomisto and Ruokolainen 1997, Clark 2002, Martins *et al.* 2003, Pinto *et al.* 2008).

Floristic similarity: The 24 locations that had their floristic similarity compared showed mainly two groups of plots (Fig. 6). Our 15 "EMBR" plots formed one group (group-1) and the remaining plots formed the other one (group- 2), excepting the "ZF2B" and "JURUA" plots. Overall, our 15 "EMB" plots shared more than 60% of their species and the comparison within group-1, revealed that some plots are grouped by their geographical proximity, where closer plots shared more species with more than 70%, such as plots14-76 and 103-144, which are all at the top position according to the topography. Our plots showed higher values when compared with Oliveira and Amaral (2004), who found values for Sorensen's similarity index that ranged from 28 to 36% among 20 plots in terra firme forests near Manaus, but falls in the range of findings for Coronado *et al.* (2008), who also found high similarity values. This fact was ratified by the Mantel test, which showed a significant positive correlation between geographical distances and species composition, i.e., the smaller the geographical distance, the more similar the plots are. However, some EMB plots seem to be clustered regardless of their proximity and of their topographic position, such as plots 15-24. Other factors might influence such cluster, which need to be investigated in future studies.

It seems that the environmental heterogeneity played a strong effect in separating plots, which could be observed for the “ZF2B” and “JURUA” plots, once the former plot is located at the base position in the topography and the “JURUA” is the farthest plot, probably having different features compared to the others. Inspite of the positive correlation between geographical distance and specie composition, the Mantel coefficient was not significant. Through the dendrogram analysis, we could better see the tendency of closer plots to share more species, like the plots ZF2P and ZF2V, which are close each other (100m apart).

When the whole 24 plots were included in the Mantel test, a positive and significant correlation was found ($R=0.3627$, $p< 0.01$), showing that closer plots tend to be more similar in species composition, and on the other hand, distant plots tend to be more different. Malheiros *et al.* (2009) comparing forests in the Amazon region, found that the closer the plots the more similar they were to each other in species composition.

The local heterogeneity could explain the low similarity within group-2 and between both groups, although these values could be considered high values for Amazon region (Coronado *et al.* 2008). It is expected that environmentally similar sites tend to have similar floristic composition, whereas environmentally different ones have different composition (Barrantes and Sandoval 2009). Also, biological factors such as dispersal and competitive abilities of species, herbivory, edaphic factors and so on, have been considered to affect the diversity in forest communities, generating several trends in alpha-diversity , which need to be better understood (Tuomisto and Ruokolainen 2005).

To sum up, our study area shows high tree diversity and calls our attention to the large occurrence of low- abundance species across the whole area and to the necessity of considering such rare species in management projects in order to prevent local extinctions. Our results fall in the range of the floristic composition and diversity’s index for Amazon terra firme forests and the comparison amongst our 15 plots in the present study and other nine in the state of Amazonas showed that the closer the plots more similar they are in species composition. Also, we point out that the mosaic of environments in Amazon terra firme forests, with regional and local variations, coupled with the biological process can be responsible for the low similarity observed between some plots compared in this study, showing once more the importance of studies that can keep such variability, helping to understand the mechanisms that allow and maintain the high tree diversity in tropical rainforests.

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ANNEX 1

List of families and species identified at 15 permanent plots at the Embrapa Experimental site, Manaus, state of Amazonas, Brazil. (APGII system).

Families	Scientific names
Anacardiaceae	*Anacardium parvifolium* Ducke
	Anacardium spruceanum Engl.
	Astronium lecointei Ducke
Anisophylleacea	*Anisophyllea manausensis* Pires & W.A.Rodrigues
Annonaceae	*Annona ambotay* Aubl.
	Bocageopsis multiflora (Mart.) R.E.Fr.
	Guatteria poeppigiana
	Guatteria sp.
	Guatterria olivacea R.R.Fr.
	Pseudoxandra coriacea R.E.Fr.
	Unonopsis duckei (R.&P.)Macba.
	Xylopia amazonica R.E. Fr.
	Xylopia brasiliensis Spreng.
	Xylopia calophylla R.E. Fr.
Apocynaceae	*Ambelania duckei* Markgr.
	Aspidosperma album (Vahl.) R. Bem.
	Aspidosperma marcgravianum Woodson
	Couma macrocarpa Barb.
	Couma sp.
	Couma utiles Mart.
	Geissospermum argenteum Woodson
	Hymatanthus sucuba (spruce)Woodson
Araliaceae	*Schefflera morototoni* (Aubl.) Frondin
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don.
	Tabebuia serratifolia (Vahl) Nichols
Bixaceae	*Bixa orellana* L.
Boraginaceae	*Cordia* sp.
Burseraceae	*Protium divaricatum* Engl.
	Protium hebetatum Daly
	Protium heptaphyllum (Aubl.) ssp. ulei (Swart) Daly
	Protium pilosissimum Engl.
	Protium rubrum Cuatrec.
	Protium subserratum Engler
	Trattinnickia burserifolia Mart.
Caryocaraceae	*Caryocar pallidum* A.C. Smith
	Caryocar villosum (Aubl.) Pers.
Celastraceae	*Maytenus guyanensis* Klotzsch

Families	**Scientific names**
Chrysobalanaceae	*Couepia bracteosa* Benth.
	Couepia canomensis (Mart.) Benth. ex Hook.f.
	Couepia longipendula Pilg.
	Licania adolphoduckei Prance
	Licania apelata (E.Mey.) Fritsch
	Licania heteromorpha Benth.
	Licania laevigata Prance
	Licania micrantha Miq.
	Licania oblongifolia Standl.
Clusiaceae	*Distomovita brasiliensis* D' Arcy
	Platonia insignis Mart.
	Symphonia globulifera L.
	Vismia japurensis Reichardt
	Vismia sp.
Combretaceae	*Buchenavia grandis* Ducke
	Terminalia dichotoma G.Meyer
Dichapetalaceae	*Tapura amazonica* Poepp. & Endl.
Elaeocarpaceae	*Sloanea excelsa* Ducke
Erythroxylaceae	*Erythroxylum amplum* Bth.
Euphorbiaceae	*Alchornea discolor* Klotzsch
	Conceveiba guianensis Aubl.
	Conceveiba martiana Baill
	Croton cajucara Benth.
	Croton lanjouwensis Jabl.
	Glycydendron amazonicum Ducke
	Hevea guianensis Aubl.
	Mabea sp.
	Mabea subsessilis Pax & K. Hoffm.
	Micranda siphonoides Benth.
	Pausandra macropetala Ducke
Fabaceae-Caesalpinioideae	*Dialium guianense* Steud.
	Eperua duckeana R.S.Cowan
	Eperua glabriflora (Ducke) R.S.Cowan
	Hymenea parvifolia Huber
	Macrolobium angustifolium (Benth.) R.S.Cowan
	Macrolobium limbatum Spruce ex Benth
	Peltogyne paniculata Benth.
	Sclerolobium helanocarpus Ducke
	Tachigali cf. myrmecophila Ducke
	Zollernia paraensis
Fabaceae-Faboideae	*Andira micrantha* Ducke
	Andira parviflora Ducke
	Andira trifoliata S.A.Mori

Families	**Scientific names**
Fabaceae-Faboideae	*Bocoa viridiflora* (Ducke) R.S.Cowan
	Diplotropis rodriguesii Lima
	Dipteryx magnifica Ducke
	Dipteryx odorata (Aubl.) Willd.
	Dipteryx polyphylla Huber
	Dipteryx punctata (Blake) Amshoff
	Dipteryx sp.
	Hymenolobium sericeum Ducke
	Ormosia grossa Rudd
	Paramachaerium ormosioides Ducke
	Platymiscium duckei Huber
	Swartzia corrugata Benth.
	Swartzia cuspidata Spruce ex Benth.
	Swartzia recurva Poepp.
	Swartzia reticulata Ducke
	Swartzia schomburgkii Benth. Var. guyanensis R.S. Cowan
	Swartzia tessmannii Harms
	Swartzia tomentifera Harms
	Swartzia ulei Harms
Fabaceae-Mimosoideae	*Abarema jupunba* (Willd.) Britton &Killip
	Abarema sp.
	Dinizia excelsa Ducke
	Enterolobium schomburgkii Benth.
	Inga alba (Sw) Willd.
	Inga cordatoalata Ducke
	Inga gracilifolia Ducke
	Inga obidensis Ducke
	Inga stipularis DC.
	Inga suberosa T.D.Penn.
	Parkia decussata Ducke
	Parkia multijuga Benth.
	Parkia nitida Miq.
	Parkia pendula (Willd.) Walp.
	Piptadenia suavolens Miq.
	Pithecellobium elegans Ducke
	Pithecellobium racemosum Ducke
	Stryphnodendron guianensis (Aubl.)Benth.
	Stryphnodendron pulcherrimum (Willd.) Hochr.
	Stryphnodendron sp.
	Zigia juruana (Harms) L.Rico
	Zigia racemosa (Ducke) Barneby & J.W. Grimes
Goupiaceae	*Goupia glabra* Aubl.
Humiriaceae	*Duckesia verrucosa* (Ducke) Cuatr.
	Endopleura uchi (Huber) Cuatrec.
	Sacoglotis matogrossensis Aubl.
	Vantanea guiannensis (Aubl.) Ducke
	Vantanea macrocarpa Ducke
	Vantanea micrantha Ducke

Families	Scientific names
Icacinaceae	*Emmotum acuminatum* (Benth.) Miers
	Emmotum aff. nitens Benth. Ex Miers
Lamiaceae	*Vitex cimosa* Bert. ex Spreng
Lauraceae	*Aniba canellila* (H.B.K.)Mez
	Aniba hostmaniana (Ness) Mez.
	Aniba megaphylla Mez
	Aniba rosaeodora Ducke
	Licania sp.
	Licaria canella (Meissn.) Kosterm.
	Licaria guianensis Aubl.
	Licaria sp.
	Mezilaurus itauba (Meissn.) Taubert ex Mez
	Ocotea cernua (Nees) Mez s.l.
	Ocotea cymbarum H.B.K.
	Ocotea sp.
	Sextonia rubra (Mez) Van der Werff
Lecythidaceae	*Cariniana* sp.
	Corythophora rimosa W.A.Rodrigues
	Couratari alta Kunth.
	Couratari guianensis Aubl.
	Couratari stellata A.C.Sm.
	Eschweilera atropetiolata S.A.Mori
	Eschweilera collina Eyma
	Eschweilera coriacea (DC.) S.A. Mori
	Eschweilera rhododendrifolia (Knuth) A.C.Sm.
	Gustavia elliptica S.A.Mori
	Lecythis barnebyi Mori
	Lecythis graciena S.A.Mori
	Lecythis poiteaui Berg.
	Lecythis prancei S.A. Mori
	Lecythis usidata Camb.
Linaceae	*Roucheria punctata* Ducke
Malpighiaceae	*Byrsonima crispa* Juss.
	Byrsonima duckeana W.R.Anderson
Malvaceae	*Apeiba echinata* Gaertner
	Lueheopsis rosea (Ducke) Burret
	Pseudobombax munguba (Mart. & Zucc) Dugand
	Scleronema micranthum Ducke
	Scleronema praecox Ducke
	Sterculia pruriens (Aubl.) K.Schum.
	Theobroma subincanum Mart.
	Theobroma sylvestre Mart.
Melastomataceae	*Miconia elaeagnoides* Cogn.
	Miconia reglelii Cogn.

Families	**Scientific names**
Melastomataceae	*Miconia* sp.
	Mouriri angulicosta Morley
	Mouriri callocarpa Ducke
	Tococa guianensis Aubl.
Meliaceae	*Carapa guianensis* Aubl.
	Guarea sp.
	Trichilia micropetala T.D.Penn.
	Trichilia septentrionales C.DC.
Monimiaceae	*Siparuna amazonica* Mart.
	Siparuna guianensis Aubl.
	Siparuna sp.
Moraceae	*Brosimum acutifolium* Huber ssp. Interjectum C.C.Berg
	Brosimum lactescens (S.Moore) C.C.Berg.
	Brosimum parinarioides Ducke
	Brosimum potabile Ducke
	Brosimum rubescens Taub.
	Brosimum utile (H.B.K.) Pittier ssp. ovatifolium (Ducke) C.C.Berg.
	Clarisia racemosa Ruiz & Pav.
	Helianthostylis sprucei Baill.
	Helicostylis scabra (Macbr.)
	Naucleopsis caloneura (Huber) Ducke
	Sorocea guilleminiana Gaudich.
Myristicaceae	*Virola michelii* Heckel
	Iryanthera coriacea Ducke
	Iryanthera juruensis Warb.
	Osteophloeum platyspermum (A.DC.) Warb.
	Virola caducifolia W.A. Rodrigues
	Virola calophylla Warb.
Myrtaceae	*Eugenia diplocampta* Diels
	Myrcia magna Legrand
	Myrcia paivae O. Berg
	Psidium araca Raddi
Nyctaginaceae	*Neea oppositifolia* Ruiz & Pav.
Olacaceae	*Minquartia guianensis* Aubl.
	Pytchopetalum olacoides Benth.
Opiliaceae	*Agonandra brasiliensis* Miers
Peraceae	*Pera heteranthera* (Schrank) I.M. Johnst.
	Pogonophora schomburgkiana Miers ex Benth.
Putranjivaceae	*Drypetes variabilis* Uittien

Families	**Scientific names**
Quiinaceae	*Lacunaria jenmani* (Oliv.)Ducke
	Touroulia guianensis Aubl.
Rubiaceae	*Albertia edulis* A. Rich.
	Chimarrhis duckeana del Prete
	Chimarrhis sp.
	Duroia fusifera Hook. F. ex K. Schum.
	Duroia saccifera (Mart.) Hook. F. ex K. Schum.
	Ferdinandusa elliptica Pohl.
	Palicourea corymbifera Mull. Arg.
	Warszewiczia schwackei K.Schum.
Salicaceae	*Casearia grandiflora* Cambess
Sapindaceaea	*Matayba* sp.
	Talisia cf. cupularis Radlk.
Sapotaceae	*Chrysophyllum sanguinolentum* (Pierre) Baehni
	Chrysophyllum sparsiflorum Klotzsch ex Miq.
	Ecclinusa guianensis Eyma
	Glycoxylon pedicellatum (Ducke) Ducke
	Manilkara amazonica (Huber) Stand.
	Manilkara bidentata (A.DC.) A. Chev.
	Micropholis guyanensis (A.DC.) Pierre ssp.duckeana (Baehni)
	Micropholis sp.
	Micropholis trunciflora Ducke
	Poteuria platyphylla (A.C.Sm.) Baehni
	Pouteria ambelaniifolia (Sandwith) T.D.Penn.
	Pouteria caimito (Ruiz & Pav.) Radlk.
	Pouteria eugenifolia (Pierre)Baehni
	Pouteria guianensis Aubl.
	Pouteria laurifolia (Gomes) Radlk
	Pouteria minima T.D.Penn.
	Pouteria oblanceolata Pires
	Pouteria peruviensis (Aubrév.) Bernardi
	Pouteria petiolata T.D. Penn.
	Pouteria reticulata (Engl.) Eyma
	Pouteria venosa (Mart.) Baehni ssp. amazonica T.D.Penn.
	Pradosia cochlearia (Lecomte) T.D.Penn
Simaroubaceae	*Simaba cedron* Planch.
	Simaba polyphylla (Cavalcante) W.Thomas
	Simarouba amara Aubl.
Solanaceae	*Duckeodendron cestoides* Kuhlm.
Ulmaceae	*Ampelocera edentula* Rusby
Urticaceae	*Cecropia concolor* Willd.
	Cecropia purpurascens C.C. Berg
	Cecropia sciadophylla Mart.

Families	**Scientific names**
Urticaceae	*Pouroma guianensis* Aubl.
	Pourouma myrmecophyla Ducke
Violaceae	*Rinorea guianensis* Aubl.
	Rinorea racemosa (Mart.) Kuntze
Vochysiaceae	*Erisma bicolor* Ducke
	Qualea acuminata Aubl.
	Qualea albiflora Warm
	Qualea paraensis Ducke
	Ruizterania cassiquiarensis (Spruce ex Warm.)
Vochysiaceae	*Vochysia vismiaefolia* Spruce ex Warm.

Artigo 2

ESTRUTURA DO COMPONENTE ARBÓREO EM 15 HA DE PARCELAS PERMANENTES DE FLORESTA DENSA DE TERRA FIRME NA AMAZÔNIA CENTRAL

HORIZONTAL STRUCTURE OF 15 HECTARES OF TERRA FIRME DENSE FOREST IN CENTRAL AMAZONIAN

RESUMO

A floresta densa de terra firme ocorre em 65% da região Amazônica e é caracterizada por possuir alta diversidade de espécies vegetais e elevada ocorrência de espécies raras. Este trabalho analisou a estrutura horizontal de 15 ha de parcelas aleatoriamente selecionadas de um conjunto de 400 ha de parcelas permanentes, localizadas no Campo Experimental da Embrapa Amazônia Ocidental, Manaus, AM, Brasil. Todos os indivíduos com DAP ≥ 10 cm foram marcados e identificados em nível de espécie em 2005. Os valores de IVI (Índice de Valor de Importância) foram separados em classes de amplitude de um (01) desvio padrão e os indivíduos distribuídos segundo classes de DAP de amplitude de 10 cm. Ao todo foram identificados 8771 indivíduos, distribuídos em 264 espécies e 53 famílias. Um maior número de indivíduos concentra-se em poucas espécies, tais como *Protium hebetatum* Daly, *Eschweilera coriacea* (DC.) S.A. Mori e *Licania oblongifolia* Standl. que somaram 21% do número total de indivíduos e 12% do IVI. Há elevada ocorrência de espécies raras (36%) e as famílias Sapotaceae, Lecythidaceae e Burseraceae somaram 39% do número total de indivíduos. A estrutura diamétrica em forma de J-invertido mostra que 80% dos indivíduos estão concentrados nas primeiras classes de 10-30 cm de DAP. Os resultados são similares aos de outros estudos desenvolvidos em florestas de terra firme na região e chamam a atenção para a elevada ocorrência de espécies raras e daquelas com baixa densidade, mas com distribuição restrita a algumas parcelas, principalmente aquelas pertencentes às menores classes de IVI e que devem merecer atenção especial nas ações de conservação da biodiversidade e manejo florestal.

Palavras-chave: Estrutura de florestas; Amazônia Central; Fitossociologia; Floresta de terra firme.

ABSTRACT

Amazonian forests are characterized by the high biological diversity with high occurrence of rare plant species in a very diversity of environments. This paper aimed to analyze the horizontal structure of 15 hectares of plots, randomly chosen from a set of 400 ha of permanent plots situated at the Experimental Site of Embrapa Amazônia Ocidental, Manaus, Amazonas State, Brazil. All individuals with DAP ≥ 10 cm were stem mapped and botanically identified in 2005. The IVI values were cut in classes with one (01) standard deviation range and the diameters into classes of 10 cm in range. Overall, 8771 individuals were identified, distributed into 264 species and 53 families. A larger number of individuals are concentrated in a few number of species, such as *Protium hebetatum* Daly, *Eschweilera coriacea* (DC.) S.A. Mori and *Licania oblongifolia* Standl, which sum up 21% of the total number of individuals and 12% of the IVI. There is a high occurrence of rare species (36%) and just the families Sapotaceae, Lecythidaceae and Burseraceae together accounted for 39% of the total number of individuals. The diametric structure has a J-inverse shape, common in tropical forests, with 80% of individuals concentrated in the first classes ranging between 10-30 cm. Our results are similar to other studies developed in terra firme tropical forests in Amazon and call our attention to the high occurrence of rare species and those with low density that show restricted occurrence to some plots, which deserve special attention in actions for biodiversity conservation and forest management.

Keywords: Phytosociology, diversity, Central Amazon, terra firme tropical rainforests.

INTRODUÇÃO

O Brasil, com aproximadamente um terço das florestas tropicais remanescentes do mundo, é um dos mais importantes locais da biodiversidade mundial (PAS, 2008). Porém, o impacto das ações antrópicas sobre os ambientes tem feito com que importantes ecossistemas sejam descaracterizados sem que se tenha conhecimento da sua estrutura fitossociológica e composição florística das espécies nos diferentes ambientes.

Na Amazônia, muitas áreas são formadas por mosaicos de habitats, com diferentes conjuntos de espécies vegetais ocorrendo em áreas adjacentes sobre diferentes substratos, onde se observa, de modo geral, que a distribuição das espécies arbóreas tropicais pode se dar devido a preferências de habitats e/ou à variações na história evolutiva das mesmas (PITMAN *et al.*, 2001; NOVAES FILHO *et al.*, 2007).

A dinâmica e estrutura das florestas têm sido relatadas de variar através da bacia Amazônica em um gradiente leste-oeste, seguindo um padrão que coincide com variações na fertilidade do solo e geologia (QUESADA *et al.*, 2009). Descrever estes padrões de variações, utilizando grandes conjuntos de dados, que contemplem os diferentes gradientes ambientais amazônicos é de suma importância para o entendimento dos mecanismos que determinam a distribuição das espécies, contribuindo, assim, para a definição de estratégias de manejo e conservação das florestas em face dos desmatamentos e das mudanças climáticas (CORONADO *et al.*, 2009).

Cerca de 65% da região Amazônica é coberta por um tipo florestal denominado floresta de terra firme, caracterizada principalmente pela elevada riqueza e diversidade de espécies, representada por poucos indivíduos de cada espécie e em geral mostrando alta dissimilaridade florística entre parcelas adjacentes, ocorrendo através de platôs e áreas de terras baixas associadas com vales de pequenos rios (PRANCE *et al.*, 1976; VELOSO *et al.*, 1991; FERREIRA e PRANCE, 1998; OLIVEIRA e MORI, 1999; LIMA FILHO *et al.*, 2001; ANDERSON *et al.*, 2009). Fatores climáticos e edáficos como climas mais chuvosos e menos sazonais, e solos relativamente mais férteis em nutrientes, têm sido citados como possíveis responsáveis por uma maior diversidade de plantas na Amazônia Ocidental (GENTRY, 1988; QUESADA *et al.* 2009). Phillips *et al.* (1994) relacionam a maior riqueza de espécies à dinâmica natural de mortalidade de árvores, onde florestas com altas taxas de mortalidade e recrutamento seriam mais diversificadas.

O conhecimento das características e estrutura das comunidades vegetais contribui para resultados mais eficientes das atividades de conservação e manejo florestal, evitando mudanças significativas na composição florística e estrutura dessas vegetações, prevenindo extinções locais e mantendo, assim, o ambiente mais estável, preservando sua identidade ecológica. Neste contexto, este trabalho objetivou descrever e analisar a estrutura horizontal de 15 hectares de floresta densa de terra firme na Amazônia Central, Manaus, Amazonas, Brasil a fim de contribuir para ampliar os conhecimentos sobre a organização das espécies na comunidade, auxiliando, assim, nas ações de conservação e manejo florestal na Amazônia.

MATERIAL E MÉTODO

Área de estudo

A área de estudo está localizada em uma floresta densa de terra firme na Amazônia Central, no Campo Experimental da Embrapa Amazônia Ocidental, Manaus, Amazonas, Brasil. A área integra projeto desenvolvido no âmbito da Rede de Monitoramento da Dinâmica de Florestas da Amazônia Brasileira-REDEFLOR com 400 ha de parcelas permanentes demarcadas.

O clima da área é do tipo "Am" na classificação de Köppen, com precipitação anual de 1.355 a 2.839 mm. A temperatura média anual é de 27,6 °C, com umidade relativa do ar variando de 84 a 90% ao longo do ano; os meses mais chuvosos vão de dezembro a maio, e os mais secos de julho a outubro, com estes meses recebendo normalmente menos do que 100 mm de chuva (RADAM, 1978). A altitude média varia de 60 a 160 m (REGIS, 1993; ANDERSON *et al.*, 2009). Os solos predominantes na área são o latossolo amarelo com textura variando de mais argilosa nos platôs a arenosa nas partes baixas, sendo ácidos e pobres em nutrientes, cobertos predominantemente pela vegetação da floresta densa de terras baixas, com dossel emergente IBGE (1999), consituídas por árvores que variam de médio a grande porte, atingindo até 55 m de altura (REGIS, 1993).

Coleta e análise de dados

Quinze parcelas de 100 x 100m foram aleatoriamente selecionadas do conjunto de 400 ha de parcelas permanentes, sendo que a maioria das parcelas (9), está situada nas áreas de platô, quatro contemplam platô e encosta, uma (01) contempla encosta e baixio e uma (01) está completamente situada no baixio. Nas 15 parcelas, todos os indivíduos com diâmetro a altura do peito (DAP) ≥ 10 cm foram plaqueteados e identificados botanicamente em nível de espécie em 2005. O material botânico foi identificado por meio de comparações a exsicatas disponíveis no herbário do Instituto Nacional de Pesquisas da Amazônia (INPA), bem como por meio de consulta a literatura especializada em espécies florestais nativas da Amazonia (RIBEIRO *et al.*, 1999). Os nomes botânicos foram conferidos na página da Web do Missouri Botanical Garden (http:// mobot.mobot.orgw3t/search/vas.htm).

O cálculo dos parâmetros estruturais da vegetação, como área basal (AB), dominância absolulta e relativa (DoA, DoR), abundância (N), densidade absoluta e relativa(DA,DR) e frequencia absoluta e relativa (FA,FR) para a composição do

Índice de Valor de Importância (IVI) foram obtidos segundo Mueller-Dumbois e Ellenberg (1974), calculados no software Mata Nativa 2 (CIENTEC, 2006). A estimativa da importância ecológica das famílias na comunidade estudada foi feita mediante o Índice de Valor de Importância Familiar (IVIF), calculado pela soma da diversidade (nº de espécies da família/nº total de espécies), densidade e dominância relativas, Mori e Boom (1983), utilizando o programa Microsoft Excel for Windows. As classes de IVI (%) foram definidas utilizando-se para o limite superior da primeira classe o valor da média menos 0.5 desvio padrão (M-0,5*desvio_padrão) e a partir daí acrescidos de 1 desvio padrão. As classes de diâmetro foram definidas com amplitude de 10 cm.

RESULTADOS E DISCUSSÃO

No total dos 15 hectares amostrados foram identificados 8771 indivíduos, pertencentes a 264 espécies e 53 famílias com DAP ≥ 10 cm. O número de árvores e área basal por parcela variou de 497-688 e de 23,4-32,7 m^2, respectivamente. As 10 espécies mais importantes na área de estudo, com base no Índice de Valor de Importância (IVI), Figura 1, representam 24% do IVI total, sendo *Protium hebetatum* Daly, *Eschweilera coriacea* (DC.) S.A. Mori, *Licania oblongifolia* Standl., *Pouteria minima* T.D.Penn. e *Ocotea cernua* (Nees) Mez s.l. as que apresentaram os maiores valores de IVI. Somente as três primeiras espécies possuem 20.7% do número total de indivíduos identificados. As famílias mais importantes segundo o Índice de Valor de Importância Familiar (IVIF), em ordem decrescente foram Sapotaceae, Lecythidaceae, Burseraceae, Fabaceae-Mimosoideae e Chrysobalanaceae (Figura 2), sendo que as três primeiras famílias agrupam aproximadamente 39% do número total de indivíduos. Há grande ocorrência de espécies raras (1 indivíduo/parcela), cujos valores variaram entre 30 a 42% do número total de espécies registradas nas parcelas amostradas. Quando se avalia a ocorrência destas espécies no conjunto total dos 15 ha este valor cai para aproximadamente 13 % (34 espécies), sendo Fabaceaae-Mimosoideae, Fabaceae-Faboideae e Fabaceae-Caesalpinoideae, em ordem decrescente, as famílias que tiveram maior número de espécies contribuindo para este valor.

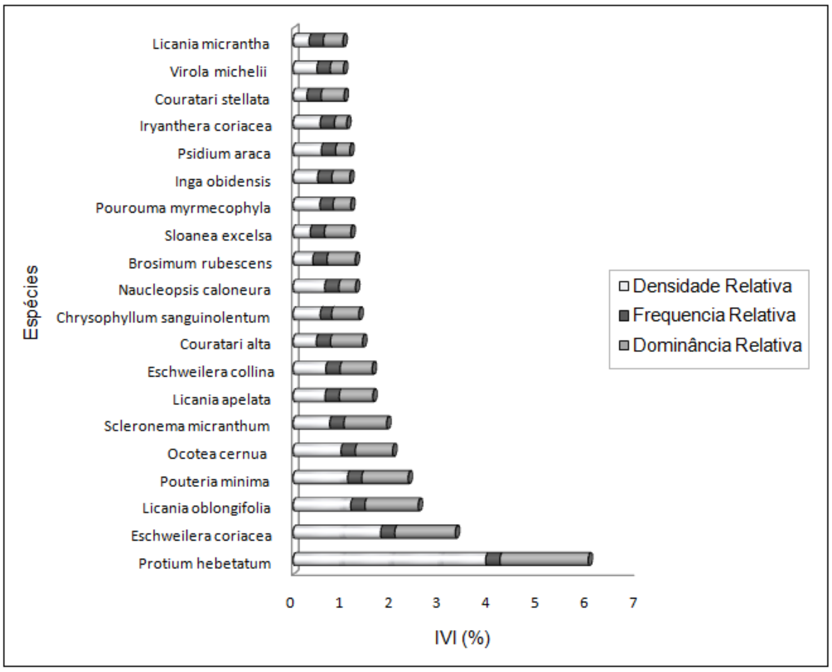

FIGURA 1: Índice de Valor de Importância-IVI(%) das 20 espécies com os maiores valores em 15 parcelas permanentes no Campo Experimental da Embrapa Amazônia Ocidental, Manaus, AM, Brasil.

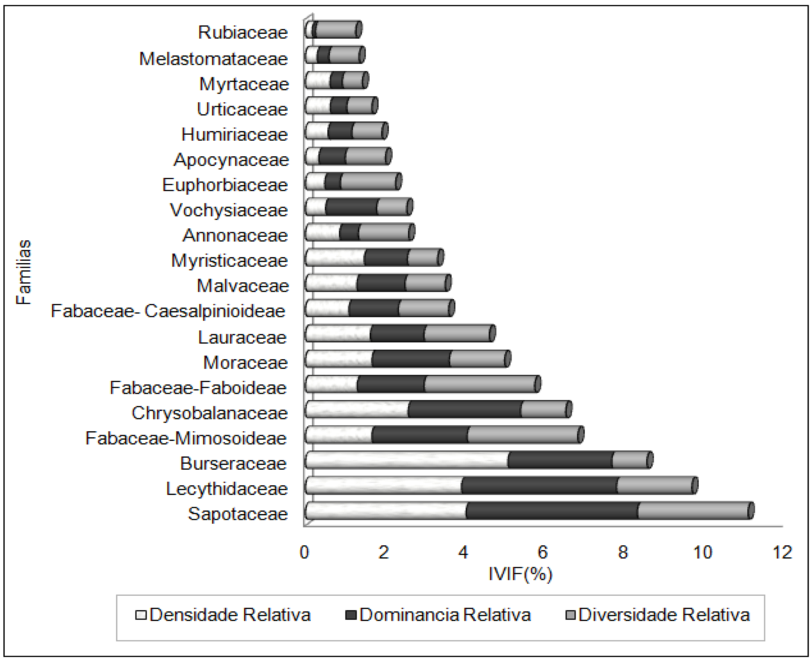

FIGURA 2: Composição do Índice de Valor de Importância Familiar – IVIF (%) para as 20 famílias com os maiores valores, no Campo Experimental da Embrapa Amazônia Ocidental, Manaus, AM, Brasil.

Observa-se grande variabilidade na ocorrência das espécies distribuídas em classes de IVI (%), dentro das 15 parcelas amostradas (Figura 3), principalmente nas duas menores classes que agrupam valores inferiores a 0,66%, as quais reúnem aproximadamente 83% das espécies identificadas na área de estudo. As parcelas 15, 150 e 273 têm maior número de espécies exclusivas dentro da menor classe (< 0,096%) e à medida que os valores de IVI vão aumentando observa-se uma distribuição mais uniforme das espécies nas 15 parcelas. Das 85 espécies agrupadas na menor classe de IVI (< 0,096%), 41 espécies aparecem com ocorrência exclusiva nas parcelas, tendo baixa densidade, com 87% destas espécies ocorrendo com apenas um (01) indivíduo e 13% de dois a seis indivíduos. *Duckesia verrucosa* (Ducke) Cuatr. (Humiriaceae), apresenta 6 indivíduos que só foram registrados na parcela 106, a qual está na posição topográfica baixio e com maior teor de umidade e textura arenosa. Neste contexto, as parcelas 15, 150 e 273 somam 39% do número de espécies com o menor valor de IVI e com ocorrência restrita a estas parcelas.

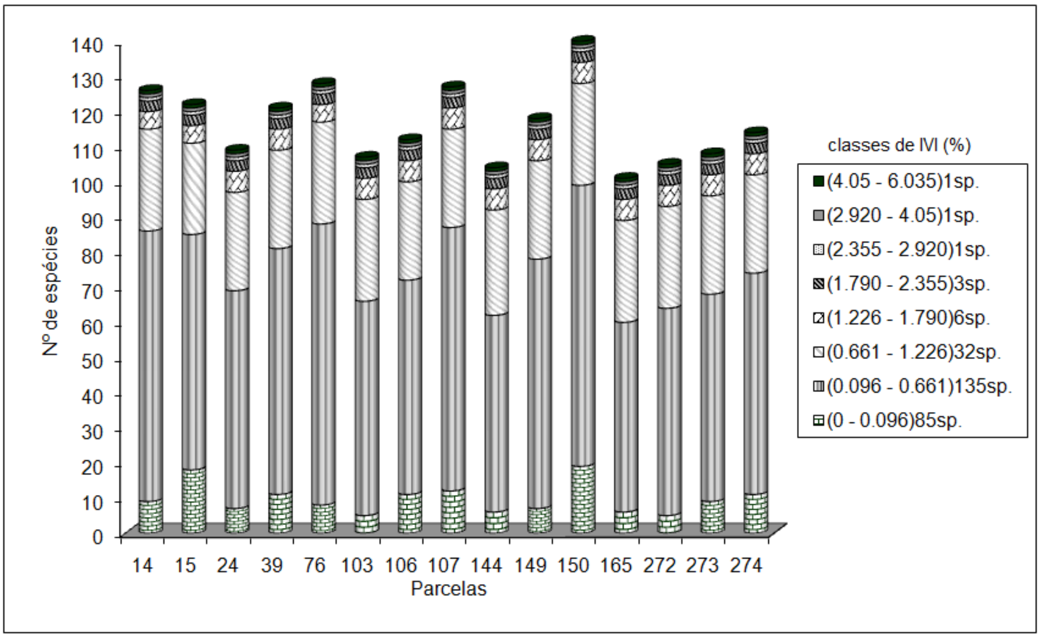

FIGURA 3: Distribuição das espécies dentro das parcelas segundo classes de IVI (%) para 15 parcelas de 100 x 100m localizadas no Campo Experimental da Embrapa Amazônia Ocidental, Manaus-AM, Brasil.

A distribuição dos indivíduos nas classes diamétricas de amplitude 10 cm (Figura 4), mostra a distribuição J-invertido, característica das florestas naturais. A amplitude total dos diâmetros variou de 10-210 cm, onde se observa a ocorrência de indivíduos em quase todas as classes diamétricas, com exceção para as classes 140-180 cm e 190-200 cm. A grande maioria dos indivíduos (61%) está distribuída na menor classe de diâmetro (10-20 cm). As duas primeiras classes (10-30 cm) concentram 80% do número total dos indivíduos nos 15 hectares amostrados. *Buchenavia grandis* Ducke (Combretaceae) e *Andira parviflora* Ducke (Fabaceae-Faboideae) ocorreram na classe diamétrica 180 - 190 cm e *Caryocar pallidum* A.C. Smith (Caryocaraceae) e *Dinizia excelsa* Ducke (Fabaceae-Mimosoideae), na maior classe (200-210 cm).

De modo geral, a floresta de terra firme, objeto do presente estudo apresenta composição florística e estrutura características desta tipologia vegetal com a maioria dos indivíduos concentrados em poucas espécies e poucas famílias concentrando o maior percentual da riqueza de espécies (MILLIKEN, 1998; LIMA FILHO *et al.*, 2004; OLIVEIRA e AMARAL, 2004; OLIVEIRA *et al.*, 2008).

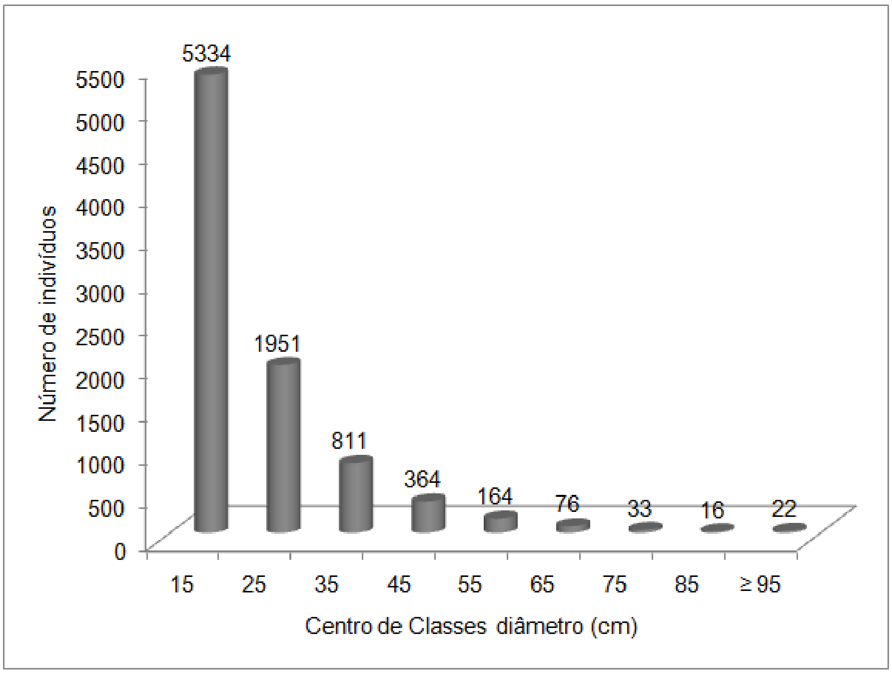

FIGURA 4: Número total de indivíduos por classes de diâmetro de amplitude 10 cm, no Campo Experimental da Embrapa Amazônia Ocidental, Manaus, AM, Brasil.

Observou-se também que as famílias com maior Valor de Importância não são em geral as mais abundantes ou de maior riqueza de espécies (Figura 2). A família Burseraceae, apesar da menor riqueza de espécies, quando comparada a Fabaceae-Mimosoideae e Fabaceae-Faboideae apresentou maior IVIF, devido principalmente ao maior número de indivíduos observados para aquela espécie. Esta família (Burseraceae) aparece com o terceiro maior IVIF e é a que possui a espécie com maior IVI na área (*Protium hebetatum*). Este fato demonstra a grande variabilidade nas florestas tropicais relacionada à abundância de indivíduos e diversidade nas famílias.

Gama *et al.* (2005) e Oliveira *et al.* (2008) relatam em seus estudos que *Protium hebetatum e Eschweilera coriacea* são as espécies mais comumente registradas nas florestas de terra firme da Amazônia, apresentando ampla distribuição geográfica e os maiores valores de abundância. Estas espécies foram também registradas no presente trabalho, com as mesmas características, onde a densidade e dominância, de modo geral, contribuíram para a maior importância das espécies na área. A maior densidade relativa observada para *Protium hebetatum* contribuiu de maneira decisiva para um maior valor de dominância e conseqüente maior valor de IVI, uma vez que as dez mais importantes espécies apresentaram valores similares de freqüência, com distribuição ampla nas parcelas amostradas.

A variabilidade na distribuição do número de espécies por classes de IVI dentro das parcelas, principalmente nas menores classes pode ser atribuída à influência das espécies raras, uma vez que as parcelas 15 e 150 foram as que tiveram a maior ocorrência destas espécies no conjunto total das 15 parcelas, sendo também as que apresentaram o maior percentual de espécies exclusivas, ocorrendo com baixa abundância. Diversos estudos relatam a ocorrência de um número expressivo de espécies raras nas florestas de terra firme da Amazônia, valores estes que se assemelham aos encontrados neste estudo, em média 34% do número total de espécies (GENTRY, 1988; FERRERIA e PRANCE, 1998; OLIVERIA *et al.*, 2008). No contexto das classes de IVI, nossos resultados mostram que algumas espécies com baixa abundância têm ocorrência restrita nas parcelas e merecem atenção especial junto com as espécies raras (1 indivíduo/parcela), no sentido de se evitar extinções locais quando das ações de manejo. Excetuando-se a primeira menor classe de IVI, pode-se considerar de modo geral, que todas as parcelas possuem espécies de todas as classes de IVI, sugerindo que com base nesta classificação, a estrutura horizontal observada encontra-se bem representada no conjunto das parcelas.

A forma da curva de distribuição dos diâmetros em J-invertido no presente estudo é típica das florestas tropicais, com alta proporção de árvores com DAP < 30cm (FERREIRA e PRANCE, 1988a; LIMA FILHO *et al.*, 2001; HAUGAASEN *et al.*, 2006). A estrutura diamétrica observada sugere que a área não tem sofrido grandes distúrbios e que a dinâmica natural de mortalidade e recrutamento de novos indivíduos, devido a ocorrência de pequenas clareiras naturais pode ser responsável pela distribuição observada (OLIVEIRA e MORI, 1999; OLIVEIRA *et al.*, 2008). A ocorrência de alguns indivíduos em classes de diâmetro maior que 80 cm também sugere que a floresta não tem sido afetada por grandes distúrbios, onde observa-se por exemplo indivíduos de *Dinizia excelsa* com DAP de aproximadamente 200 cm.

CONCLUSÕES

A floresta densa de terra firme estudada apresenta grande ocorrência espécies raras e de espécies com baixa densidade e de distribuição restrita a algumas parcelas. De modo geral há um número pequeno de espécies concentrando a maior proporção do número de indivíduos observados e poucas famílias concentrando um maior número de espécies. A variabilidade no número de espécies nas menores classes de valores de IVI, ao longo das parcelas, aliado às características acima citadas ressaltam a importância do estabelecimento de estratégias diferenciadas de manejo e conservação para as florestas densas de terra firme na Amazônia Central, a fim de se evitar alterações que comprometam sua composição e estrutura, prevenindo extinções locais de espécies.

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Artigo 3

Spatial structure of tree species community in a “terra firme” Amazon forest near Manaus, Brazil

Abstract The role of species-environment relationships in structuring the spatial distribution of tree species communities at different sampling unit sizes were investigated in a “terra firme” tropical rainforest in the Brazilian Amazon. We stem-mapped all trees with diameter at breast height ≥ 10.0 cm in 2005 at the Embrapa Experimental Site, Manaus, Amazonas State. Specifically, we determined the relationships of tree species with soil properties using canonical correspondence analysis based on nine soil variables and 68 tree species. From the canonical correspondence analysis, we group the species into two groups: one where species occur mainly in wet and sandy sites; and another where species occur mainly in dry and clay sites. Then, to determine whether each group presents some spatial aggregation, we used Ripley`s *K* uni- and bivariate functions, analyzing 32 plots ranging in size from 2,500 m^2 to 20,000 m^2. For the two groups, a significant spatial aggregation was found only at sampling unit sizes larger than 10,000 m^2, particularly for those species found in clay soils and drier environments, and when the sampling units investigated seemed to meet the species requirements. Soil variables, topographic position and plant dispersal types influenced the spatial aggregation of species in a varied range of mainly intermediate to large distances (≥20m). Based on our findings, we conclude that environmental heterogeneity and the minimum sample unit sizes of 10,000 m^2 should be considered in forest dynamic studies to characterize patterns and understand the spatial processes structuring the “terra firme” tropical rainforest in the Brazilian Amazon.

Keywords: Canonical correspondence analysis, Ripley`s *K*, Spatial point patterns, Species diversity, Amazon forest, Soil nutrients.

Introduction

Identification of spatial structure is a key step in understanding the ecological processes structuring the distribution of plants in nature. Quantifying and relating the underlying generative processes that create these structures will provide crucial information to help us decipher the factors that structure and maintain ecological diversity (Illian et al. 2008; Rossi 1994). In tropical Amazon forests, large numbers of species coexist, with high species diversity and low density of individuals per species (Condit et al. 2000). Indeed, several studies have recorded 150-350 tree species co-occurring in a single hectare, including only trees with stem diameters larger than 10 cm (Amaral 1996; Ferreira and Prance 1998; Lima et al. 2001; Oliveira and Amaral 2005). Individuals of various species and sizes can be spatially associated with one another, presenting structures that may result from complex forest dynamics, such as dispersal, growth, and mortality, interaction of silvicultural management, land use and climate, with a extremely large number of potential inter-and intra-species interactions (Comas and Mateu 2007; Jombart et al. 2009; Legendre and Fortin 1989; Shimatani and Kubota 2004).

Rainforest plant species have been found to be associated with particular edaphic, topographic, or successional conditions, according to the results of many studies which involved mainly soil gradients, due to their importance to plant diversity (Clark et al. 1998; Jones et al. 2007; Tuomisto and Ruokolainen 1994; Tuomisto 2006; Valencia et al. 2004). While generalist species occur in all types of soils, other species have strong relationships to soil variables. Then, finding out how species are organized in space according to environmental heterogeneity (spatial dependence), dispersal and competition (spatial autocorrelation) may reveal patterns that can help to understand the biological processes which generate such structures (Illian et al. 2008; Law et al. 2009; Legendre and Legendre 1998).

Species distribution is also influenced by many environmental variables, inducing spatial patterns mostly at broad scales (Wagner and Fortin 2005). In contrast, biotic processes such as dispersal and competition can give rise to spatial autocorrelation, which might result in intermediate to small-scale spatial structuring (Fortin and Dale 2005; Legendre 1993). The observed spatial pattern often results from a combination of several processes operating on different spatial and temporal scales.

The quantification of spatial structure, however, is directly related and limited by the study area (extent) and the sampling size unit (grain) at which the analysis is conducted (Fortin and Dale 2005; Massant at al. 2009, Wiens 1989). We hypothesized that tree species are structured due to soil nutrients and that our ability to detect spatial structure is also influenced by the size of the sampling units analyzed. To test this, we first used canonical correspondence analysis (CCA) to relate species distribution to soil variables and separate species according to the gradient of soil variation, and then Ripley`s *K* analysis to investigate how species assemblages are locally spatially structured in a “terra firme” tropical rainforest near Manaus, Amazonas State, Brazil.

Methods

Study area

The study area is located in a Western Amazon “terra firme” dense forest, at the Experimental site of Embrapa Western Amazonia (Manaus, state of Amazonas, Brazil), at the coordinates 59°59’42.6” W and 2°32’49.7” S, belonging to the 400 ha permanent plots project in Brazilian Amazon started in 2005. 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 1999), but with a degree of local variation in topography and edaphic conditions.

The upland areas ("terra firme") 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 (Regis 1993).

Field sampling

In order to investigate the effect of soil variables structuring the tree community, we first used 15 plots of 50 × 50 m, selected to reflect the range of environmental variation in the study area, to collect soil samples and to relate soil variables to species composition (Fig. 1a). After that, we used 32 plots, distributed in five different sizes of sampling units across the study area, aiming to identify to what sampling-unit size the spatial dependence between soil variables and species could be detected: (1) 15 plots of 2,500 m^2 (Fig. 1a); (2) six plots of irregular shapes, with areas ranging from 4,270 to 5,870 m^2 (Fig. 1b); (3) nine plots of 10,000 m^2 each (Fig. 2a); (4) one plot of 14,300 m^2 (Fig. 2b); and (5) one plot of 20,000 m^2 (Fig. 2b). In these plots there is a gradient, mainly in texture from the clayey to sandy plots in west-east direction.

In these five sizes of sampling units, all trees with dbh $\geq$ 10 cm were stem-mapped (*x*-*y* coordinates) in 2005. The trees were identified to species level, and in each plot their topographic positions, i.e., top, slope, and base, were recorded (Fig. 1 and Fig. 2). Because the study area covers two Universal Transverse Mercator (UTM) zones, all trees were georeferenced to the Local Transverse Mercator (zone 21 and central meridian W60), placing the data into a single zone, although they did not extended for more than 6 degree.

Canonical Correspondence Analysis (CCA)

To determine whether or not species were related to soil properties, a canonical correspondence analysis was performed (Jongman *et al.* 1995; Legendre and Legendre 1998), using soil variables sampled between 0-20 cm depth at 15 plots of 2,500 m^2 (Fig. 1a).

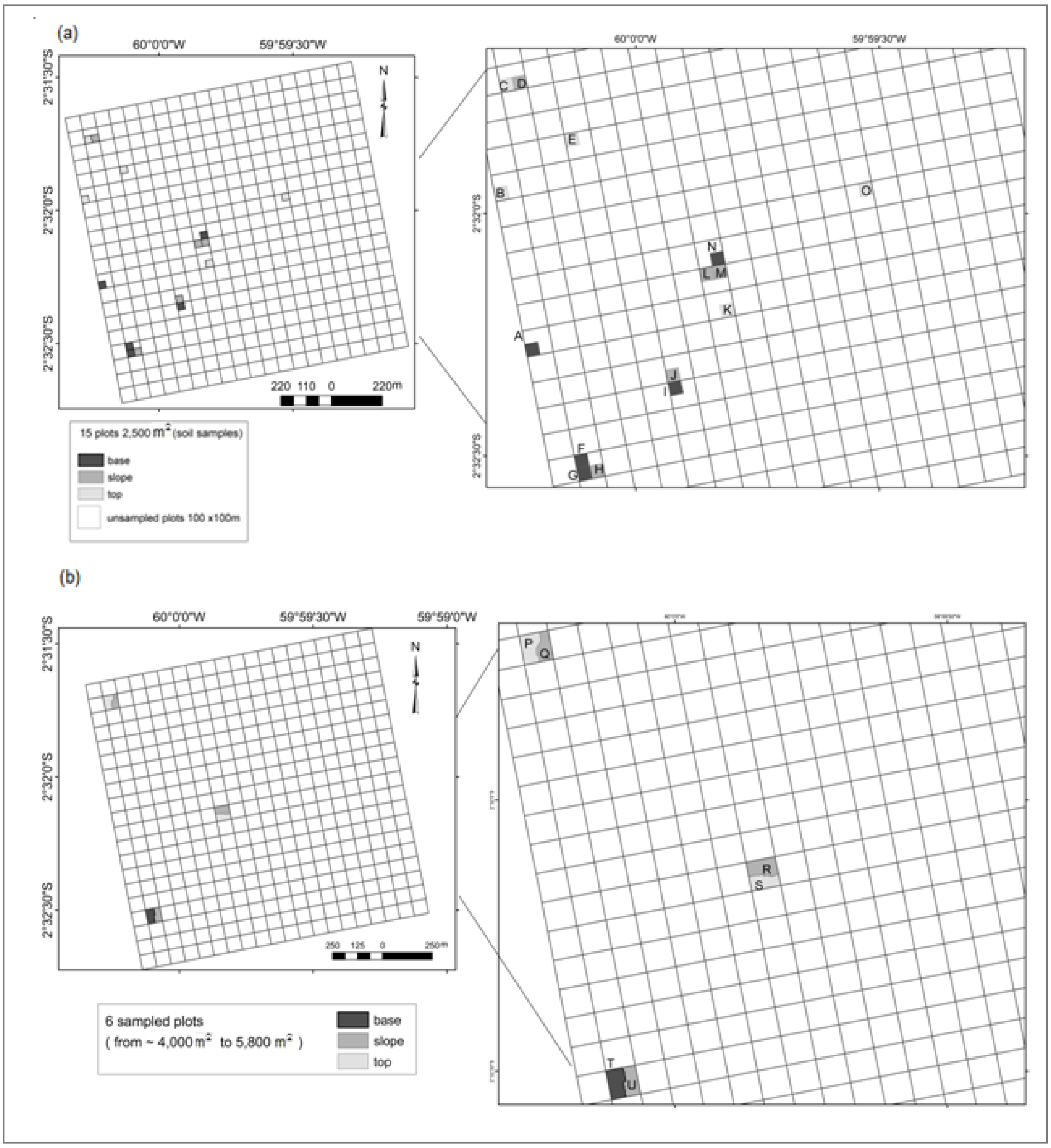

Fig. 1 Location of sample units at different sizes across study area: (a) fifteen plots of 2,500 m^2 where soil samples were collected. (b) Six plots of sizes ranging from ~ 4,000 to 5,800 m^2 where Ripley`s *K* was performed. The variation on the grey colors represents the topographic position of the plots

Each sample was a composite of 3 subsamples, separated at least 10 m from each other. Chemical (macro/micronutrients) and physical (texture) analyses were carried out for each soil sample and then nine soil variables were used at CCA: soil pH, organic matter (OM), concentration of P, Fe, Zn, Mn, aluminum toxicity (m%), sum of bases-SB (Ca, Mg, K, Na), and percentage of sand (S). Then, from the 264 species recorded at the 15 plots, the most abundant species (present everywhere) and the rare ones (up to four individuals) were excluded, resulting in 68 species retained for the CCA. The software PAST (PAleontological STatistics) was used to perform the CCA (Hammer and Harper 2009).

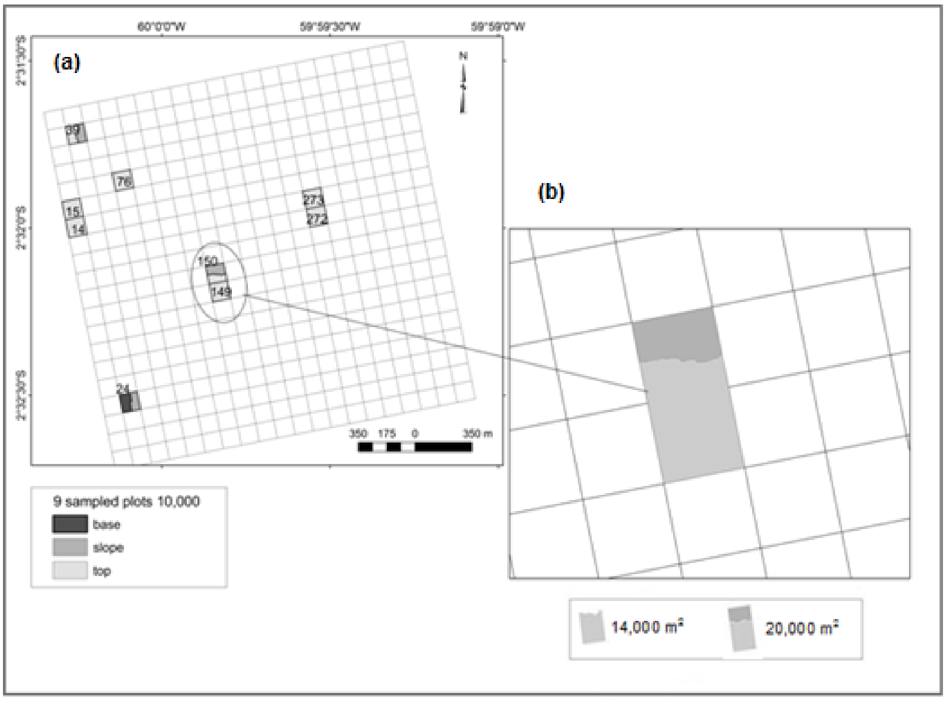

Fig. 2 Location of sampling units of different sizes: (a) nine plots of 10,000 m^2; (b) one plot of 14,000 m^2 and one plot of 20,000 m^2

As our intent was to study the spatial structure of species assemblage (hereafter community), we separate species in two groups using their scores in the two axes of CCA greater than or equal to |0.5|, avoiding species too close to the origin axes. After, we performed the point pattern analysis considering these two groups of species analyzed at the five sampling unit sizes, comprising 32plots.

Point Pattern Analysis

Spatial point processes are stochastic models that serve as appropriate tools for the analysis of patterns in ecological communities, representing the locations of objects in two- or more-dimensional space (Illian and Burslem 2007; Wiegand and Moloney 2004). To investigate the spatial structure of the community in the study area according to environmental factors (soil variables), we used the uni- and bivariate Ripley`s K analyses, applied to the species selected from the CCA (Fortin and Dale 2005; Illian et al. 2008; Shimatani and Kubota 2004; Wiegand and Moloney 2004). The study was conducted across the five sampling unit sizes, and the results were plotted as "$L(r) - r$" instead of K, which is a transformation of the Poisson K function to the straight line, with a constant value=0, making it easier to assess the deviation from the theoretical function. The bivariate case was used to compare Group 1 and Group 2 of species identified from the CCA, testing for dependence or independence of the process affecting the distribution of species in each group (Franklin and Rey 2007).

Monte Carlo tests were carried out, with a probability level of 5%, to test the empirical functions against the theoretical one, constructing simultaneous envelopes for the critical values under the null hypothesis of Complete Spatial Randomness (CSR). The test rejects the null hypothesis if the graph of the observed function lies outside the linearized envelope at any value of "r" distance (Baddeley 2008). The spatial analysis was performed by using the Spatstat package, in R software.

Results

The CCA, based on the 15 plots of 50 × 50 m, separated the species scores into two groups along the first two axes, which accounted for 52% of the composition variation (Fig. 3 and Table 1-online Resource1). Group 1 related 21 species to areas having sandy soil, higher P concentration, higher moisture content, lower Fe concentration, less organic matter and less acidity, and in general at the lowest position (base) according to the topography. Group 2 related 31 species to areas with lower moisture, higher clay, and higher organic-matter (OM) content.

The first CCA axis showed that the composition of species is correlated mainly with the concentration of Mn, OM, Zn, and sand. The second one axis indicated species correlated with the P and Fe concentrations and aluminum toxicity (m). Laurance et al. (1999) studied the relationship between soils and Amazon forest biomass in forests near to our study area, finding that clay areas were also associated with higher OM content and more-acid sites having less P and high aluminum saturation.

In our study area, considering the 15 plots of 50 x 50 m, the ones with higher contents of clay and OM (plots B, C, D, E, Fig. 1a) are those having, on average, larger numbers of individuals and basal area (*n*=150 and BA=7.021 m^2, respectively), and more mean number of species, compared with plots having more sand and P content (*n*= 103 and BA=4.33), such as plots A, F, I, N, and in general at the lowest position in the landscape (Fig. 1a and Fig. 3).

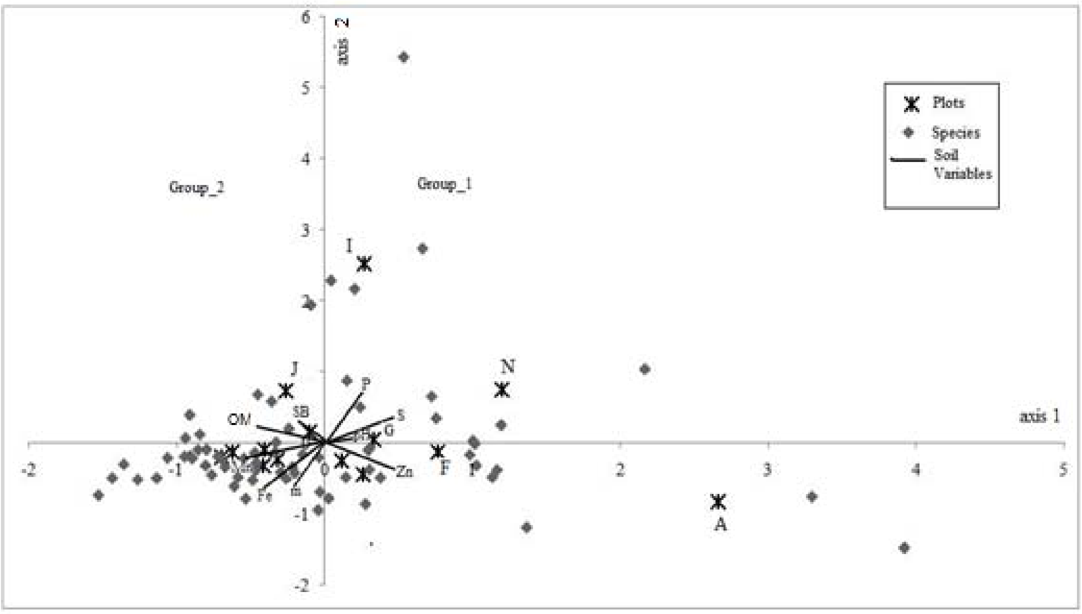

Fig. 3 CCA triplot based on 68 species, 15 plots and nine soil variables, for upland tropical rain forest data, at the Embrapa Experimental Site, Manaus, Amazonas, Brazil. (✱A,I,N,F are in general plots in the Group_1 side with sandy and wetter soils, and ✱ J and others in Group_ 2 side are plots with clayey and drier soils).

Of the 53 families identified over all the 15 mapped 50 x 50-m plots, 31 were represented in the two groups of species studied. Only six families, the Annonaceae, Euphorbiaceae, Fabaceae-Mimosoideae, Lecythidaceae, Meliaceae, and Sapotaceae were common to both groups. The species in the plots with more humid, sandy soils (Group 1) represented 13 families, of which Burseraceae, Sapotaceae, Malvaceae, Fabaceae-Caesalpinioideae, and Fabaceae-Mimosoideae comprised 69% of the total number of individuals in this group. Species in the plots with drier and more-acid soils with higher clay and OM contents (Group 2) represented 18 families, with Sapotaceae, Lecythidaceae, Annonaceae, Moraceae, and Lauraceae comprising 55% of the total number of individuals.

Some species were well separated in both groups by the CCA axes, occurring in plots with different soil conditions. Within Group 1, species such as *Abarema jupunba* (Willd.) Britton & Killip, *Eperua duckeana* R.S. Cowan, *Erythroxylum amplum* Bth., *Macrolobium limbatum* Spruce ex Benth, and *Carapa guianensis* Aubl. were found mainly near plots with more sand, P, and OM (plot I, Fig. 3), and more moisture content (Silva, 2010, personal communication). In the same Group 1, the soil variation, mainly in OM and moisture, seemed to favor different arrangements of species in plots having less-humid soils with less OM (plots N and F), but similar sand content, such as *Theobroma subincanum* Mart., *Guatterria olivacea* R.R.Fr., *Simarouba amara* Aubl., *Trattinnickia burserifolia* Mart., *Tapura amazonica* Poepp. & Endl., *Protium pilosissimum* Engl., *Chrysophyllum sanguinolentum* (Pierre) Baehni, *Inga alba* (Sw) Willd., and *Sterculia pruriens* (Aubl.) K. Schum. Within Group 2, we observed that *Xylopia calophylla* R.E. Fr., *Manilkara bidentata* (A.DC.) A. Chev., *Goupia glabra* Aubl., *Lecythis graciena* S.A. Mori and *Distomovita brasiliensis* D'Arcy, among others, occurred in drier, clayey soils with more OM (plots C and D, mainly), compared with the species in Group 1. In general, the more humid and sandy plots were in the lowest topographic position, along stream valleys, and the drier clayey plots were on plateaus (top position).

The largest proportion of species (68%) growing in the sandy and wetter plots (Group 1) have small, light seeds, followed by 18% with large-sized seeds (Camargo et al. 2008; Martinez et al. 1997; Roosmalen 1985). Forty-seven percent of species occurring in the more-acid, clay, and drier plots (Group 2) have small seeds, followed by twenty-eight percent of species with medium-sized seeds. These traits may have an important influence on the spatial patterns displayed by the two groups of species, related to their seed dispersal.

The point pattern analysis performed for the two groups individually showed that the CCA was helpful to reveal structure in the species assemblage, only when the sample unit size was large enough to allow the detection of spatial dependence. That is, from the sample unit sizes of 2,500 m^2 up to 5,870 m^2, the univariate Ripley`s *K* analyses did not detect any significant spatial pattern for the two groups. The bivariate analysis comparing the two groups also did not show significant evidence of dependence between species occurring in the sandy and wetter plots, and those in the more-acid and drier plots considering the same sample sizes cited above.

As the sample unit sizes increased, some degree of structure began to appear. This was observed for five out of nine plots with 10,000 m^2 where species showed some structure within both groups, which are presented at Fig. 4. Species in drier, more-acid plots (Group 2) showed aggregation over small to large scales, with some variation in the resulting patterns across plots (Fig. 4 a, b, c). For species in the sandy and wetter plots (Group 1), aggregation was observed for distances from 25 m up to 55 m (Fig. 4 d, e).

The same tendency of showing spatial pattern was observed when the sample unit size of 14,000 m^2 was analyzed for species in the drier, more acid plots (Group 2), with a clearer pattern for distances larger than 22 m (Fig. 5d). However, species in the sandy and wetter plots (Group 1) did not reveal a different pattern from CSR for the univariate analyses (Fig. 5a).

The bivariate analyses of species occurring in the sandy, wetter plots (Group 1) and in drier, more-acid plots (Group 2), also in the sample size unit of 14,000 m^2, showed attraction between species for distances around 30 m and larger, with more strength in the direction from Group 1 to Group 2, once more confirming that the soil characteristics in this plot are favorable to species that occur in the drier, more-acid plots, that is, species of Group 2 (Fig. 5 b, c).

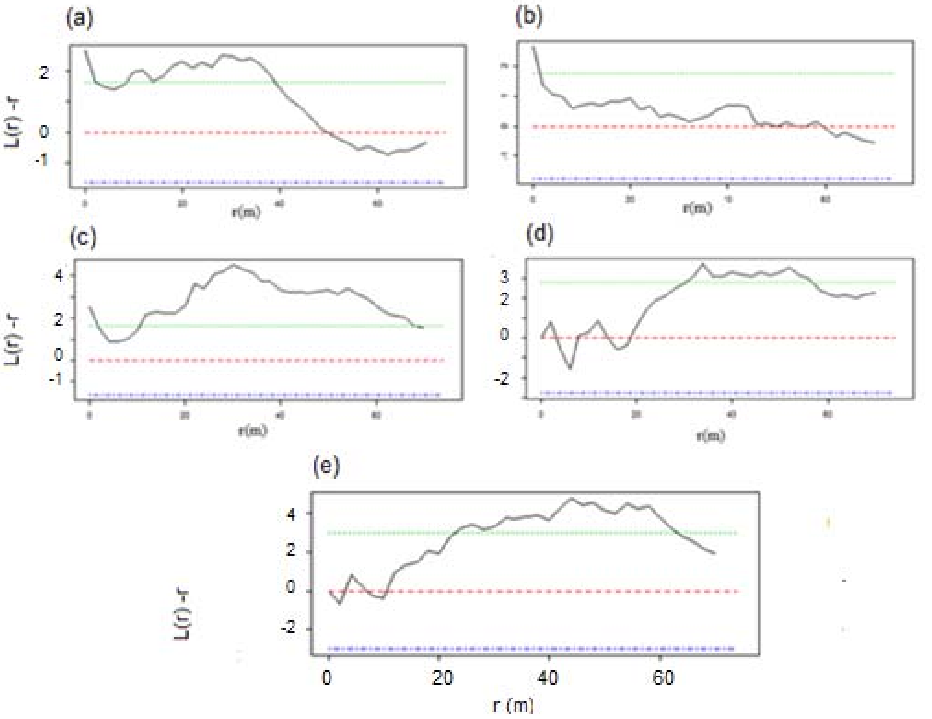

Fig. 4 Ripley`s function "*L(r)-r*", univariate analysis at 10,000 m^2 plots in the Embrapa Experimental Site. (a) Plot 15, (b) Plot 76, and (c) Plot 149, where species of Group 2 showed different patterns from Complete Spatial Randomness-CSR; (d) Plot 150; and (e) Plot 273, where species of Group 1 showed significant patterns. Upper and lower dotted lines represent the critical envelope under the null hypothesis of CSR (dotted line on zero value)

The effect of the environmental factors (soil variables) structuring the distribution of species was better observed in the largest sample unit size of 20,000 m^2 (combined plots 149 and 150, Fig. 2b). The analysis carried out including all species occurring in that plot, without using the CCA and disregarding the species groups showed a random distribution (Fig. 6a). On the other hand, when the analysis was done using species selected from the CCA (Groups 1 and 2 together), the resulting pattern was aggregated for distances larger than 30m (Fig. 6b). The greatest part of this plot is positioned at top position according to topography (Fig. 2b).

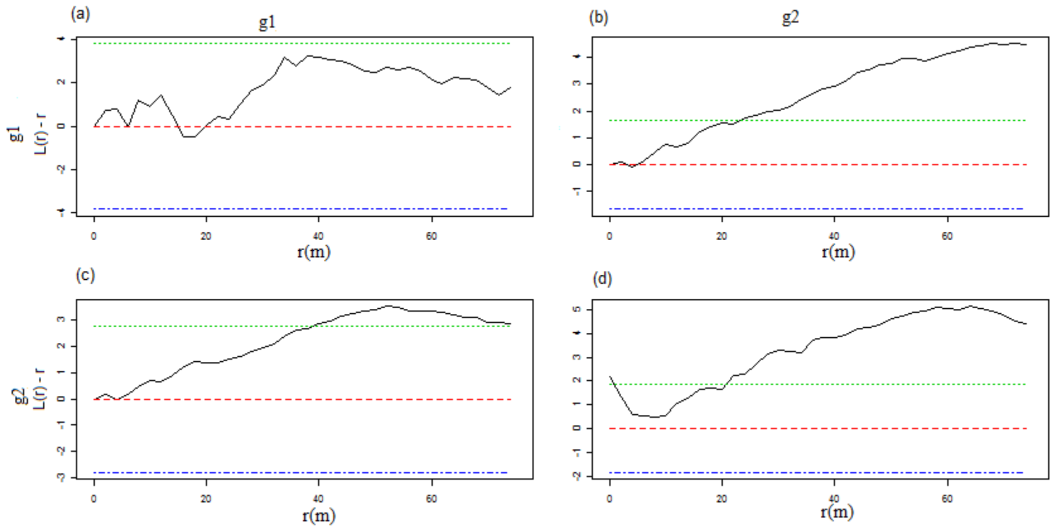

Fig. 5 Ripley`s function "*L(r)-r*", univariate/bivariate analysis at ~ 14,000 m^2 (combination of plots 149 and 150 at the top position), in the Embrapa Experimental Site. (a) and (d) are univariate analyses for Group 1 (g1) and Group 2 (g2), respectively; (b) and (c) are the bivariate analyses between Group 1 and Group 2

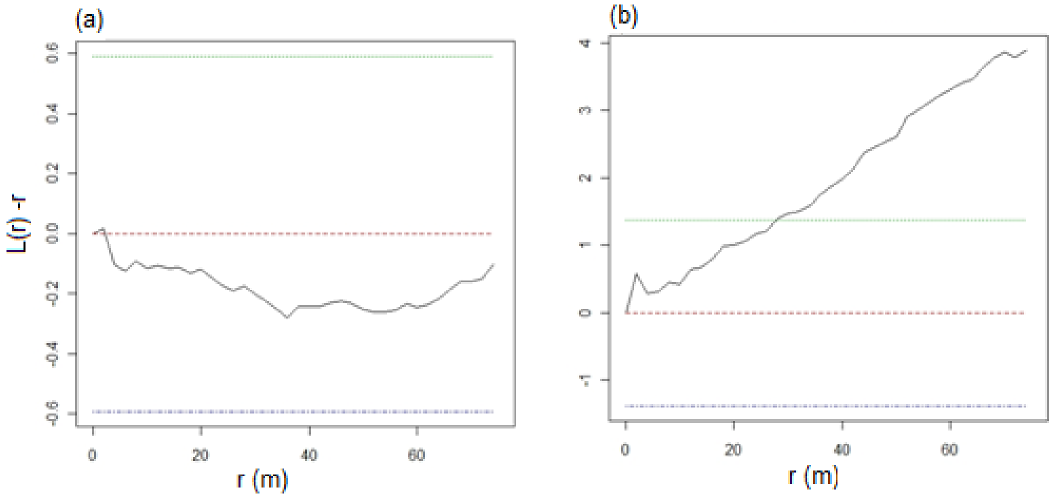

Fig. 6 Ripley`s function "*L(r)-r*", for the plot with 20,000 m^2 (combined plots 149 and 150). (a) all species in the plot are considered, without separation into groups; (b) species found in both groups (Group 1 and Group 2) are analyzed together

Discussion

Direct gradient analysis-CCA identifies the compositional gradient in vegetation as a response to measured environmental factors, which are often spatially structured (Wagner 2003). The interactions between living communities and their environment, and among the organisms themselves, occur at definite spatial and temporal scales, and give rise to spatial patterns that must be assessed in order to better understand the processes structuring these communities (Bocard et al. 2004; Jombart et al. 2009).

The results found in our study have shown that environmental and ecological factors are driving the way that tree species are organized in this forest, with a strong effect of spatial dependence among species and soil variables, which could be identified at the intermediate sample unit size (10,000 m^2) and more obviously for the sizes larger than or equal to 14,000 m^2. Poulsen et al. (2006) found that differences in elevation and soil factors were highly correlated with floristic differences within a 1-ha plot in a tropical rainforest in Ecuador, indicating that soil factors may have played an important role for distribution and beta diversity of plants, even at the local scale. Also, Coronado et al. (2009) found that soil fertility was a good predictor for studies on floristic patterns in the Amazon Basin.

Observed spatial patterns often result from a combination of several processes operating on different spatial and temporal scales (Fortin and Dale 2005). In the present study, the observed variation in the patterns, especially associated with species growing in drier, clayey soils, Group 2 (Fig. 4 a, b, c) could also be explained by ecological processes: a high proportion (60%) of the species in this group are canopy species with small and medium-sized seeds, which might have their seeds dispersed over wide distances. Processes generating aggregation at short distances, such as dispersal and competition, should be better investigated in future studies, using stem diameters smaller than 10 cm.

Many studies conducted in tropical rainforests have indicated that species respond differently to environmental factors, and soil variables are commonly studied because of their importance in explaining variations in the distribution and performance of species (Baltzer et al. 2007; Jones et al. 2006; Tuomisto 2006). Forest structure and dynamics have been noted to vary across the Amazon Basin in an east-west gradient, in a pattern that coincides with variations in soil fertility and geology, even at regional scales (Quesada et al. 2009). In the present study, despite the general low fertility throughout the study area, local gradients could be detected. Our plots ranged from plateaus to lowland areas in stream valleys, which form a gradient in topography and soil conditions, mainly in texture in the east-west, and also in the northwest-southwest directions (Fig. 1a and Fig. 3). Phillips et al. (2004) suggested that an edaphic resource gradient, mediated by soil quality, was likely the cause of the observed floristic gradient in their study of pattern and process in Amazon tree turnover.

The ordination of species along the gradient of soil variables (CCA) in our study area, allowed us to group species occurring in plots with different soil features, which resulted in differences in the spatial patterns for those species. The observed differences in the two groups were directly affected by the variations in the topographic position of the sampling units (plots), which were also responsible for the variations in soil features. The largest number of plots located in the top position, with generally drier and more-acid soils, met the requirements of species in Group 2, which were more frequently found in plots with these soil characteristics. Coronado et al. (2009), in their multi-scale comparisons of tree composition in Amazon "terra firme" forests, found a floristic east-west gradient in a large, regional-scale study conducted in the Amazon Basin. They also observed that species of Lecythidaceae and Sapotaceae were characteristically found on poorer soils. Our study showed similar results at the local scale, with Lecythidaceae and Sapotaceae having large numbers of both species and individuals over the entire study area. We observed local differences in the occurrence of these two families in the two groups, with species of Lecythidaceae occurring more in acid clayey soils (Group 2), and less in moister sandy soils. Therefore, it is expected that the families Lecythidaceae and Sapotaceae more strongly influenced the observed spatial patterns across the plots situated mainly in the top position (plateaus).

In the sampling unit size of 14,000 m^2, strong aggregation was observed for species in Group 2, whose soil requirements seem to match with the features of this plot, which is completely within the top position of the landscape (Fig. 1b and Fig. 5d). No similar pattern was observed for species in Group 1, reinforcing the effect of soil variations mediated by the topography (Fig. 5a). Future investigations that include explicit spatial information on soil variables, and plots located over the entire topographical variation of the area, mainly in the base (low) position, can help to better characterize the responses of the species growing in moister sandy soils (Group 1).

An important aspect is the effect of the size of the sampling units, to allow us to visualize the spatial structure of the species and /or community depending on our goals. Cunha (2003) studied the spatial patterns of three tropical tree species with dbh $\geq$ 35 cm in Pará State, Brazil, aiming to identify and interpret these patterns with a view toward application in forest management projects. He suggested that 100 ha should be the minimum unit size; this conclusion was probably influenced by the minimum diameter used, resulting in a small number of individuals above this class. Such a low number of individuals per species is expected for the Amazon forest conditions, and requires larger areas to attain a comprehensive view of these patterns. In the present study, a minimum sampling unit size of 10,000 m^2 was necessary to obtain a better view of the spatial dependence of species distributions on soil variables.

Overall, for the larger sampling unit sizes (14,000 m^2 and 20,000 m^2), the soil variables played an important role, with strong aggregation being found for species preferring more clayey and drier plots (Group 2), when the set of species selected from the CCA was used for these plots (Figs. 5 and 6). The soil requirements of these species seemed to be satisfied by these two larger sampling units. The minimum size of 10,000 m^2 shows the importance of using this value for studies assessing the effect of soil variables on forest communities.

Conclusion

Our results contribute to the knowledge of the spatial structure of the Amazon tropical tree community, in particular for the “terra firme” tropical rainforests. Our findings showed that the spatial structure of the tree species has been driven both by ecological processes (dispersal, competition) and by soil variables mainly, and that the species respond differently to these factors. The observed soil gradients of fertility and texture seem to repeat the same tendency observed at broad and regional scales noted in several studies across the Amazon Basin. The species are organized in general along the gradient of OM, moisture, and texture, and spatial structure was better revealed when the patterns were investigated in plots that met the species requirements. However, the effect of these factors was only observable from sample unit sizes larger than 10,000 m^2, which reflected the environmental heterogeneity, characterized by the soil variables and topographic position. These results provide important information for the design of sampling units used in studies of forest dynamics for management purposes and also conservation programs. Such studies must include the environmental heterogeneity based on an appropriate scale of analysis, in order to better understand, characterize, and protect the structure of “terra firme” tree species communities in the Amazon region.

Acknowledgments

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Online Resource 1

Online Resource 1

Spatial structure of tree species community in a “terra firme” Amazon rainforest near Manaus, Brazil

Table 1 List of species resulting from CCA, grouped in two groups and used for Ripley’s *K* analysis in five different sampling unit sizes at the Experimental site of Embrapa, Manaus, Amazonas, Brazil.

Group	Scientific name	Family
g1	*Abarema jupunba*(Willd.) Britton &Killip	Fabaceae-Mimosoideae
g1	*Aparisthmium cordatum* Baill.	Euphorbiaceae
g1	*Carapa guianensis* Aubl.	Meliaceae
g1	*Chrysophyllum sanguinolentum* (Pierre) Baehni	Sapotaceae
g1	*Endopleura uchi* (Huber) Cuatrec.	Humiriaceae
g1	*Eperua duckeana* R.S.Cowan	Fabaceae-Caesalpinioideae
g1	*Erythroxylum amplum* Bth.	Erythroxylaceae
g1	*Eschweilera truncata* A.C.Sm.	Lecythidaceae
g1	*Eschweilera wachenheimii* (Benoist) Sandwith	Lecythidaceae
g1	*Guatterria olivacea* R.R.Fr.	Annonaceae
g1	*Inga alba* (Sw) Willd.	Fabaceae-Mimosoideae
g1	*Inga suberosa* T.D.Penn.	Fabaceae-Mimosoideae
g1	*Macrolobium limbatum* Spruce ex Benth	Fabaceae-Caesalpinioideae
g1	*Protium heptaphyllum* (Aubl.) ssp. ulei (Swart) Daly	Burseraceae
g1	*Protium pilosissimum* Engl.	Burseraceae
g1	*Simarouba amara* Aubl.	Simaroubaceae
g1	*Sterculia pruriens* (Aubl.) K.Schum.	Malvaceae
g1	*Tapura amazonica* Poepp. & Endl.	Dichapetalaceae
g1	*Theobroma subincanum* Mart.	Malvaceae
g1	*Theobroma sylvestre* Mart.	Malvaceae
g1	*Trattinnickia burserifolia* Mart.	Burseraceae
g2	*Agonandra brasiliensis* Miers	Opiliaceae
g2	*Aspidosperma marcgravianum* Woodson	Apocynaceae
g2	*Couratari alta* Kunth.	Lecythidaceae
g2	*Distomovita brasiliensis* D' Arcy	Clusiaceae
g2	*Eschweilera atropetiolata* S.A.Mori	Lecythidaceae
g2	*Geissospermum argenteum* Woodson	Apocynaceae
g2	*Goupia glabra* Aubl.	Goupiaceae
g2	*Helicostylis scabra* (Macbr.)	Moraceae
g2	*Helianthostylis sprucei* Baill.	Moraceae
g2	*Hevea guianensis* Aubl.	Euphorbiaceae
g2	*Lecythis graciena* S.A.Mori	Lecythidaceae
g2	*Lecythis usidata* Camb.	Lecythidaceae
g2	*Licaria guianensis* Aubl.	Lauraceae
g2	*Licania* sp.	Lauraceae
g2	*Mabea* sp.	Euphorbiaceae
g2	*Manilkara bidentata* (A.DC.) A. Chev.	Sapotaceae
g2	*Micropholis trunciflora* Ducke	Sapotaceae
g2	*Mouriri callocarpa* Ducke	Melastomataceae
g2	*Neea oppositifolia* Ruiz & Pav.	Nyctaginaceae
g2	*Pithecellobium elegans* Ducke	Fabaceae-Mimosoideae

Group	Scientific name	Family
g2	*Pouteria caimito* (Ruiz & Pav.) Radlk.	Sapotaceae
g2	*Pouteria laurifolia* (Gomes) Radlk.	Sapotaceae
g2	*Pouteria venosa* (Mart.) Baehni ssp. amazonica T.D.Penn.	Sapotaceae
g2	*Pytchopetalum olacoides* Benth.	Olacaceae
g2	*Rinorea racemosa* (Mart.) Kuntze	Violaceae
g2	*Stryphnodendron* sp.	Fabaceae-Mimosoideae
g2	*Swartzia recurva* Poepp.	Fabaceae-Faboideae
g2	*Talisia* cf. *cupularis* Radlk.	Sapindaceaea
g2	*Trichilia micropetala* T.D.Penn.	Meliaceae
g2	*Unonopsis duckei* (R.&P.)Macba.	Annonaceae
g2	*Xylopia calophylla* R.E. Fr.	Annonaceae

Artigo 4

Neighbour`s Identity of Commercial Tropical Tree Species in a Tropical Rainforest Near Manaus, Brazil.

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 ≥ 10.0 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.

Key words: neighbourhood analysis; tropical tree species; central Amazonian; *terra firme* forest.

1. 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 (Mouquet et al., 2002; Cardinale et al., 2004; Illian and Burslem, 2007). Understanding the impact of biodiversity loss on ecosystems requires an understanding of the processes that structure communities and the mechanisms that sustain biodiversity (Hubbell et al., 2001; Condit et al., 2002; Castilho et al., 2010). 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 (Peters, 2003). Spatial patterns of trees in forest stands reflect, indeed, the 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.

Tropical forests, one of the world's most species-rich terrestrial ecosystems, are the focus of ongoing attempts to describe, interpret and understand the importance of such mechanisms for community-level properties, such as species richness and abundance (Peters, 2003), 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 (Greig-Smith, 1979; Smith and Grant, 1986; Law et al., 2009).

It has been recognised that coexistence is in part determined by the inter- and intra-specific interactions in a community (Mouer, 1993; Murrel et al., 2001), 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 (Hubbell, 1990; Law et al., 2003), because plants compete with their immediate neighbours for limited resources above or below ground, or for both (Schneider et al., 2006). 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 (Moustakas et al., 2008; Potvin and Dutilleul, 2009).

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 (Condit et al., 2000; Leigh Jr. et al., 2004; Vogt et al., 2010). 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 (Vanclay, 1991). 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.

Taxonomic proximity might be expected to increase overlap in resource requirements or the likelihood of shared enemies, augmenting the strength of interactions among neighbouring species, which also could contribute to species coexistence (Uriarte et al., 2004). These authors found in their studies at the Barro Colorado Island (BCI), Panamá that families and species differed in the response to neighbour groupings where for most legumes, the taxonomic identity or light guild of the neighbours had distinct effects on sapling growth. So, the variation among species in response to crowding or to the identity of neighbouring species is likely to contribute to the maintenance of species diversity in tropical forests (Uriarte et al., 2004; Potvin and Dutilleul, 2009).

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.

2. Methods

2.1. *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, having an area of 2-ha, 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, 1999). 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 (Regis, 1993). 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 (Laurance et al., 2004).

2.2. Field sampling and species information

At the 2-ha study area (100mx200m), 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 the species having only one (01) individual and about 68 percent from 1 to 5 individuals (Fig. 1).

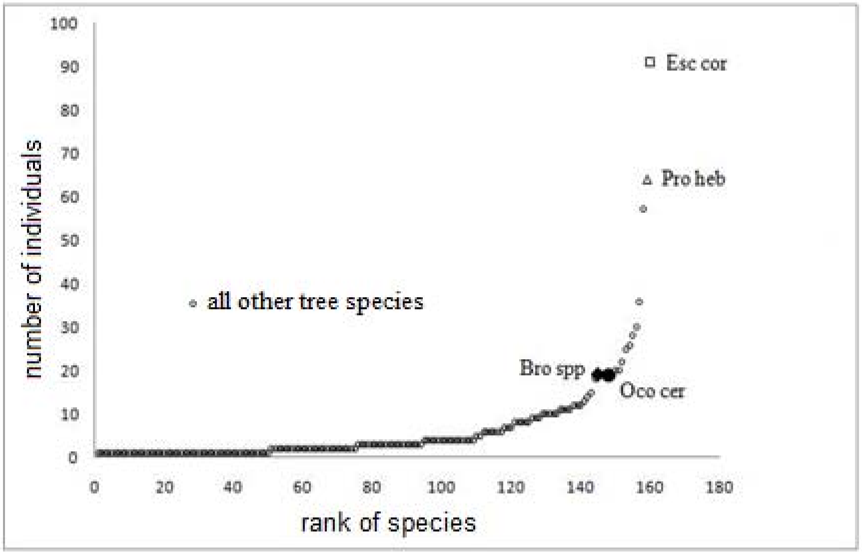


Fig.1. Number of individuals per species at the 2-ha study area, highlighting the four commercial species studied.

From the list of species identified at the 2-ha plot, four commercial tree species largely used by 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 on, 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, are generally 20 to 30 meters tall, present high density wood and small seeds. According to studies of Marimon et al. (2008), 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 (Nelson and Oliveira, 2001; Lopes, 2007). 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 and Mori, 1978).

Ocotea cernua- lauraceae family, produces small fruits and trees occupy the midstorey and canopy position (Comita et al., 2007). 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 (Ribeiro et al., 1994). It is typical understory species, medium tall and has medium size fruits and seeds, with mainly endozoocoric dispersal (Andrade and Higuchi, 2009).

2.3. 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, 2008), 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 results 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 (Fortin and Dale, 2005); (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.

3. Results

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.

3.1. 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 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.

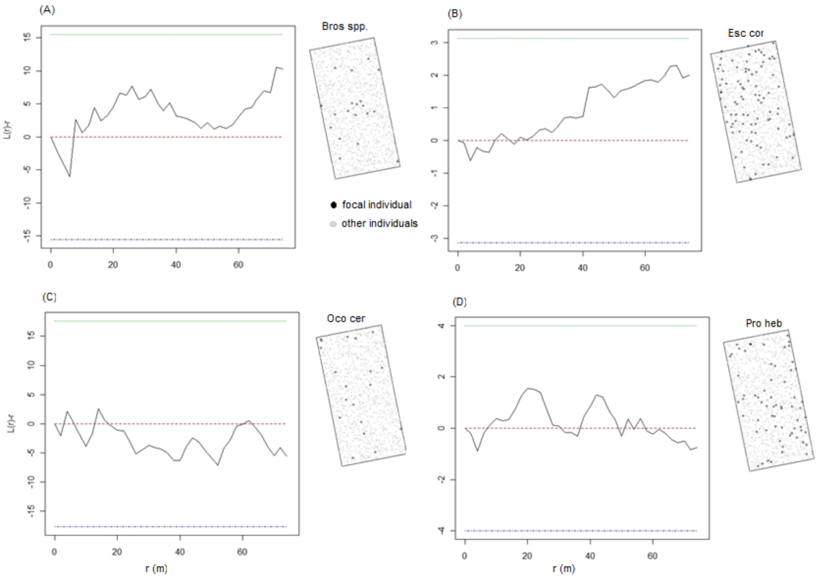


Fig. 2. Ripley`s function “*L(r)-r*” to the four species studied. (A) *Brosimum* spp.; (B) *Eschweilera coriacea*, (C) *Ocotea cernua*, and (D) *Protium hebetatum*.Dotted upper and lower lines are the simultaneous critical envelopes of 95% based on complete spatial randomness.

The analyses aiming to investigate the taxonomic pattern in the occurrence of neighbours of focal species are presented below for each focal species individually, and the complete list of neighbour species is presented at Appendix.

(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.

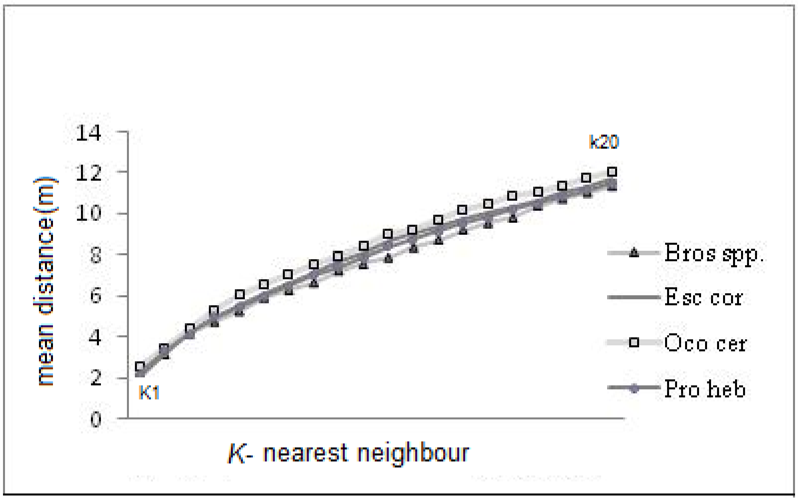


Fig. 3. Mean distance from focal trees of the four commercial tree species up to the 20th nearest neighbour at 2-ha study area.

In spite of the low mean proportion of conspecific trees along the 20-*k*-*n*earest 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).

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

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

The total number of species registered at the first *k*-nearest neighbour (*k*1) 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.

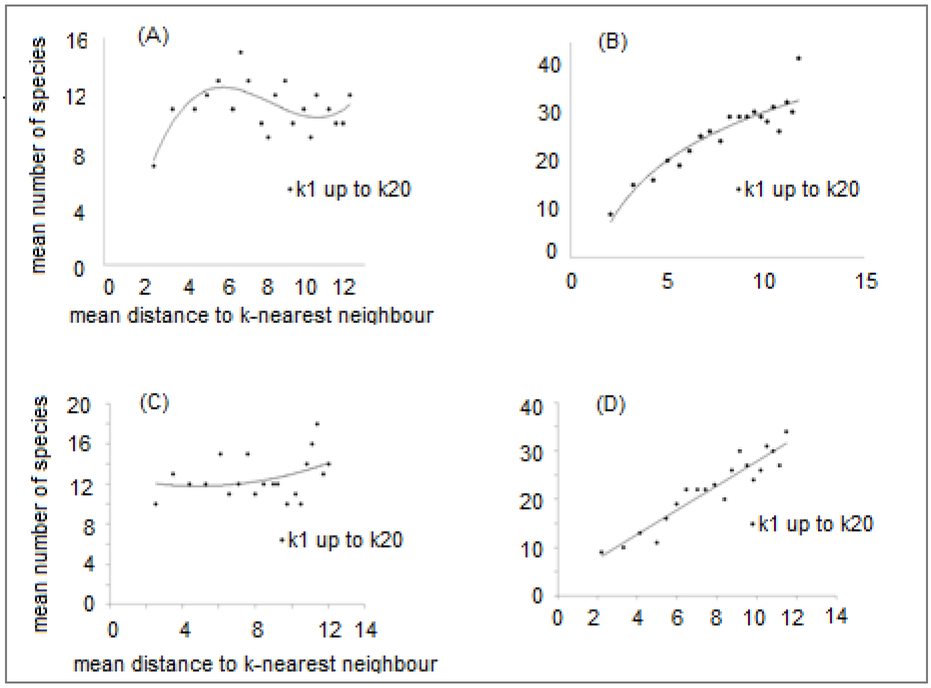
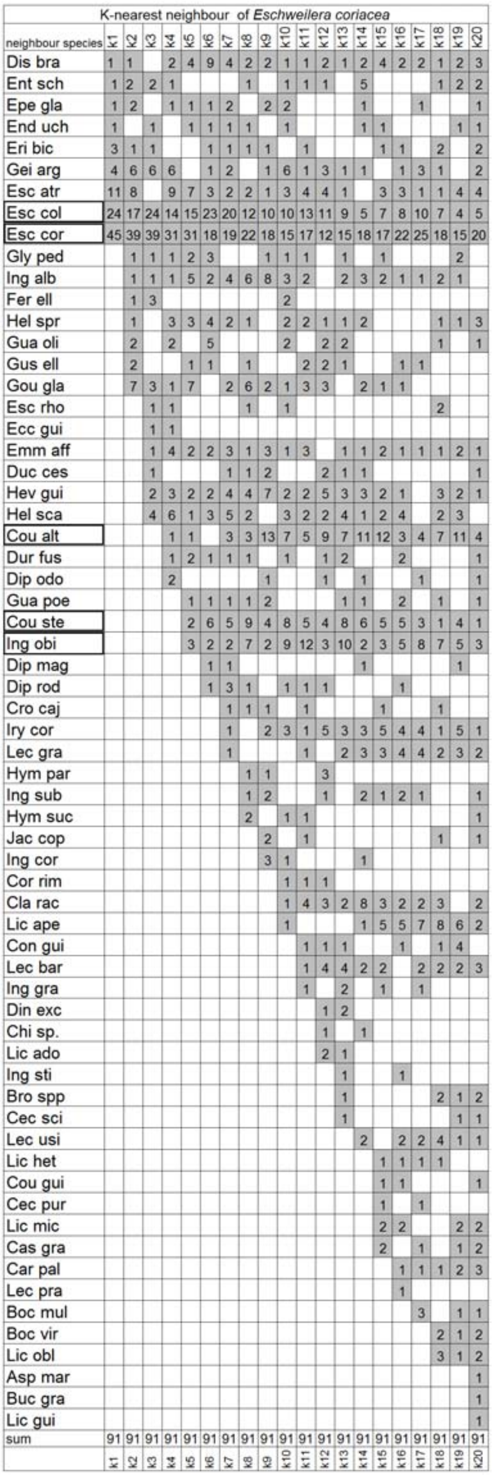


Fig. 5. Number of species by the mean distance registered up to the 20-*k*nearest neighbours of four focal species at the study area. (A) *Bros*imum spp. (Bro spp), (B) *Eschweilera coriacea* (Esc cor), (C) *Ocotea cernua* (Oco cer), and (D) *Protium hebetatum* (Pro heb).

(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 some degree of 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 decreases 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".

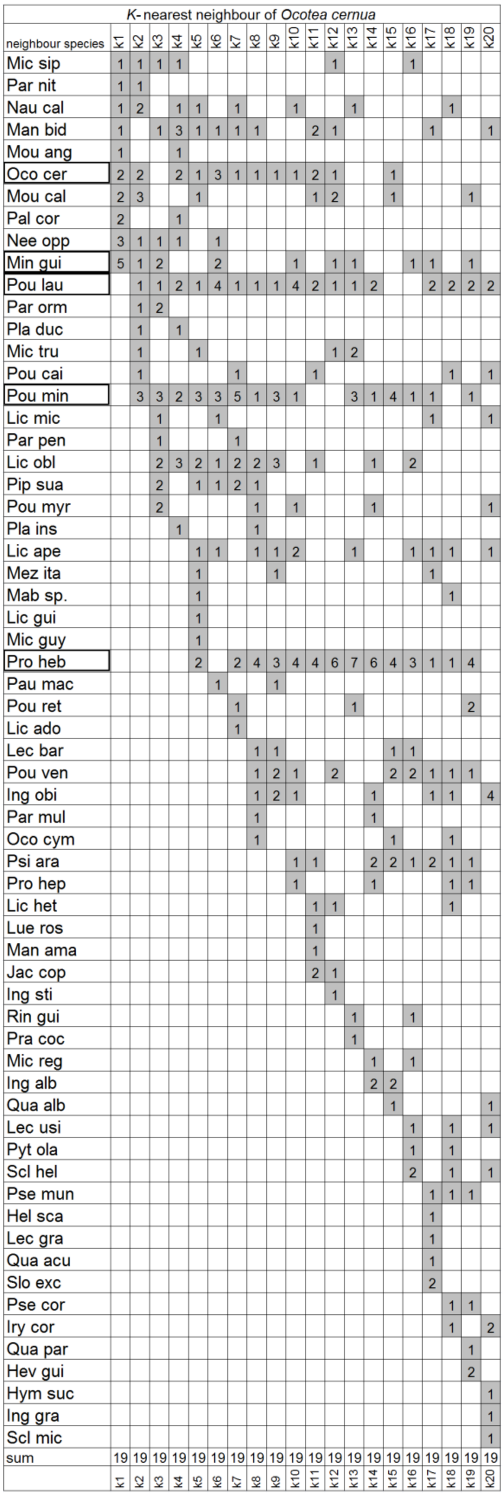
Considering the other species, there is no visible pattern in their occurrence due to the low frequency values (below 4 %) for both short and high distances. This could be ratified by the tendency of fast increase in the number of species from the first *k*-nearest neighbour, with the highest value to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



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

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



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

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

(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.

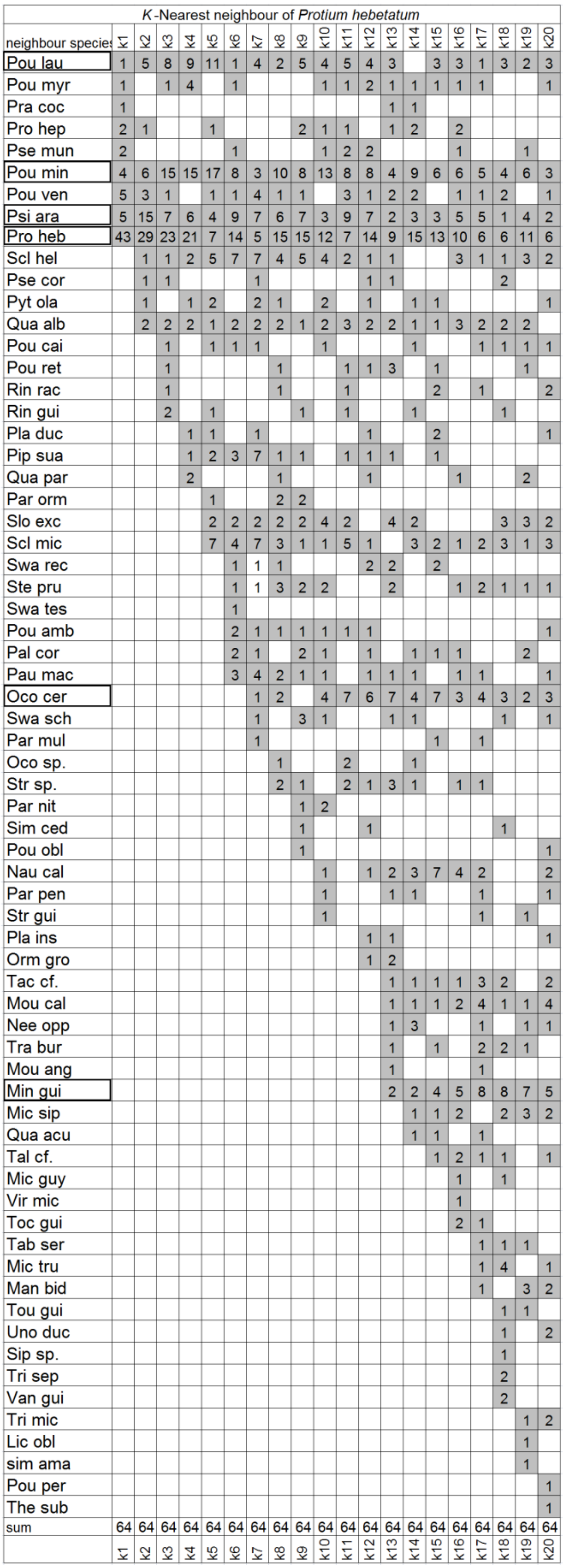
The mean richness at each focal tree is 14 species and the mean proportion of conspecifics 5 percent, with SD equal to 0.90 individuals. At shorter distances, within the first four nearest, the relative frequency of species is in general below 15 percent, with no tendency of association among species 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 (*k*1).

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 the focal species 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 *k*th 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 20*k*s-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).



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

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

4. 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. Condit et al. (2000) and Vogt et al. (2010) observed in their studies that the frequency with which individuals have other individuals of the same or different species as their neighbours depended less on the relative abundance than on the particular spatial pattern, where it is expected that intraspecific encounters could be much more frequent than interspecific ones when species exhibit aggregated patterns.

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 (Lopes, 2007).

Connel et al. (1984) studied the effect of distance to neighbour on mortality of both seedling and saplings, in a tropical rainforest in Australia, finding that mortality was significantly higher when conspecific neighbours were closer for the most of the species investigated. 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 (47 and 63 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 *k*th-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 the 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.

5. Conclusions

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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Appendix:Neighbour species of four focal tree species at the Embrapa experimental site, Manaus, state of Amazonas, Brazil.

Species Code	**Scientific Names**	**Family**
Ago bra	Agonandra brasiliensis Miers	Opiliaceae
Amb duc	Ambelania duckei Markgr.	Apocynaceae
Ani can	Aniba canellila (H.B.K.)Mez.	Lauraceae
Ani hos	Aniba hostmaniana (Ness) Mez.	Lauraceae
Ani meg	Aniba megaphylla Mez	Lauraceae
Ani ros	Aniba rosaeodora Ducke	Lauraceae
Ann amb	Annona ambotay Aubl.	Annonaceae
Ape ech	Apeiba echinata Gaertner	Malvaceae
Asp alb	Aspidosperma album (Vahl.) R. Bem.	Apocynaceae
Asp mar	Aspidosperma marcgravianum Woodson	Apocynaceae
Ast lec	Astronium lecointei Ducke	Anacardiaceae
Boc mul	Bocageopsis multiflora (Mart.) R.E.Fr.	Annonaceae
Boc vir	Bocoa viridiflora (Ducke) R.S.Cowan	Fabaceae-Faboideae
Bro spp	*Brosimum lactescens* (S.Moore) C.C.Berg	Moraceae
Bro spp	*Brosimum acutifolium* Huber ssp. Interjectum C.C.Berg	Moraceae
Bro spp	*Brosimum utile* (H.B.K.) Pittier ssp. ovatifolium (Ducke) C.C.Berg.	Moraceae
Bro spp	*Brosimum rubescens* Taub.	Moraceae
Buc gra	Buchenavia grandis Ducke	Combretaceae
Car pal	Caryocar pallidum A.C. Smith	Caryocaraceae
Cas gra	Casearia grandiflora Cambess	Salicaceae
Cec pur	Cecropia purpurascens C.C. Berg	Urticaceae
Cec sci	Cecropia sciadophylla Mart.	Urticaceae
Chi duc	Chimarrhis duckeana del Prete	Rubiaceae
Chi sp.	Chimarrhis sp.	Rubiaceae
Cla rac	Clarisia racemosa Ruiz & Pav.	Moraceae
Con gui	Conceveiba guianensis Aubl.	Euphorbiaceae
Cor rim	Corythophora rimosa W.A.Rodrigues	Lecythidaceae
Cou alt	Couratari alta Kunth.	Lecythidaceae
Cou gui	Couratari guianensis Aubl.	Lecythidaceae
Cou ste	Couratari stellata A.C.Sm.	Lecythidaceae
Cro caj	Croton cajucara Benth.	Euphorbiaceae
Din exc	Dinizia excelsa Ducke	Fabaceae-Mimosoideae
Dip mag	Dipteryx magnifica Ducke	Fabaceae-Faboideae
Dip odo	Dipteryx odorata (Aubl.) Willd.	Fabaceae-Faboideae
Dip rod	Diplotropis rodriguesii Lima	Fabaceae-Faboideae
Dis bra	Distomovita brasiliensis D' Arcy	Clusiaceae
Duc ces	*Duckeodendron cestoides* Kuhlm.	Solanaceae
Dur fus	*Duroia fusifera* Hook. F. ex K. Schum.	Rubiaceae
Ecc gui	*Ecclinusa guianensis* Eyma	Sapotaceae
Emm aff	*Emmotum aff. nitens* Benth. Ex Miers	Icacinaceae
End uch	*Endopleura uchi* (Huber) Cuatrec.	Humiriaceae
Ent sch	*Enterolobium schomburgkii* Benth.	Fabaceae-

Species Code	**Scientific Names**	**Family**
		Mimosoideae
Epe gla	*Eperua glabriflora* (Ducke) R.S.Cowan	Fabaceae-Caesalpinioideae
Eri bic	*Erisma bicolor* Ducke	Vochysiaceae
Esc atr	*Eschweilera atropetiolata* S.A.*Mori*	Lecythidaceae
Esc col	*Eschweilera collina* Eyma	Lecythidaceae
Esc cor	*Eschweilera coriacea* (DC.) S.A. Mori	Lecythidaceae
Esc rho	*Eschweilera rhododendrifolia* (Knuth) A.C.Sm.	Lecythidaceae
Fer ell	*Ferdinandusa elliptica* Pohl.	Rubiaceae
Gei arg	*Geissospermum argenteum* Woodson	Apocynaceae
Gly ped	*Glycoxylon pedicellatum* (Ducke) Ducke	Sapotaceae
Gou gla	*Goupia glabra* Aubl.	Goupiaceae
Gua oli	*Guatterria olivacea* R.R.Fr.	Annonaceae
Gua poe	*Guatteria poeppigiana*	Annonaceae
Gus ell	*Gustavia elliptica* S.A.Mori	Lecythidaceae
Hel sca	*Helicostylis scabra* (Macbr.)	Moraceae
Hel spr	*Helianthostylis sprucei* Baill.	Moraceae
Hev gui	*Hevea guianensis* Aubl.	Euphorbiaceae
Hym par	*Hymenea parvifolia* Huber	Fabaceae-Caesalpinioideae
Hym suc	*Hymatanthus sucuba* (spruce)Woodson	Apocynaceae
Ing alb	*Inga alba* (Sw) Willd.	Fabaceae-Mimosoideae
Ing cor	*Inga cordatoalata* Ducke	Fabaceae-Mimosoideae
Ing gra	*Inga gracilifolia* Ducke	Fabaceae-Mimosoideae
Ing obi	*Inga obidensis* Ducke	Fabaceae-Mimosoideae
Ing sti	*Inga stipularis* DC.	Fabaceae-Mimosoideae
Ing sub	*Inga suberosa* T.D.Penn.	Fabaceae-Mimosoideae
Iry cor	*Iryanthera coriacea* Ducke	Myristicaceae
Jac cop	*Jacaranda copaia* (Aubl.) D. Don.	Bignoniaceae
Lec bar	*Lecythis barnebyi* Mori	Lecythidaceae
Lec gra	*Lecythis graciena* S.A.Mori	Lecythidaceae
Lec pra	*Lecythis prancei* S.A. Mori	Lecythidaceae
Lec usi	*Lecythis usidata* Camb.	Lecythidaceae
Lic ado	*Licania adolphoduckei* Prance	Chrysobalanaceae
Lic ape	*Licania apelata* (E.Mey.) Fritsch	Chrysobalanaceae
Lic gui	*Licaria guianensis* Aubl.	Lauraceae
Lic het	*Licania heteromorpha* Benth.	Chrysobalanaceae
Lic mic	*Licania micrantha* Miq.	Chrysobalanaceae
Lic obl	*Licania oblongifolia* Standl.	Chrysobalanaceae
Lue ros	*Lueheopsis rosea* (Ducke) Burret	Malvaceae
Mab sp.	*Mabea* sp.	Euphorbiaceae
Man ama	*Manilkara amazonica* (Huber) Stand.	Sapotaceae
Man bid	*Manilkara bidentata* (A.DC.) A. Chev.	Sapotaceae
Mez ita	*Mezilaurus itauba* (Meissn.) Taubert ex Mez	Lauraceae
Mic guy	*Micropholis guyanensis* (A.DC.) Pierre ssp.duckeana (Baehni)	Sapotaceae
Mic reg	*Miconia reglelii* Cogn.	Melastomataceae

Species Code	**Scientific Names**	**Family**
Mic sip	*Micranda siphonoides* Benth.	Euphorbiaceae
Mic tru	*Micropholis trunciflora* Ducke	Sapotaceae
Min gui	*Minquartia guianensis* Aubl.	Olacaceae
Mou ang	*Mouriri angulicosta* Morley	Melastomataceae
Mou cal	*Mouriri callocarpa* Ducke	Melastomataceae
Nau cal	*Naucleopsis caloneura* (Huber) Ducke	Moraceae
Nee opp	*Neea oppositifolia* Ruiz & Pav.	Nyctaginaceae
Oco cer	*Ocotea cernua* (Nees) Mez s.l.	Lauraceae
Oco cym	*Ocotea cymbarum* H.B.K.	Lauraceae
Oco sp.	*Ocotea* sp.	Lauraceae
Orm gro	*Ormosia grossa* Rudd	Fabaceae-Faboideae
Pal cor	*Palicourea corymbifera* Mull. Arg.	Rubiaceae
Par mul	*Parkia multijuga* Benth.	Fabaceae-Mimosoideae
Par nit	*Parkia nitida* Miq.	Fabaceae-Mimosoideae
Par orm	*Paramachaerium ormosioides* Ducke	Fabaceae-Faboideae
Par pen	*Parkia pendula* (Willd.) Walp.	Fabaceae-Mimosoideae
Pau mac	*Pausandra macropetala* Ducke	Euphorbiaceae
Pip sua	*Piptadenia suavolens* Miq.	Fabaceae-Mimosoideae
Pla duc	*Platymiscium duckei* Huber	Fabaceae-Faboideae
Pla ins	*Platonia insignis* Mart.	Clusiaceae
Pou amb	*Pouteria ambelaniifolia* (Sandwith) T.D.Penn.	Sapotaceae
Pou cai	*Pouteria caimito* (Ruiz & Pav.) Radlk.	Sapotaceae
Pou lau	*Pouteria laurifolia* (Gomes) Radlk	Sapotaceae
Pou min	*Pourouma minor* Benoist	Urticaceae
Pou myr	*Pourouma myrmecophyla* Ducke	Urticaceae
Pou obl	*Pouteria oblanceolata* Pires	Sapotaceae
Pou per	*Pouteria peruviensis* (Aubrév.) Bernardi	Sapotaceae
Pou ret	*Pouteria reticulata* (Engl.) Eyma	Sapotaceae
Pou ven	*Pouteria venosa* (Mart.) Baehni ssp. amazonica T.D.Penn.	Sapotaceae
Pra coc	*Pradosia cochlearia* (Lecomte) T.D.Penn	Sapotaceae
Pro heb	*Protium hebetatum* Daly	Burseraceae
Pro hep	*Protium heptaphyllum* (Aubl.) ssp. ulei (Swart) Daly	Burseraceae
Pse cor	*Pseudoxandra coriacea* R.E.Fr.	Annonaceae
Pse mun	*Pseudobombax munguba* (Mart. & Zucc) Dugand	Malvaceae
Psi ara	*Psidium araca* Raddi	Myrtaceae
Pyt ola	*Pytchopetalum olacoides* Benth.	Olacaceae
Qua acu	*Qualea acuminata* Aubl.	Vochysiaceae
Qua alb	*Qualea albiflora* Warm	Vochysiaceae
Qua par	*Qualea paraensis* Ducke	Vochysiaceae
Rin gui	*Rinorea guianensis* Aubl.	Violaceae
Rin rac	*Rinorea racemosa* (Mart.) Kuntze	Violaceae
Scl hel	*Sclerolobium helanocarpus* Ducke	Fabaceae-Caesalpinioideae

Species Code	**Scientific Names**	**Family**
Scl mic	*Scleronema micranthum* Ducke	Malvaceae
sim ama	*Simarouba amara* Aubl.	Simaroubaceae
Sim ced	*Simaba cedron* Planch.	Simaroubaceae
Sip sp.	*Siparuna* sp.	Monimiaceae
Slo exc	*Sloanea excelsa* Ducke	Elaeocarpaceae
Ste pru	*Sterculia pruriens* (Aubl.) K.Schum.	Malvaceae
Str gui	*Stryphnodendron guianensis* (Aubl.)Benth.	Fabaceae-Mimosoideae
Str sp.	*Stryphnodendron* sp.	Fabaceae-Mimosoideae
Swa rec	*Swartzia recurva* Poepp.	Fabaceae-Faboideae
Swa sch	*Swartzia schomburgkii* Benth. Var. guyanensis R.S. Cowan	Fabaceae-Faboideae
Swa tes	*Swartzia tessmannii* Harms	Fabaceae-Faboideae
Tab ser	*Tabebuia serratifolia* (Vahl) Nichols	Bignoniaceae
Tac cf.	*Tachigali cf. myrmecophila* Ducke	Fabaceae-Caesalpinioideae
Tal cf.	*Talisia cf. cupularis* Radlk.	Sapindaceaea
The sub	*Theobroma subincanum* Mart.	Malvaceae
Toc gui	*Tococa guianensis* Aubl.	Melastomataceae
Tou gui	*Touroulia guianensis* Aubl.	Quiinaceae
Tra bur	*Trattinnickia burserifolia* Mart.	Burseraceae
Tri mic	*Trichilia micropetala* T.D.Penn.	Meliaceae
Tri sep	*Trichilia septentrionales* C.DC.	Meliaceae
Uno duc	*Unonopsis duckei* (R.&P.)Macba.	Annonaceae
Van gui	*Vantanea guiannensis* (Aubl.) Ducke	Humiriaceae
Vir mic	*Virola michelii* Heckel	Myristicaceae

CONCLUSÕES GERAIS

A complexidade das interações bióticas e abióticas que ocorrem nas comunidades vegetais da Amazônia, ressalta a importância de se ampliar os conhecimentos acerca destas interações, visando subsidiar, ações de restauração, manejo florestal e conservação de espécies tropicais. Neste contexto, esta tese traz importantes contribuições para o conhecimento da composição florística e estrutura das espécies arbóreas da floresta densa de terra firme na Amazônia, a partir da análise de um conjunto de 15 hectares de parcelas permanentes, as quais contemplaram diferentes variações ambientais na área de estudo. Não se obervou predomínio de uma espécie sobre as demais, apesar das espécies *Protium hebetatum* e *Eschweilera coriaceae* terem apresentado os maiores valores de IVI(%). A ocorrência de um grande número de espécies raras chama a atenção, principalmente para as ações de exploração florestal em áreas com semelhantes caracterísitcas a do presente estudo, a fim de que se evitem extinções locais de espécies.

Observou-se que as variações na composição florística, em escala local, seguem os padrões observados em outros estudos em escalas regionais e continentais, em um gradiente de fertilidade e textura que variam no sentido leste-oeste. As espécies mostraram um nível de organização espacial que foi evidenciado a partir de uma ordenação das mesmas segundo um gradiente edáfico e topográfico, que somente começaram a ser visualizados em unidades de amostras de tamanho igual a 1.0 ha, sendo mais evidente no tamanho amostral de 1.4 ha, o que mostra a importância do tamanho adequado de unidades amostrais para estudos que objetivam avaliar processos resultantes do efeito de fatores abióticos e bióticos estruturando comunidades vegetais.

A análise de vizinhança de espécies de interesse comercial contribuiu para uma maior compreensão das interações que ocorrem na comunidade do ponto de vista dos indivíduos das espécies focais. Observou-se que há um padrão taxonômico associado às espécies estudadas, principalmente relacionado à ocorrência de conspecíficos a curtas distâncias dos indivíduos focais e também de espécies raras, os quais merecem atenção especial nas ações de manejo de espécies de interesse, as quais devem atentar para a redução de danos a indivíduos da espécie de interesse, bem como a espécies raras, procurando-se manter e/ou restaurar a estrutura da floresta e consequentemente preservar as funções ecológicas das espécies.

A oportunidade de se trabalhar um conjunto maior de dados e o uso de métodos de análise muitivariada e análise espacial permitiram uma compreensão muito maior da área de estudo e das possíveis interações entre as espécies, os quais certamente contribuirão para o avanço no conhecimento ecológico das florestas tropicais e para o manejo, conservação e restauração das florestas de terra firme na Amazônia.