

Disentangling structural patterns of natural forest fragments in a savanna matrix in the eastern Brazilian Amazon

Iêda Leão do AMARAL^{1*}, William Ernest MAGNUSSON¹, Francisca Dionízia de Almeida MATOS¹, Ana Luisa K. ALBERNAZ², Yuri Oliveira FEITOSA¹, Jean-Louis GUILLAUMET³

¹ Instituto Nacional de Pesquisas da Amazônia, Coordenação de Pesquisa em Biodiversidade, Caixa Postal 2223, CEP 69.080-971, Manaus, AM, Brasil.

² Museu Paraense Emílio Goeldi, Coordenação de Ciências da Terra e Ecologia, Campus de Pesquisa, Av. Perimetral 1901, CEP 66.077-530, Terra Firme, Belém, PA, Brasil.

³ Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, 16, rue Buffon, 75005 Paris, França

* Corresponding author: iamaral@inpa.gov.br

ABSTRACT

Natural fragments are an important source of richness for the management and conservation of a local flora. The objective of this study was to evaluate the effect of fragmentation on the structure and composition of the plant communities of forest fragments (FF) in Alter do Chão, eastern Brazilian Amazonia. The study sample consisted of 25 FF and nine continuous forest (CF) sites. We compared plant density and species richness between site categories by t-tests, analyzed the differences in composition by cluster analysis, and assessed the effect of fragment size and distance to CF on the basal area and diameter of FF assemblages by linear regression. Individual trees and shrubs with DBH ≥ 1.27 cm were measured in 2x250 m plots. 17,078 individuals were recorded - 75.32% in FF and 24.68% in CF, comprising 475 species, 216 genera and 64 families. Myrtaceae and Fabaceae were the most abundant families in both FF and CF. Average species richness in FF and CF was statistically different. The 20 species with the highest importance values were similar in FF and CF. The average plant diameter was similar in FF and CF, suggesting that both are "mature" forests composed of thin individuals. Average diameter and total basal area showed a negative relationship with distance to CF and fragment area, respectively. Similarity analysis revealed two groups, one composed exclusively of portions of fragmented forest. Fragments and continuous forest differed in species composition, but were similar in structure. Diameter distribution in fragments was similar to that of primary forests.

KEYWORDS: Bray-Curtis, Cluster analysis, diameter structure, small trees.

Desvendando padrões estruturais de fragmentos florestais na Amazônia Oriental

RESUMO

Fragmentos naturais constituem importante fonte de recursos para o manejo e conservação da flora local. Este trabalho avaliou o efeito da fragmentação sobre a estrutura e a composição das comunidades de plantas de fragmentos florestais (FF), em Alter do Chão, na Amazônia oriental brasileira. Foram amostrados 25 sítios em FF e nove em floresta contínua (CF). Analisamos a diferença na densidade de plantas e na riqueza de espécies entre FF e CF por teste-t, e na composição por análise de agrupamento. Utilizou-se regressão linear para avaliar o efeito do tamanho dos fragmentos e distância à CF sobre a área basal e diâmetro. Os indivíduos com DAP $\geq 1,27$ cm foram medidos em parcelas de 2x250 m. Foram registrados 17.078 indivíduos, 75,32% nos FF e 24,68% na CF, distribuídos em 475 espécies, 216 gêneros e 64 famílias. As famílias Myrtaceae e Fabaceae foram as mais abundantes em ambos FF e CF. A riqueza média diferiu significativamente entre FF e CF. As 20 espécies com maior valor de importância foram semelhantes nos FF e CF. O diâmetro médio nos FF e CF foi semelhante, sugerindo tratar-se em ambos casos de florestas "maduras" compostas por indivíduos finos. O diâmetro médio e a área basal total mostraram relação negativa com a distância à CF e área dos fragmentos, respectivamente. A análise de similaridade revelou dois grupos, um deles composto exclusivamente por fragmentos. Composicionalmente, os fragmentos diferiram da floresta contínua, sendo estruturalmente semelhantes entre si, evidenciando distribuição diamétrica semelhante à das florestas primárias.

PALAVRAS CHAVES: Bray-Curtis, análise de agrupamento, estrutura diamétrica, pequenas árvores.

INTRODUCTION

Forest fragmentation is the result of either natural or anthropic processes that can divide or reduce large areas of existing forest cover into smaller, disjunct, parts (Cerqueira *et al.* 2003). Fragmented habitats or islands of different habitats can be produced by a variety of natural processes, which must be distinguished if fragment composition is to be correctly interpreted. Forest islands are isolated forest fragments, found in open areas of savanna-forest contact zones in the Neotropics (Huber *et al.* 2006).

Old natural fragments have served as source material for restoration and have important role in the planning, management and conservation of native local flora. As well as being essential for the development of rational strategies for use of natural resources, they help maintain water quality and prevent erosion (Peters *et al.* 1989), especially when embedded in the savanna matrix.

The Amazon region also contains some very old forest fragments, their generating processes being a matter of debate among researchers. Alter do Chão, Pará State, has natural forest fragments within savanna areas. Their origin is unclear, given that 4000 years ago the whole region was covered by continuous forest and there are no obvious differences in the topography or soil characteristics between the fragments and the surrounding savanna (Sanaiotti *et al.* 2002). Some authors suggest that such forest fragments may have been caused by fires set by Amerindians, which could have favored the establishment and subsequent perpetuation of grasslands in forest areas in the Amazon (Serena 1984), or that they may have been produced by other processes, including natural climatic fluctuations, soil heterogeneities, topographic variation, river and sea hydrodynamics and hydrological processes in periodically flooded areas (Constantino *et al.* 2003).

There is very little information about the diversity, floristic composition and structure of forest fragments within Amazonian savannas (Prado 2000), although there are reports concerning the influence of topography, soil and watercourse proximity on their composition, richness and diversity (Sette-Silva 1997). According to Tabarelli *et al.* (2004), fragmentation does not occur in isolation, and its effect will be amplified when associated with the synergistic effects of other events threatening tree cover in neotropical forests.

The forest fragments in Alter do Chão were scientifically documented for the first time by Bates (1892), who described them as forest islands, insular in form and distribution and surrounded by grass. The antiquity of the forest fragments in Alter do Chão provides an opportunity to study the composition and the structure of forest patches that have been isolated for a long time and compare them to continuous forest in the same region. Thus this study aimed at investigating

whether differences existed between plant structure and species composition of the forest fragments and continuous forest in Alter do Chão, and the relation of fragment area and distance from continuous forest with these parameters.

MATERIALS AND METHODS

Study area

Situated on the right bank of the Tapajós River, the Alter do Chão district (centered on 2°31' S and 55°00' W) occupies an area of approximately 1,706 km² and lies some 30 km from Santarém, Pará State, Brazil. The area has isolated forest fragments lying within a savanna matrix, as well as a large area of continuous native forest (Figure 1). The climate is Am, according to the Köppen classification, characterized as being hot and humid, with a dry period between July-November, with September being the driest month (34 mm average precipitation). The rainy season lasts from January to June, with April being the wettest month (346 mm precipitation). On average, five months have less than 100 mm rainfall (range 34-85 mm). Average annual rainfall is 1,991 mm, and average annual temperature 25.9 °C (range 20.2-32.2 °C (Climate-data.org 2014)).

At Alter do Chão, dense *terra firme* rainforest occupies the higher regions, and open rainforest with palm trees occupies lower-lying areas. Seasonally-flooded forest (*igapó*) occurs close to water bodies. There are also continuous strips of white sand beaches along the margins of rivers and tributaries. Savanna vegetation occurs in many areas, and is composed of a graminoid-dominated landscape, interspersed with shrubs and trees with twisted trunks, most with thick bark, large canopies and leathery leaves (Miranda 1993). At the study site, the savanna is surrounded by tropical semi-deciduous forest (IBGE 2012) which also forms the forest fragments, known locally as "*ilhas de mata*" (forest islands) that lie within the savanna. Secondary vegetation occurs in areas where human activities, such as agriculture and logging, have occurred. Even after many years of regeneration, these are still structurally different from the primary forest (Albernaz 2001).

Data collection

Data were collected from 1998 to 2001 in forest fragments (FF) and continuous forest (CF) composed of Semi-deciduous Forest (IBGE 2012). The area, perimeter and degree of isolation of fragments were calculated from Landsat satellite TM-5 images, orbits/point 227/62 1999, to identify forests, with fragment profiles converted to vector format and their areas calculated in ArcView 3.2 software (ESRI 1996). The continuous-forest area sampled covered hundreds of hectares and the sampling units were established between 1-10 kilometers from each other.

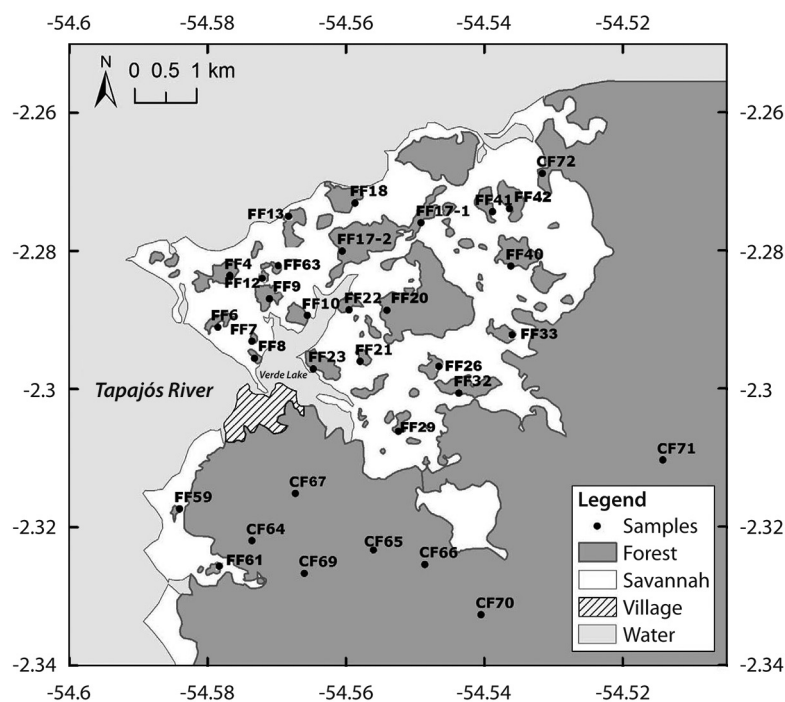


Figure 1. Map of part of the Alter do Chão region, Santarém, Brazil, showing the distribution of forests, savannas, the town of Alter do Chão, the major water bodies and the location (in black) of sample sites. FF=forest fragment, CF=continuous forest. (Source: Albernaz 2001).

In total 34 sampling points were analyzed; 25 in FF and nine in CF. Within all nine CF sites and 23 of 25 FF sites, four subplots of 2m x 250m (2000 m²) were established. The exceptions were two very small fragments where only two subplots (1000 m²) were established. The subplots were arranged perpendicular to the fragment edge, 50 m apart from it, and parallel to each other, separated by 50 m.

Individual trees and shrubs with a minimum of 4 cm in circumference at breast height (CAP), corresponding to 1.27 cm in diameter at breast height (DBH) at 1.30 m above the ground, were measured, numbered and labeled with aluminum tags and botanical samples were collected for later species identification. Identification was carried out by morphological comparison to specimens in the Herbarium of the National Institute of Amazonian Research (INPA), as well as by consulting literature and taxon experts (see acknowledgements). Taxonomic classification of specimens followed the Angiosperm Phylogeny Group (APG III 2009), as presented in the updated classification on the group website (<http://floradobrasil.jbrj.gov.br/reflora>. Accessed from 12/10/2016 to 01/15/2017). Unidentified botanical samples were morphotyped to the lowest possible taxon level and reference material was incorporated into the INPA herbarium collection. Further information on the complete species list is available at <http://ppbio.inpa.gov>.

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Data analysis

Plant density, species richness and DBH distribution were compared between FF and CF using t-tests in the R statistical platform (R Core Team 2014). Phytosociological parameters were estimated following Mueller-Dombois and ElleMBERG (2003). For this, forest fragments (FF) were categorized into small (SF), medium (MF) and large (LF), based on the mean area of the fragments (44.62 ha); where fragments with an area below 50% of the average value (2.4-22.34 ha, N=13) were classified as small, those in the range 22.34-67.01 ha (N=10) as medium, and those above 67.01 h as large (N=2).

The structural profiles of forest fragments and continuous forest were analyzed as the frequency distribution of DBH classes. As the forest had many thin individuals, a class amplitude of 5 cm was adopted (Soares *et al.* 2007). The effect of fragment area (F_A), sampled area (S_A), and distance of fragments to CF (D_{CF}) on two dependent variables, mean DBH (DBH_M) and total basal area (T_{BA}), was analyzed using multiple linear regression. The difference in species composition between fragments and continuous forest was analyzed with a cluster analysis based on a matrix of relative abundance in each fragment, using an ecological distance matrix between the pairs

of sampling units (Bray-Curtis 1957). Difference was expressed in terms of between-site variance in species content (Kindt and Coe 2005), using hierarchical clustering methods and the unweighted pair-group average (UPGM) distance algorithm for all members in the groups. Ordination was done with the PAST program - Paleontological Statistic Software Package (Hammer *et al.* 2001).

RESULTS

Overall 17,078 individuals were sampled, 12863 (75.32%) in FF and 4215 (24.68%) in CF. These were classified into 475 species, in 216 genera from 64 families. Out of the total number of individuals, 264 were identified only to family level. Of these, 54.54% belonged to Myrtaceae, a family difficult to identify by comparative morphology of sterile material; 479 individuals were identified only to genus level (2.80%), and 80 (0.47%) could not be identified to any taxonomic level below angiosperm.

A total of 387 species were recorded from the fragments, distributed in 185 genera from 60 families. The highest number of individuals was recorded in the SF (6119 individuals), followed by MF (5430) and LF (1314 individuals). In CF, the 4215 individuals recorded belonged to 320 species in 168 genera from 61 families. A t-test revealed no difference between the average plant density in the two forest environments (FF = 2673.24; CF = 2330.34; $t = 0.8432$, $df = 32$, $p = 0.405$).

The families with the highest numbers of individuals in both forest types were Myrtaceae, Fabaceae, Salicaceae, Sapindaceae, Lauraceae and Euphorbiaceae (in descending order). Together these accounted for 46.58% of total plants sampled. Two of these families, Fabaceae and Myrtaceae, were part of the 10 most diverse families, accounted for 51.68% of overall species richness (Figure 2), and contributed 20 species that accounted for 41.75% of the total number of individuals (Figure 3). The genera *Eugenia*, *Inga*, *Swartzia*, *Myrcia*, *Casearea* and *Miconia* together contributed the highest number of species (79: 16.6% of the total). The remainder (211 genera) commonly occur in other types of vegetation in the Amazon and Atlantic Forest. Some species of *Miconia*, *Casearea* and other genera were associated with forest edges and occur in anthropogenic and natural clearings. At the edges, it was common to find *Miconia* and/or *Casearea* species, often with many juveniles.

Of the 475 species found, 113 (23.74%) were common to both FF and CF. Of these, three had the highest densities: *Ocotea longifolia* Kunth (649 individuals), *Casearia javitensis* Kunth (623) and *Myrcia splendens* DC (916). Twenty species were considered generalists, with *Tapirira guianensis* Aubl., *Handroanthus serratifolia* (Vahl) S.O.Grose, *Bellucia grossularioides* Triana, *Casearia javitensis* Kunth and *Simarouba*

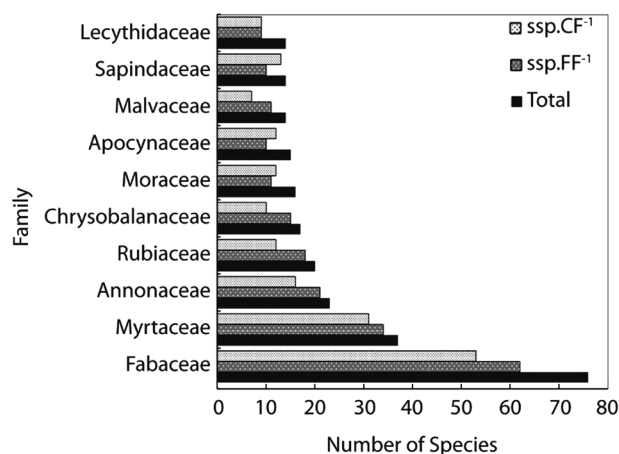


Figure 2. The 10 families with the greatest species richness in FF and CF sampling sites in Alter do Chão.

amara Aubl. being considered generalists able to prosper in a variety of environments (Cavalcanti and Tabarelli 2004). Forty species are known to occur in FF and savanna areas in other regions of the country (Northeast, Central-West and Southeast), and in Alter do Chão 33 of these were found in the FF (Magnusson *et al.* 2008).

Nine species (2% of the total) are listed as vulnerable by IBAMA (2008): *Bowdichia nitida* Spruce, *Dimorphandra parviflora* Spruce ex Benth, *Platymiscium trinitatis* Benth, *Swartzia leptopetala* Benth, *Swartzia macrocarpa* Spruce, *Mezilaurus ita-uba* Taub. ex Mez, *Ocotea cujumarum* Mart, *Eschweilera micranta*, Miers and *Pouteria venosa* (Mart.) Baehni. However, these species were abundant locally in FF and CF.

Mean species richness differed significantly between FF and CF assemblages at the 95% confidence level (FF = 86.48; CF = 109.67; $P = 0.012$). Richness within the fragments was no greater than that between them ($P = 0.24$), but differed from continuous forest ($P = 0.017$).

The phytosociological analysis of assemblages from fragments and continuous forest showed that, for the 20 species of each fragment grouped with highest IV (importance value), the relative values of density, frequency and dominance, when expressed as IV indexes, were numerically similar between environments, and deviations from the means of these parameters were small ($IV_{20spp} = 109.74 + 6.45$; $Den_{20spp} = 43.71 + 1.38$; $Freq_{20spp} = 16.24 + 3.04$; $Dom_{20spp} = 49.82 + 4.56$). Among the 20 more important species, only three had high IV scores in all environments (6.25%). Of the other species, 18.75% occurred in LF, 16.67% in MF, 10.42% in SF, and 16.67% in CF. The remaining 35.42% occurred in two or three of the four groups, respectively (Table 1).

No striking structural differences in DBH frequency distribution were found between groups. However, there were

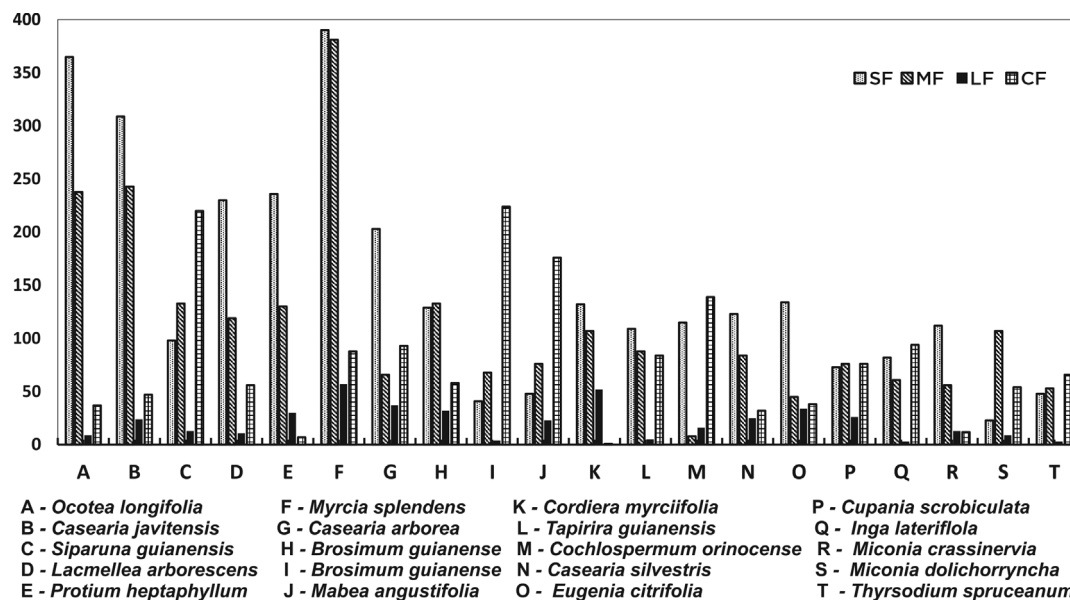


Figure 3. The 20 species with the widest distribution in forest fragments and continuous forest in Alter do Chão. SF = small fragment, MF = medium fragment, LF = large fragment, CF = continuous fragment.

Table 1. Phytosociological parameters for 47 species, emphasizing the 20 most important, for each sampled habitat, ordered by size of location (CF= continuous forest, SF= small fragments, MF= medium fragments, LF= large fragments) showing Density (Den) and Importance Value (IV) estimates.

Species	Family	CF		SF		MF		LF	
		Den (%)	VI (%)	Den (%)	VI (%)	Den (%)	VI (%)	Den (%)	VI (%)
<i>Brosimum guianense</i> (Aubl.) Huber ex Ducke	Moraceae	1.38	3.06	2.11	4.12	2.45	4.62	2.43	4.88
<i>Casearia arborea</i> (Rich.) Urb.	Salicaceae	2.21	3.99	3.32	5.75	1.22	4.08	2.81	5.93
<i>Myrcia splendens</i> (Sw.) DC.	Myrtaceae	2,09	4,48	6,37	10,58	7,02	10,79	4,34	7,64
<i>Casearia javitensis</i> Kunth	Salicaceae	1.16	3.35	5.05	7.57	4.48	6.86	-	-
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	1.99	6.57	1.78	5.65	1.62	4.36	-	-
<i>Dialium guianense</i> (Aubl.) Sandwith	Fabaceae	0.95	8.52	0.59	4.08	0.87	5.01	-	-
<i>Ocotea longifolia</i> Kunth	Lauraceae	0.88	3.96	5.96	18.55	4.38	14.93	-	-
<i>Cochlospermum orinocense</i> (Kunth.) Steud.	Bixaceae	3.30	11.8	1.88	8.57	-	-	1.21	10.10
<i>Dequelia spruceana</i> (Benth.) AMG Azevedo	Fabaceae	1.92	5.43	-	-	-	-	1.97	4,00
<i>Hymenaea parvifolia</i> Huber	Fabaceae	0.38	6.78	-	-	-	-	1.44	6.52
<i>Annona exsucca</i> (DC.) A.DC.	Annonaceae	0.76	3.00	-	-	-	-	1.36	5.46
<i>Siparuna guianensis</i> Aubl.	Siparunaceae	5.22	7.03	-	-	2.45	3.81	-	-
<i>Casearia silvestris</i> Sw.	Salicaceae	-	-	2.01	4.63	1.55	3.69	1.90	4.16

Table 1. Continuação

Species	Family	CF		SF		MF		LF	
		Den (%)	VI (%)	Den (%)	VI (%)	Den (%)	VI (%)	Den (%)	VI (%)
<i>Protium heptaphyllum</i> (Aubl.) Marchand	Burseraceae	-	-	3.86	7.52	2.39	4.94	2.28	4.35
<i>Hevea brasiliensis</i> (Willd. ex Juss.) Müll. Arg.	Euphorbiaceae	-	-	0.60	4.26	1.23	5.45	-	-
<i>Lacmellea arborescens</i> (Mull.Arg.) Markgr.	Apocynaceae	-	-	3.76	6.66	2.19	4.30	-	-
<i>Byrsonima spicata</i> (Cav.) Rich. ex Kunth	Malpighiaceae	-	-	0.70	4.63	-	-	0.60	4.95
<i>Eugenia citrifolia</i> Poir.	Myrtaceae	-	-	2.12	4.22	-	-	2.58	5.62
<i>Cecropia palmata</i> Willd.	Urticaceae	4.58	5.91	-	-	-	-	-	-
<i>Chamaecrista apoucouita</i> (Aubl.) Irwin & Barneby	Fabaceae	1.14	4.91	-	-	-	-	-	-
<i>Cupania scrobiculata</i> L.C.Rich.	Sapindaceae	1.80	3.18	-	-	-	-	-	-
<i>Ecclinusa lanceolata</i> (Mart. & Eich. ex Miq.) Pierre	Spotaceae	0.81	2.83	-	-	-	-	-	-
<i>Inga lateriflora</i> Miq.	Fabaceae	2.23	4.00	-	-	-	-	-	-
<i>Lindackeria paludosa</i> (Benth.) Gilg.	Achariaceae	1.78	4.01	-	-	-	-	-	-
<i>Mabea angustifolia</i> Spruce ex Benth.	Euphorbiaceae	4.18	6.03	-	-	-	-	-	-
<i>Solanum distichophyllum</i> Sendth.	Solanaceae	5.31	6.26	-	-	-	-	-	-
<i>Aspidosperma multiflorum</i> A.DC.	Apocynaceae	-	-	0.15	3.65	-	-	-	-
<i>Mezilaurus ita-uba</i> (Meisn.) Taub. ex Mez	Lauraceae	-	-	1.27	4.05	-	-	-	-
<i>Miconia crassinervia</i> Cogn.	Melastomataceae	-	-	1.83	3.51	-	-	-	-
<i>Sclerobium paniculatum</i> Vogel	Fabaceae	-	-	0.92	4.86	-	-	-	-
<i>Simarouba amara</i> Aubl.	Simaroubaceae	-	-	1.31	5.58	-	-	-	-
<i>Eschweilera obversa</i> (O.Berg) Miers	Lecythidaceae	-	-	-	-	1.44	5.91	-	-
<i>Glycydendron amazonicum</i> Ducke	Euphorbiaceae	-	-	-	-	0.88	3.77	-	-
<i>Guatteria foliosa</i> Benth.	Annonaceae	-	-	-	-	1.20	4.41	-	-
<i>Maprounea guianensis</i> Aubl.	Euphorbiaceae	-	-	-	-	1.57	5.90	-	-
<i>Matayba inelegans</i> Radlk.	Sapindaceae	-	-	-	-	3.54	5.09	-	-
<i>Sacoglottis matogrossensis</i> Malme	Humiriaceae	-	-	-	-	0.37	3.77	-	-
<i>Swartzia recurva</i> Poepp.	Fabaceae	-	-	-	-	1.56	4.48	-	-

Table 1. Continuação

Species	Family	CF		SF		MF		LF	
		Den (%)	VI (%)	Den (%)	VI (%)	Den (%)	VI (%)	Den (%)	VI (%)
<i>Cordia myrciifolia</i> (K.Schum) Pers. & Delprete	Rubiaceae	-	-	-	-	-	-	3.95	4.75
<i>Croton cajucara</i> Benth.	Euphorbiaceae	-	-	-	-	-	-	3.95	4.75
<i>Eugenia patens</i> Poir.	Myrtaceae	-	-	-	-	-	-	1.21	4.00
<i>Geissospermum argenteum</i> Woodson	Apocynaceae	-	-	-	-	-	-	2.13	3.81
<i>Abarema mataybifolia</i> (Sand.) Barneby & Irwin	Fabaceae	-	-	-	-	-	-	1.67	7.30
<i>Bocageopsis multiflora</i> (Mart.) R.E.Fries	Annonaceae	-	-	-	-	-	-	0.98	4.08
<i>Lecythis pisonis</i> Cambess.	Lecythidaceae	-	-	-	-	-	-	1.06	6.01
<i>Warszewiczia coccinea</i> (Vahl) Klotzsch	Rubiaceae	-	-	-	-	-	-	2.35	3.50
<i>Xylopia frutescens</i> Aubl.	Annonaceae	-	-	-	-	-	-	3.80	7.70
Total 1 (20 species)		43.49	104.2	45.66	115.38	42.39	107.0	43.30	108.80
Total 2 (Other species)		56.51	195.8	54.34	180.97	57.61	192.9	56.70	191.20
Total (%)		100	300	100	300	100	300	100	300

significant differences in the three DBH classes between FF and CF, with 57% and 63% of all individuals, respectively, being in the first size class (1.27-5 cm DBH). The frequency of the second class decreased dramatically to 23%, while for the third it was approximately 10%. These three size classes comprised some 97% of individuals (Figure 4), leaving only about 3% for the other eight classes. Species with notably higher DBH included *Hymenaea parvifolia* Huber (139.73 cm), *Duguetia echinophora* Chorus. (117.77 cm) and *Aspidosperma multiflorum* A.DC. (111.40 cm). A t-test comparison showed that mean DBH was similar between FF and CF (FF = 7.03; CF = 7.09, $t = 0.11$, $df = 32$, $p = 0.9131$), suggesting that FF and CF are structurally similar, both a developing forest and a “mature” forest comprising many thin individuals.

Multiple linear regression showed that the effect of predictive variables, FF area (F_A) and sampled area (S_A), lacked a defined relationship with the structural variable mean DBH (DBH_M) of FF, while distance to CF (D_{CF}) had a negative relationship, as indicated by the adjustment of the equation: $DBH_M = 7.395 - 0.00614 * F_A - 0.0003 * D_{CF} + 0.00064 * S_A$ ($r^2 = 0.53$; $F_{21,3} = 7.85$, $P = 0.0011$) (Figure 5). For the effect of the predictive variables on total basal area (T_{BA}), the multiple linear regression showed that the predictors F_A and S_A had, respectively, negative and positive relationships with the dependent variable, while D_{CF} showed

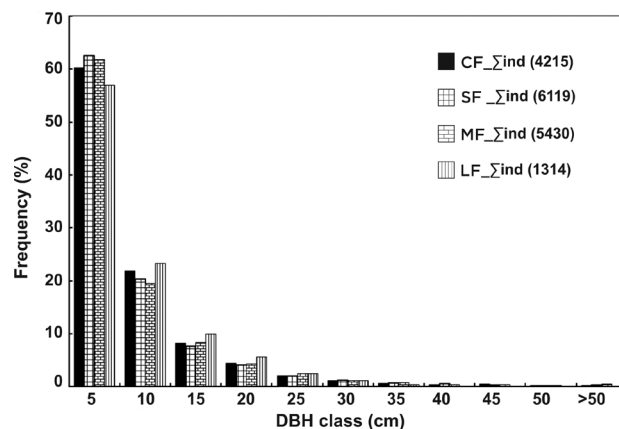


Figure 4. Grouping of individuals by DBH classes (≥ 1.27 cm), in forest fragments and continuous forest in Alter do Chão, with the respective percentages for individuals in each class.

no apparent relationship with T_{BA} ($T_{BA} = -0.9654 - 0.0109 * F_A - 0.000016 * D_{CF} + 0.002873 * S_A$; $r^2 = 0.53$, $P = 0.0011$) (Figure 6).

Cluster analysis indicated the presence of two groups (GI and GII). GII was homogeneous, composed only of samples from FF, all close to each other, close to Verde Lake and the Tapajós River (Figure 7). The floristic composition within GI was more variable, forming three subgroups (GI.1,

GI.2 and GI.3), with similarity percentages ranging from 30 to 57%, except for CF72 that had a similarity value at the 25% limit. The first subgroup, GI.1, consisted primarily of continuous-forest samples (70%), but there were three fragments (FF17.1, FF32 and FF40), especially FF32 and FF40, that were closer to the continuous forest area. The second, GI.2, was composed entirely of fragments and had

similarity values that ranged from 45 to 57%, of which four were very close to bodies of water, and two were distant from the others, but near continuous forest and water bodies. The third, GI.3, was formed by three fragments that were all close to each other and two continuous-forest samples. Except for the CF72 sample in GI.3, similarity values for fragments and other continuous-forest samples exceeded 30%.

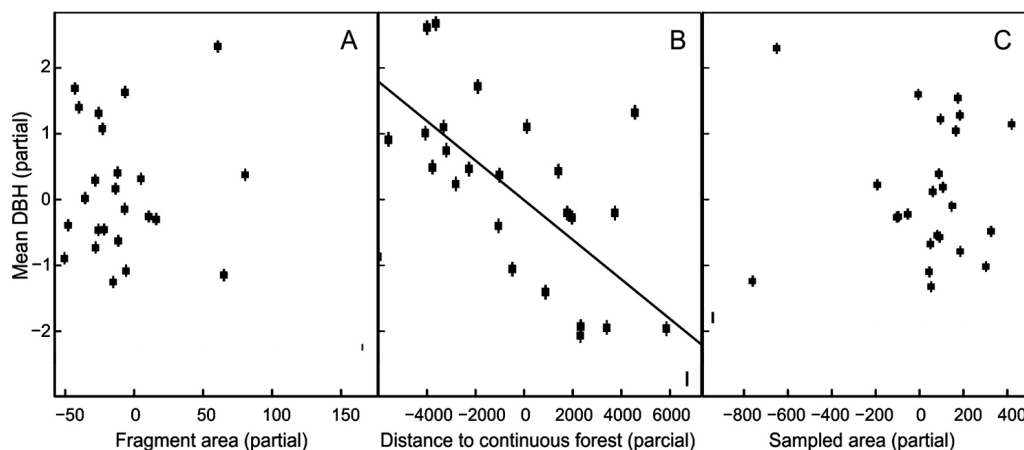


Figure 5. Partial regression plots of mean DBH (DBH_M) on forest fragment area (FF_A), sampled area (S_A) and distance to continuous forest (D_{CF}) of forest fragments sampled in Alter do Chão.

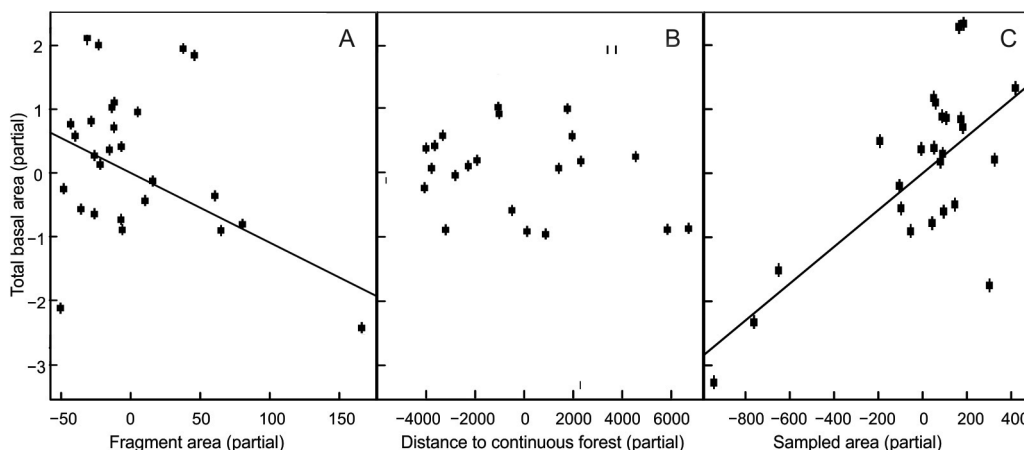


Figure 6. Partial regression plots of total basal area (T_{BA}) on forest fragment area (FF_A), sampled area (S_A) and distance to continuous forest (D_{CF}) of forest fragments sampled in Alter do Chão.

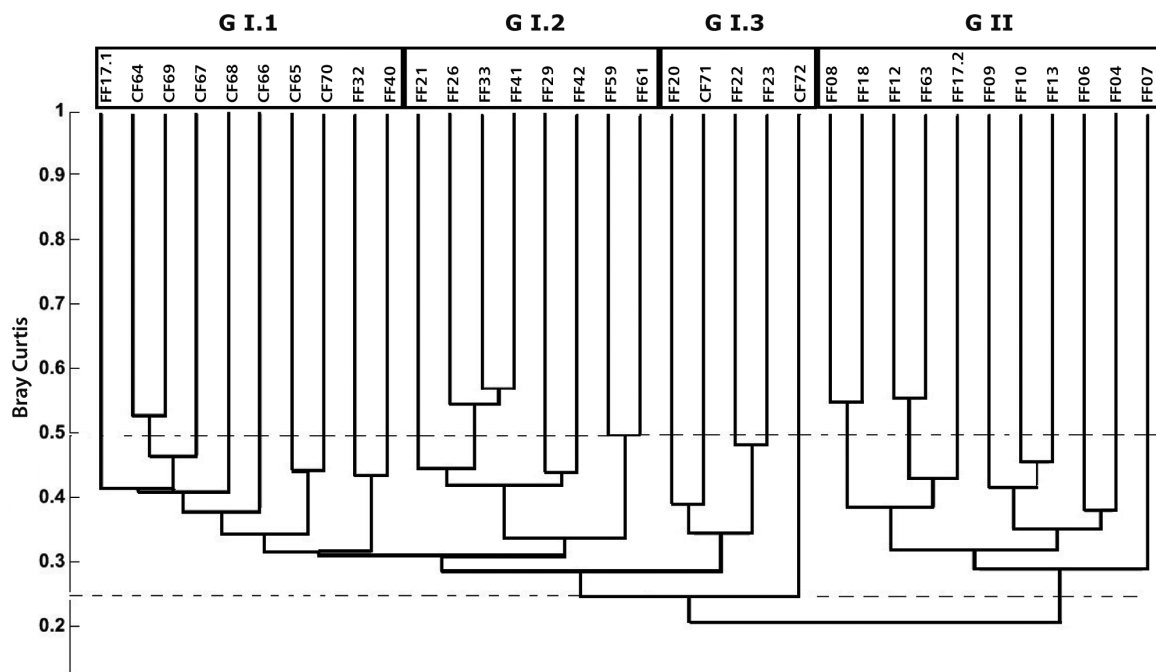


Figure 7. Cluster analysis dendrogram (UPGM), based upon Bray-Curtis similarity indices, for FF and CF sample sites in Alter do Chão, showing the groups and subgroups derived by the analysis.

DISCUSSION

Myrtaceae, Fabaceae, Salicaceae, Sapindaceae, Euphorbiaceae and Lauraceae were the most abundant families. These taxa are always present whenever native floras are sampled in the Amazon (Matos and Amaral 1999). Indeed the Fabaceae always appears among the three most abundant families in the Amazon (ter Steege *et al.* 2006 and 2013), both in old (Santos *et al.* 2013) and recent forest fragments (Rankin-de-Merona *et al.* 1992), as well as various types of forests. In studies using DBH ≥ 10 cm, Fabaceae is considered hyperdominant, with other families are not part of hyperdominant groups because most of their individuals are small and thin (ter Steege *et al.* 2013).

The abundance of Myrtaceae in forest fragments has also been reported for the Atlantic Forest (Oliveira-Filho and Fontes 2000, Durigan *et al.* 2008), which shows both the great range of this family and/or the capacity of its members to adapt to fragmented areas, since there are large differences between the Amazon and Atlantic Forest biomes. Fabaceae had the greatest species richness, and it is commonly cited as the richest family in other Amazon forest types (Pitman *et al.* 2002, Oliveira *et al.* 2004, ter Steege *et al.* 2013). Myrtaceae and Fabaceae were considered by Miranda *et al.* (2002) as the richest families in forest areas within the Roraima savannas, while Santos *et al.* (2013) cited Fabaceae as the most abundant and richest family in forest fragments from Boa Vista

savanna in the central Brazilian Cerrado. Their fruits being a food source for medium- and large-sized frugivores, which facilitates dispersal (Catharino *et al.* 2006), can explain their presence in both secondary and mature forest. Thus, in the Alter do Chão fragments, the abundance and species diversity of many families do not differ from other forest types, even when isolated from continuous forest.

Trees are the predominant plant life form in tropical forest, and in the current study. Even using smaller DBH ranges, where more variation in life forms can occur, our results did not differ from other investigations that used higher DBH boundaries, where trees are the dominant life (rather than, e.g. shrubs or lianas). According to Maas and Westra (1993), of the 292 plant families in neotropical forests, 140 contain tree species. This is the dominant biological type, accounting for about 80% of individuals with DBH ≥ 10 cm.

Many widely-distributed tropical forest species tend to be locally abundant in some areas and relatively rare in others (Hubell and Foster 1986). This can be seen, in the current study, with *Ocotea longifolia*, *Casearia javitensis* and *Myrcia splendens*. All these had large numbers of individuals in both FF and CF, unlike the most abundant species in most areas of Amazon forest, such as *Eschweilera* spp. and *Pouteria* spp.

The phytosociological organization of FF and CF groups showed that the 20 species with the highest IV

were numerically similar, showing that the most influential parameter was abundance. High density of species tends to be typical for the region (Araújo *et al.* 2009). In the 47 species set derived from the 20 most abundant species in FF and CF sites, 41 appear in the general lists of species in both analyzed environments. Species considered superabundant were those that had the highest IV, both in FF and CF, showing the influence of abundance in phytosociological structuring. The number and size of sampling units used (Balduino *et al.* 2005) probably explain this pattern, in part.

As in other types of tropical forests, the majority of individuals were concentrated in the first DBH class in both FF and CF. This characteristic of native tropical forests indicates a positive balance between recruitment and mortality, and is characteristic of self-regenerating vegetation assemblages (Silva Júnior 1999). Almost all individuals were concentrated in the first three size classes, showing that the local forest is composed of thin individuals and that FF and CF are structurally similar. Despite the selective exploitation of the environment by the local people, the large number of individual plants indicates that their component species are not vulnerable to extinction. Apart from *Mezilaurus ita-uba*, which occurs in several DBH classes (1.27 to 40.42 cm), the upper classes were occupied by only three individuals and, as the species has great commercial value, these may be subject to local extinction.

In our study, trees were recorded in all 11 DBH classes, indicating that, structurally, FF and CF forests are probably mature, stable and highly likely to continue perpetuating their constituent species. The smallest diameter trees (1.27 – 5 cm DBH) were twice as abundant as in the second size class (5.0 cm > DBH ≤ 10.0 cm), and five times more abundant than in the third size class, showing the ecological importance of small-trees in the structure, diversity and biomass to tropical forests (Memiaghe *et al.* 2016).

Our study suggests that isolation of forest fragmentation influences mean DBH in fragments. However, there is a limit to the form of this relationship (Navarrete and Menge 1997). A possible explanation is that the distance of smaller fragments from the continuous forest influences the fragments assemblage structure, possibly due to reduction in habitat quality.

Muller-Dubois and Ellenberg (2003) proposed that, for two areas to be considered alike, they must have at least 25% of species in common. Based on this criterion, cluster analysis revealed high similarity levels among our sampling sites. While the lowest similarities obtained were between samples CF72 and FF07, the remaining comparisons revealed similarity values greater than 33%. In Bray-Curtis index value calculations, the outcome of the groupings can be influenced by the abundances of species. Similarity in species composition occurs when the analysis is focused on the same type of

vegetation (Rodrigues and Nave 2000). In the GI.1 subgroup, the observed similarity was mostly influenced by the 25 most abundant species that made up the subset, and the distances between samples varied from 30 to 53%, with FF near to CF and the largest fragment. One of the factors that influenced the grouping was fragment size and isolation: two were very close, while others were distant from each other, indicating that distance is an aggregation factor (Kuntz *et al.* 2009). Four fragments with extreme distributions - two in the north and two adjacent in the south of the study area - had a species composition of 28 dominant species. For the GI.3 subgroup, the smallest grouping came from a large fragment (FF20), which was similar to CF71 (41%), so that this fragment was compositionally more like an area of continuous forest. The floristic distinctions within the GI group may be due to the influence of soil factors of hydrogeomorphological and/or anthropogenic origin (Kuntz *et al.* 2009).

In group GII, formed only by fragments, similarity ranged from 27 to 59%, and the distance was the most important factor to influence similarity, since all component FF were close to each other and distant from the CF. Fragment size was also important since only one (FF17-2) was considered to be of large size and most of the others were small. Proximity to each other and to water bodies, and isolation from CF appeared to be the factors that most influenced group composition, despite environmental factors usually having the greatest influence on species groupings (Cottenie 2005).

CONCLUSION

Despite their long history of isolation, the Alter do Chão forest fragments still support a significant proportion of the continuous forest species assemblage. Most of the species present in the fragments belong to Seasonally Semideciduous and Dense *Terra Firme* Forest, corroborating the notion that floristic composition and similarity were little changed, being at an advanced succession stage. DBH distribution patterns showed that both the forest fragments and continuous forest are at a mature stage. Some of the locally most abundant species recorded in this qualitative and quantitative study appear on the 2008 IBAMA list of vulnerable species. However, we urge caution when considering directories of endangered species, especially those that occur in the Amazon, where there are many areas that have had few or no collections. The species listed were common at Alter do Chão, and we have found them frequently in other places in the Amazon. Basing conservation priorities only on these lists may not be a useful strategy.

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