ISSN 0104-7760
v.26 n.4 2020

Ana Maria Moreira Fernandes[1a+], Maria de Lourdes Pinheiro Ruivo[2a], Antônio Carlos Lola Costa[1b]

FLORISTIC COMPOSITION AND DIVERSITY IN TERRA FIRME FOREST UNDER WATER STRESS IN THE AMAZON

FERNANDES, A. M. M.; RUIVO, M. DE L. P.; COSTA, A. C. L. Floristic composition and diversity in terra firme forest under water stress in the Amazon. **CERNE**, v. 26, n. 4, p.403-413, 2020.

HIGHLIGHTS

Fabaceae was the family with the highest richness of species.

The floristic composition did not show significant variation in areas with and without rainfall exclusion.

Species diversity was slightly greater in areas of rainfall exclusion.

Exclusion of rainfall at ground level did not significantly affect forest conservation.

Keywords:
Diversity
Richness
Rainfall exclusion

ABSTRACT

The studies on floristic composition are an aid in the understanding of the structure and dynamics of the plant communities, fundamental parameters for its management and conservation. Thus, the objective of this work was to evaluate the floristic composition, species richness, Shannon's diversity and models of species abundance over a 10-year period (2005 to 2015) in two terra firme forest areas, with and without water deficit in the soil. Data were collected in 98 subplots denominated A (control) and 98 subplots B (rainwater exclusion), each measuring 10 m x 10 m, of which plants species with diameter at breast height (DBH≥10 cm) were listed. The Fabaceae (33), Sapotaceae (27), Chrysobalanaceae (15) and Burseraceae (13) families were the most representated in the study areas. A small decrease was found in the observed species richness in area A, but the community evenness and the Shannon diversity index remained constant, and a small increase was found in the observed species richness in area B, which may have contributed to a increase in the diversity index over time. The Zipf and Zipf-Mandelbrot models adjusted for the plant communities of areas A and B, respectively, indicate that such areas indicate good ecological conditions for the establishment of late colonizing species. Thus, it can be inferred that water deficiency in the soil did not significantly affect the conservation of the forest under study.

Historic:
Received 13/02/2020
Accepted 21/09/2020

+Correspondence:
moreirafernandesanamaria@gmail.com

DOI:
10.1590/01047760202026042730

(cc) BY

[1]Federal University of Pará, Guamá, Belém, PA, Brasil. ORCID: 0000-0003-2959-8387[a], 0000-0001-8140-4020[b]
[2] Museu Paraense Emílio Goeldi, São Brás, Belém, PA, Brasil. ORCID:0000-0002-6222-5534[a]

INTRODUCTION

The Amazon biome represents about 30% of all remaining tropical rainforests in the world, in which the Amazon Rainforest stands out for providing a multitude of ecological assets and essential services to the quality of human life (Sfb, 2010). This biome has been raising the interest in long-term studies due to the anthropic pressure that has been occurring in this region associated with climate change (Tabarelli et al., 2013).

The climatic changes, particularly those in relation to changes in the water balance in some regions or even regarding temperature variation out of the regular standards may modify distribution and survival of the species (Cordeiro et al., 2008). Thus, there is great concern about the effects of drought on the rainforest, further considering that the rates of net increase in above-ground biomass are decreasing (Stark et al., 2014; Doughty et al., 2015; Feldpausch et al., 2016).

Knowledge and understaning of the complex dynamics of rainforests arise with the floristic composition survey. Studies on floristics changes not only improve understanding of the ecology of tropical forests and their response to local and regional disturbances, but also the ability to predict how future global climatic changes may influence some vital services provided by these ecosystems (Feeley et al., 2011).

Studies on the forest structure and floristic composition in the Amazon demonstrate that the terra firme forests are usually highly diverse, with few representative individuals per species (Andrade et al., 2017), and are located in higher areas, with variations in the structure of the canopy (Pereira et al., 2012) and can grow in deep oligotrophic clayey-sandy yellow Latosols of tertiary origin (Almeida et al., 1993).

A pattern shown in the literature is that, in Tropical Forests, few species are locally common, others, moderately common and most of them are rare (Magurran, 2013). Knowledge about the abundance and rarity of species is important for the policy of conservation and the use of its tools (Hewitt et al., 2016).

Thus, understanding the behavior of species in plant communities through the analysis of floristic composition is the onset for understanding the ecosystems of tropical forests and, according to Feeley et al. (2011), investigating changes in floristic composition should be a clear research priority considering the context of the influence of global climate changes on natural ecosystems (Oliveira, 2014).

Therefore, this study was based on an experiment denominated Esecaflor (Study of forest drought) which sought to exclude the maximum amount of rainwater in contact with the soil in order to simulate a possible drought caused by the occurrence of the El Niño event (CAI et al., 2014). We test the hypothesis that the reduction of water in the forest soil may have negatively affected the development of the forest in terms of floristic composition, species richness, Shannon's diversity and abundance of species over time, considering that the water deficit may be a stress factor for the plants (Chagas et al., 2012).

As a result, the objective of this study was to evaluate the changes floristic composition, richness, diversitiy and abundance models of a plant community over a 10-year period (from 2005 to 2015) in two terra firme forest areas with and withouth soil water shortage in the Caxiuanã National Forest.

MATERIAL AND METHODS

Study area

The study was carried out in a primary terra firme forest located within the Caxiuanã National Forest (FLONA) (latitude: 01°42'30" S and longitude: 51°31'45" W), belonging to Ferreira Pena Scientific Station (ECFPn) of the Paraense Emílio Goeld Museum.

Dense terra firme forest is the largest and most diverse environment in ECFPn, occupying approximately 85% of the area, and grows in deep oligotrophic clayey-sandy yellow Latosols of tertiary origin (Almeida et al., 1993).

According to the classification of Köppen, the climate in Caxiuanã is of the hot and humid-tropical type and climatic subtype "Am" with a short dry season (Oliveira et al, 2008; Marengo et al, 2011). The average annual temperature is around 26.7°C, with an average minimum temperature of 23°C and a maximum of 32.7°C (Costa and Moraes, 2002). The Caxiuanã area has an annual average of 2,011.2 mm of rain, where the rainy period is from December to May (1,871.2 mm, representing 84.6%), and the dry period between June and November – 340.4 mm, representing 15.4% (Icmbio, 2012; Silva Junior et al, 2013).

Plant sampling

This study was carried out by analyzing the data collected on the experimental site of the "Study of the Drought of the Forest" (Esecaflor) project developed under the LBA (Large Scale Biosphere-Atmosphere Experiment in the Amazon) program. The Esecaflor experiment started in January 2002, but for the aims sampling of this study, it was considered the survey of data from the 2005 to 2015 period.

Data collection was carried out in area A denominated control and in area B (rainwater exclusion), separated by a distance of 50 meters, totaling 98 contiguous subplots of 10 mx 10 m in each study area, where plants species (trees and shrub) with a diameter at breast height (DBH ≥10 cm) were listed. Identification of the species was carried out by a botanical technician of the Museu Paraense Emílio Goeldi (MPEG), but specimens were not deposited in any herbarium. The floristic inventory was always conducted by the same MPEG team, with a researcher and three technicians. The species were classified into families recognized by the Angiosperm Phylogeny Group IV (Apg IV, 2016). The scientific names of the species have been confirmed and updated using The Plant List database (http:www.theplantlist.org).

For the exclusion of rainwater in area B, a cover of the area was constructed using approximately 5,000 panels of 0.50 x 3.0 meters of clear, wood-framed plastic cladding, which were installed at a height 1.5 to 4 meters above the ground. This cover was kept permanently clean, replacing the panels in case of damage caused by falling branches, fruits and occasionally trees (Costa et al., 2007). In the same area, twenty wooden gutters were built 0.3 x 0.3 x 100 m in width, depth and length, respectively, and were placed parallel to a distance of 5 m, with a height of around 4 m in the central part of the plot and 1.5 m on the sides. The gutters were also covered with the same plastic material as the panels, which facilitated the drainage of water into the side trenches that direct these flows to discharge points distant from the parcel (Oliveira, 2014).

Data analysis

Data of the community were analyzed over the 2005-2015 period, defined on the basis of four surveys which corresponded to the years 2005, 2008, 2011 and 2015. Species richness was recorded for each inventory year in areas A and B and their estimates were calculated using five non-parametric richness estimators: ICE, Chao 2, Jackknife 1, Jackknife 2 and Bootstrap, considered efficient tools to estimate the species richness of an area (Magurran, 2013). The calculations were made using the EstimateS software version 9.1.0 (Colwell, 2013). Community diversity was determined for each surveyed year by means of the Shannon's index (H') and evenness (J') index (Magurran, 2013).

Data analysis was performed with the Past software version 3.23 (Hammer, 2013). Species diversity were compared among inventories using diversity profiles (Tóthmérész, 1995) through the use of the Hill series which corresponds to a generalization best known in the ecological literature (Hill, 1973), given by [1] where N_a is the diversity index for the parameter a ($a \geq 0, a \neq 1$) and ps corresponds the proportion of abundance of the species. The graphics were performed with the vegan package version 2.5-3 (Oksanen et al., 2018) of software R version 3.5.1 (R core team, 2018).

$$N_a = (p_1^a + p_2^a + p_3^a + \ldots + p_s^a)^{1/(1-a)} \quad [1]$$

Species abundance distribution in plant community in areas A and B was evaluated using five ecological species abundance models: Broken stick (Null Model), Niche-Preemption, Log-normal, Zipf and Zipf-Mandelbrot, in which the selection of the best fit model was based on the smallest values of the Akaike information criteria (AIC), Bayesian information criteria (BIC) and Deviance (model adjustment residuals), which indicate the best ecological model (Oksanen et al., 2018). Rare species were defined as those represented by one to four individuals.

The models to be tested in this study were chosen to assess the degree of evenness of the community and to evaluate its successional process throughout the study. For data processing, we used the vegan package version 2.5-3 (Oksanen et al., 2018) of software R version 3.5.1 (R core team, 2018).

RESULTS

Flora, species richness and Shannon's diversity

Over the study period (2005-2015), a totalvariation from 517 to 474 individuals distributed in 36 families, 88 genera and 201 species were recorded in area A. Table 1 show the 26 most abundant species above 4 individuals, with the trees predominants. The botanical families with the highest species richness were Fabaceae (31), Sapotaceae (27), Chrysobalanaceae (15), Burseraceae (13) and Lecythidaceae (8), together representing 46.77% of the total recorded species throughout the survey.

The three most abundant species in area A were *Rinorea guianensis* Aubl. (range from 56 to 50 individuals; total relative abundance 10.8% in 2005 and also in 2015), *Vouacapoua americana* Aubl. (22 to 21 individuals; total relative abundance 4.3% in 2005 and 4.4% in 2015, respectively) and *Pouteria decorticans* T.D. Penn. (18 individuals, total relative abundance 3.5% in 2005 and 3.8% in 2015) (Table 1).

From 2005 to 2015, the variation in the number of species in area A was very small (from 183 to 179) and

TABLE 1 Alphabetically ordered sampling of the most abundant species in the area A of the terra firme forest in this study (2005-2015), Flona de Caxiuanã, Pará. Where: TR = tree and SH = shrub.

Family	Species	Habit	2005	2015
Annonaceae	*Bocageopsis multiflora* (Mart.) R.E.Fr.	TR	8	7
Lecythidaceae	*Couratari multiflora* (Sm.) Eyma	TR	12	10
Lecythidaceae	*Eschweilera coriacea* (DC.) S.A.Mori	TR	8	8
Lecythidaceae	*Eschweilera grandiflora* (Aubl.) Sandwith	TR	9	6
Lecythidaceae	*Eschweilera pedicellata* (Rich.) S.A.Mori	TR	7	6
Chrysobalanaceae	*Licania heteromorpha* Benth.	TR	5	5
Chrysobalanaceae	*Licania membranacea* Sagot ex Laness.	TR	6	5
Chrysobalanaceae	*Licania octandra* (Hoffmanns. ex Roem. & Schult.) Kuntze	TR	15	12
Sapotaceae	*Manilkara huberi* (Ducke) Standl.	TR	5	-
Sapotaceae	*Manilkara bidentata* (A. DC.) A.Chev.	TR	10	10
Sapotaceae	*Micropholis venulosa* (Mart. & Eichler ex Miq.) Pierre	TR	7	7
Olacaceae	*Minquartia guianensis* Aubl.	TR	9	9
Sapotaceae	*Pouteria* sp.	TR	5	-
Sapotaceae	*Pouteria anomala* (Pires) T.D.Penn.	TR	6	6
Sapotaceae	*Pouteria cladantha* Sandwith	TR	6	6
Sapotaceae	*Pouteria decorticans* T.D. Penn.	TR	18	18
Sapotaceae	*Pouteria guianensis* Aubl.	TR	5	-
Sapotaceae	*Pouteria oppositifolia* (Ducke) Baehni	TR	13	14
Burseraceae	*Protium tenuifolium* (Engl.) Engl.	TR	10	9
Violaceae	*Rinorea guianensis* Aubl.	TR	56	50
Rubiaceae	*Stachyarrhena spicata* Hook. f.	SH	7	5
Fabaceae	*Swartzia racemosa* Benth.	TR	13	11
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	TR	6	-
Myristicaceae	*Virola michelii* Heckel	TR	5	-
Fabaceae	*Vouacapoua americana* Aubl.	TR	22	21
Fabaceae	*Zygia racemosa* (Ducke) Barneby & J.W. Grimes	TR	6	6
	Sub-total		279	231
	Other species		238	243
	Total		517	474

community equability remained constant, which contributed to maintaining the Shannon's diversity index (Table 2). In addition, the diversity profiles of the inventories showed absence of significant differences in community diversity (observed by overlapping curves - Figure 1) and over 80% of rare species.

TABLE 2 Vegetation characteristics for area A in 2005-2015 period in the terra firme forest, Flona de Caxiuanã, Pará. Where: ICE, Chao2, Jackknife1 (first order estimator), Jackknife2 (second order estimator) and Bootstrap are the non-parametric richness estimators; Sobs = observed richness; Sobs% = percentage of the observed richness in relation to the estimated richness of each estimator; rare sp. (%) = Percentage of rare species; H '= Shannon's diversity index, J' = evenness and N = number of individuals.

	2005	2008	2011	2015
1-ICE	388.89	366.93	389.06	377.1
2-Chao2	343.48	325.97	351.51	355.01
3-Jackknife1	286.93	274.98	284.93	282.93
4-Jackknife2	356.82	340.95	356.76	355.73
5-Bootstrap	226.59	217.6	224.38	222.34
Sobs	183	176	181	179
Sobs% 1	47.06	47.96	46.52	47.46
Sobs% 2	53.28	53.99	51.49	50.42
Sobs% 3	63.78	64.00	63.52	63.26
Sobs% 4	51.29	51.62	50.73	50.31
Sobs% 5	80.76	80.88	80.66	80.50
Rare sp. (%)	85.79	85.8	86.19	87.71
H'	4.57	4.53	4.57	4,58
J'	0.88	0.88	0.88	0.88
N	517	500	503	474

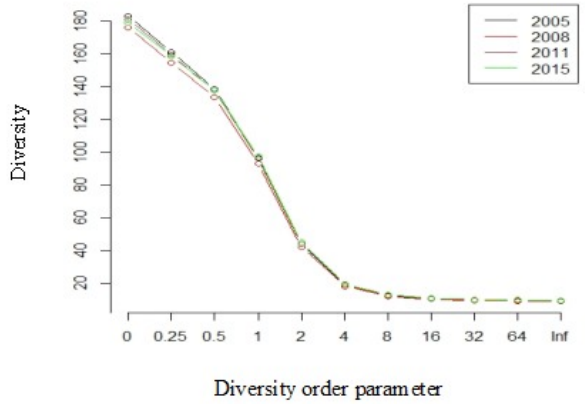

FIGURE 1 Diversity profiles for area A during the period from 2005 to 2015 using the Hill Series in the terra firme forest, Flona de Caxiuanã, Pará.

The richness estimates in area A were higher than the richness observed in the study period, which represented 47.06% in 2005 and 47.47% in 2015 through the Ice estimator - the lowest values of the estimators used. However, according to the Bootstrap estimator, it was observed 80.76% in 2005 and 80.51% in 2015 - the highest values of the estimators used (Table 2).

The ecological model of species abundance distribution that best described and fit the ecological community of area A was Zipf (Figure 2).

In the abovementioned period, area B (rainwater exclusion) recorded a totalvariation from 477 to 426 individuals distributed in 35 families, 92 genera and 210 species. Table 3 show the 31 most abundant species above 4 individuals, with the trees predominants. The plant families with the highest species richness were Fabaceae (33), Sapotaceae (25), Burseraceae (11), Chrysobalanaceae (9) and Lecythidaceae (9), together representing 41.43% of the total recorded species.

The three most abundant species in area B were *Tetragastris panamensis* (Engl.) Kuntze (range from 17 to 15 individuals, total relative abundance 3.56% in 2005 and 3.52% in 2015), *Manilkara bidentata* (A.DC.) A.Chev. (15 individuals, total relative abundance of 3.14% in 2005 and 3.52% in 2015) and *Minquartia guianensis* Aubl. (range from 15 to 14 individuals, total relative abundance of 3.14% in 2005 and 3.29% in 2015) (Table 3).

From 2005 to 2015, the number of species in area B varied from 173 to 185, while the equability did not change, in addition to more than 80% of rare species (Table 4). Thus, this small variation in richness may have contributed to the variation in community diversity - as seen in the diversity profile graph - which shows that diversity was higher in 2015 compared to the other years of the study (Figure 3).

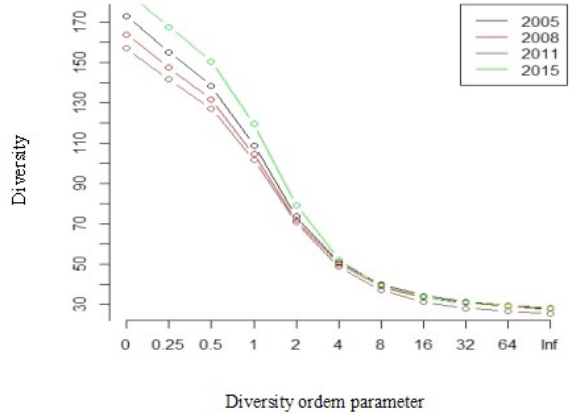

FIGURE 3 Diversity profiles for area B during the period from 2005 to 2015 using the Hill Series in the terra firme forest, Flona de Caxiuanã, Pará.

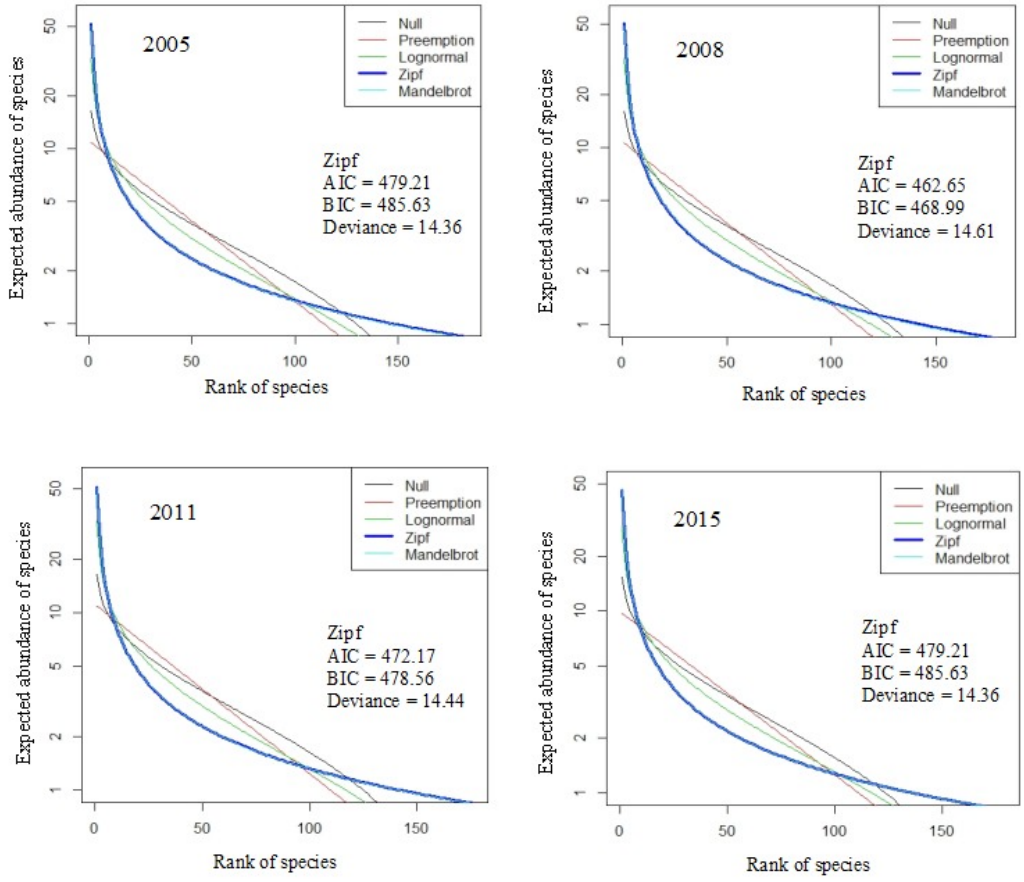

FIGURE 2 Curves of the five ecological models of species abundance distribution adopted from 2005 to 2015 for area A in the terra firme forest, Flona de Caxiuanã, Pará. AIC = Akaike Information Criteria and BIC = Bayesian Information Criteria both from the Zipf model - which best fit the data.

TABLE 3 Alphabetically ordered sampling of the most abundant species in area B of the terra firme forest in this study (2005-2015), Flona de Caxiuanã, Pará. Where: TR = tree and SH = shrub.

Family	Species	Habit	2005	2015
Sapotaceae	*Chrysophyllum prieurii* A.DC.	TR	6	6
Annonaceae	*Duguetia echinophora* R.E.Fr.	TR	5	-
Lecythidaceae	*Eschweilera coriacea* (DC.) S.A.Mori	TR	14	11
Lecythidaceae	*Eschweilera grandiflora* (Aubl.) Sandwith	TR	5	-
Lecythidaceae	*Eschweilera pedicellata* (Rich.) S.A.Mori	TR	5	5
Annonaceae	*Guatteria poeppigiana* Mart.	TR	6	-
Chrysobalanaceae	*Hirtella bicornis* Mart. & Zucc.	TR	7	6
Fabaceae	*Inga gracilifolia* Ducke	TR	6	6
Fabaceae	*Inga alba* (Sw.) Willd.	TR	5	6
Lecythidaceae	*Lecythis confertiflora* (A.C.Sm.) S.A.Mori	TR	9	8
Lecythidaceae	*Lecythis idatimon* Aubl.	TR	10	8
Chrysobalanaceae	*Licania octandra* (Hoffmanns. ex Schult.) Kuntze	TR	6	6
Sapotaceae	*Manilkara bidentata* (A.DC.) A.Chev.	TR	15	15
Sapotaceae	*Micropholis venulosa* (Mart. & Eichler ex Miq.) Pierre	TR	8	-
Olacaceae	*Minquartia guianensis* Aubl.	TR	15	14
Melastomataceae	*Mouriri duckeana* Morley	TR	7	6
Ochnaceae	*Ouratea* sp.	TR	12	8
Sapotaceae	*Pouteria decorticans* T.D. Penn.	TR	13	10
Sapotaceae	*Pouteria jariensis* Pires & T.D.Penn.	TR	6	6
Sapotaceae	*Pouteria* sp.	TR	11	6
Sapotaceae	*Pouteria anomala* (Pires) T.D. Penn.	TR	5	5
Sapotaceae	*Pouteria oppositifolia* (Ducke) Baehni	TR	-	5
Sapotaceae	*Pouteria venosa* (Mart.) Baehni	TR	6	6
Burseraceae	*Protium tenuifolium* (Engl.) Engl.	TR	11	10
Fabaceae	*Sclerolobium* sp.	TR	5	5
Rubiaceae	*Stachyarrhena spicata* Hook. f.	SH	12	9
Fabaceae	*Swartzia racemosa* Benth.	TR	11	11
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	TR	17	15
Fabaceae	*Vouacapoua americana* Aubl.	TR	8	8
Annonaceae	*Xylopia nitida* Dunal	TR	10	6
Fabaceae	*Zygia racemosa* (Ducke) Barneby & J.W. Grimes	TR	-	5
	Sub-total		256	212
	Other species		221	214
	Total		477	426

TABLE 4 Vegetation characteristics for area B in 2005-2015 period in the terra firme forest, Flona de Caxiuanã, Pará. ICE, Chao2, Bootstrap, Jackknife1 (first order estimator) and Jackknife2 (second order estimator) are the non-parametric richness estimators; Sobs = observed richness; Sobs% = percentage of the observed richness in relation to the estimated richness of each estimator; Rare sp. (%) = Percentage of rare species; H'= Shannon's diversity index, J' = evenness and N = number of individuals.

	2005	2008	2011	2015
1-ICE	361.14	359.45	315.77	506.37
2-Chao2	383.89	392.05	363.32	525.33
3-Jackknife1	270.99	259.02	245.09	306.74
4-Jackknife2	345.67	333.67	313.86	405.91
5-Bootstrap	213.14	202.53	192.87	233.58
Sobs	173	164	157	185
Sobs% 1	47.90	45.63	49.72	36.53
Sobs% 2	45.06	41.83	43.21	35.22
Sobs% 3	63.84	63.32	64.06	60.31
Sobs% 4	50.05	49.15	50.02	45.58
Sobs% 5	81.17	80.98	81.40	79.20
Rare sp. (%)	83.24	83.54	81.53	85.41
H'	4.69	4.65	4.62	4.78
J'	0.91	0.91	0.91	0.92
N	477	444	431	426

Richness estimates in area B were higher than the richness observed in the study period, which represented 45.06% in 2005 and 35.22% in 2015 - the smallest values of the estimators used in the study. However, according to the Bootstrap estimator, it was observed 80.76% in 2005 and 79.20% in 2015 - the highest values of the estimators (Table 4).

The ecological model of species abundance distribution that best described and adjusted the ecological community of rainwater exclusion areas was Zipf-Mandelbrot, as it presented the lowest information values for AIC, BIC and residues (Figure 4).

In these ten years of evaluation, regarding the number of species, it was observed that twenty-five disappeared due to mortality in area A and twenty-one in area B; also, a gain of seventeen species was observed in the former and thirty-seven in the latter. Regarding abundance, higher mortality was found in area B, with negative balance between loss and gain of individuals (Table 5).

DISCUSSION

General aspects on floristic composition, richness and diversity

It was recorded in both areas A and B, that over the study period (2005-2015), the most expressive botanical families that had prominence in terms of number of species were Fabaceae, Sapotaceae, Chrysobalanaceae,

TABLE 5 Change in richness and abundance of species from the initial 2005 survey to the final survey in 2015 in the study areas in the dry land forest, Flona de Caxiuanã, Pará.

	Area A	Area B
Initial total richness	183	173
Species loss	21 (12.02%)	25 (14.45%)
Species gain	17 (9.29%)	37 (21.39%)
Final total richness	179	185
Initial total abundance	517	477
Loss of individuals	63 (12.19%)	95 (19.92%)
Gain of individuals	20 (3.87%)	44 (9.22%)
Final total abundance	474	426

Burseraceae, Lecythidaceae, in which Fabaceae was the family with the greatest species richness. Other studies carried out in the Amazon have shown similar results, which emphasize the predominance of the Fabaceae family in number of species (Lisboa et al., 1997; Oliveira et al., 2008; Salomão et al., 2012). In the study by Lisboa et al. (1997), however, it was considered the division of legumes into three distinct families (Fabaceae, Caesalpiniaceae and Mimosaceae) and not included as belonging only to the Fabaceae family, but if added and represented in a single group (Fabaceae) would become the family with the largest species richness.

Thus, in terms of floristic composition in relation to the number of botanical family species in both A and B areas of this study, predominance of practically the same families already mentioned in these areas was found, with little variation in the number of representative species over the period of this study, even if the forest was disturbed due to water exclusion. Such fact demonstrates that the forest may be showing resilience of species with respect to disturbance suffered due to water deficit in the soil. By considering that the water deficit of this study was an attempt to simulate the effects of climate change, a study using climate and ecological models in tropical forest areas showed that forests may lose part of their carbon stock through climate change, but that the Amazon rainforest would show resilience to climate change (Davidson et al., 2012; Huntingford et al., 2013; Butt el., 2014).

By considering the most species in areas A and B, it was found that there was little variation in terms of number of individuals of the species throughout the study period and that the species *Rinorea guianensis* Aubl. stood out in terms of number of individuals followed by other more abundant species (*Vouacapoua americana* Aubl. and

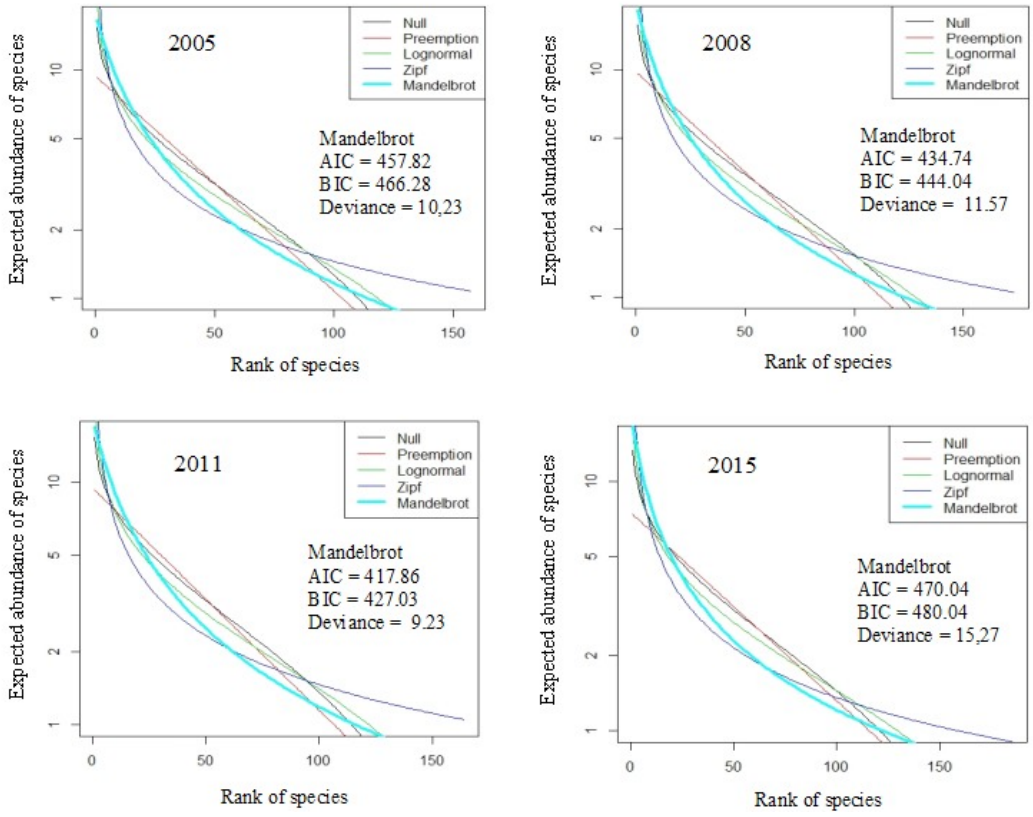

FIGURE 4 Curves of the five ecological models of species abundance distribution adopted in the period from 2005 to 2015 for area B in the Flona de Caxiuanã terra firme forest, state of Pará. AIC = Akaike Information Criterion and BIC = Bayesian Information Criterion both of the Mandelbrot model - which best fit the data.

Pouteria decorticans T.D. Penn.). Other floristics studies also recorded the occurrence of these species in terra firme forest (Amaral et al., 2009; Ferreira et al., 2015; Mendes et al., 2013).

Regarding the rare species of this study, it is quite evident a high percentage over 80% compared to the most abundant ones during the period from 2005 to 2015 in areas A and B, some of that is due to the fact that over the study period, other species achieved DBH of 10 cm and were included in the study. Almeida et al. (1993), in an area of 13 hectares, recorded the presence of 375 rare species represented by 1 to 4 individuals. Rare species are particularly sensitive to local extinction because of being represented by a small number of individuals and their conservation is of great importance for the maintenance and functioning of diverse forest ecosystems (Ferreira et al., 2015).

Although richness has been high in plots A and B, estimates of the potential number of species calculated using Bootstrap estimator were even higher. Thus, even though the observed richness has been high, the sample of this study was not sufficient to represent the total richness potential of the areas. The richness recorded over the study period was very close to another floristic study carried out in dry land forest at the Caxiuanã Scientific Station, where the average species richness was 189 per hectare (Almeida et al., 1993).

The small variation in richness and the constancy of equability in area A in 2005-2015 period is consistent with the theory that tropical forests, free of major anthropogenic disturbance or interference, generally does not change much in floristic composition (Swaine et al., 1987). In area B, a greater variation was found in the richness, contributing to a slight change in the diversity index in 2015 compared to other years. Thus, it is inferred that these areas subjected to water deficit for the plants generated this species richness variation with a positive balance between gain and loss in number of species, but with a negative balance between gain and loss of number of individuals. Thus, the mortality of species may have promoted the emergence and establishment of some species over time, as the death of species provides opening of clearings, consequently causing modification in the environmental conditions, brightness, temperature and humidity (Burslem and Whitmore, 1999).

It was observed that in the study areas, the predominant identified species were the secondary late. Furthermore, considering that the late species are generally of great size and more demanding in their environmental conditions, besides starting their presence in medium stages of succession, it is inferred that the areas under study may be moving towards resilience.

Shannon's diversity indices and equability found in this study are considered high, describing uniform plant communities. Therefore, they can be considered stable and adequately maintained.

Species abundance distribution models

The ecological models of species abundance distribution best adjusted to areas A and B were Zipf and Zipf-Mandelbrot, respectively. The results of the models are interpreted as a successional process in which late colonizing species have greater needs for a specialized niche and the presence of one species is due to dependence on previous physical and ecological conditions (Magurran, 2013).

According to Whittaker (1972), in a resource gradient, species evolve to occupy different positions over this gradient, therefore, showing variations in abundance distribution patterns according to environmental variation. In this regard, the results of the abundance distributions adjustments of this study show that they did not undergo major changes with the disturbance caused by water stress, considering that the community data were better explained by ecological models that describe more stable environments in a more mature successional stage, with little disturbance (Magurran, 2013).

CONCLUSIONS

The study showed that the plant community did not show any significant variations in terms of floristic composition, species richness, diversity and abundance distribution in forest areas without water exclusion in the soil compared to areas with water exclusion over ten years of study.

Also, the best ecological models adjusted to the data of the study characterized an environment reflecting a successional process, which postulates that late colonizers have more specific requirements when conditioned to requirements of previous environmental conditions for their establishment and, thus, it is inferred that the plant community is in the maturity stage.

Thus, it can be understood that the forest is well established, presenting itself as a dynamic system that is in an adequate state of conservation and that the water restriction in the soil over the ten years of study was not sufficient to so expressively interfere in the conservation status of the environment. This study suggests that over ten years, the forest has proved resilient to a possible climatic change caused by drought.

ACKNOWLEDGEMENTS

The execution of this study was possible due to the support granted by "Estudo da Seca da Floresta"

(ESECAFLOR/LBA). We also thank the anonymous revisers for the important suggestions that helped to improve this paper.

REFERENCES

ALMEIDA, S. S; LISBOA, P. L. B.; SILVA, A. S. L. Diversidade florística de uma comunidade arbórea na Estação Científica Ferreira Penna, Caxiuanã, Pará. **Boletim Museu Paraense Emílio Goeldi**, v. 9, n. 1, p. 93-188, 1993.

AMARAL, D. D.; ALMEIDA, S. S.; COSTA, D. C. T. Contribuições ao manejo florestal de espécies de valor madeireiro e não madeireiro na Floresta Nacional de Caxiuanã. In: LISBOA, P. L. B. **Caxiuanã**: Desafios para a conservação de uma Floresta Nacional na Amazônia. Belém: Museu Paraense Emílio Goeldi, 2009. p.199-221.

ANDRADE, R. T. G.; PANSINI S.; SAMPAIO, A. F.; RIBEIRO, M. S; CABRAL, G. S.; MANZATTO, A. G. Fitossociologia de uma floresta de terra firme na Amazônia Sul-Ocidental, Rondônia, Brasil. **Biota Amazônica**, v. 7, n. 2, p. 36-43, 2017.

APG. The Angiosperm Phylogeny Group. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. The Linnean Society of London, **Botanical Journal the Linnean Society**, v. 181, p. 1-20, 2016.

BURSLEM, D. F. R. P.; WHITMORE, T. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forests. **Journal of Vegetation Science**. v. 10, n. 6, p. 767-776, 1999.

BUTT, N. et al. Shifting dynamics of climate-functional groups in old growth Amazonian forests. **Plant Ecology and Diversity**, v. 7, n. 1-2, p. 267-279, 2014.

CAI, W. et al. Increasing frequency of extreme El Niño events due to greenhouse warming. **Nature Climate Change**, v. 4, p. 111-116, 2014.

CHAGAS, G. F. B. et al. Impactos da redução da pluviometria na biomassa. **Revista Brasileira de Engenharia Agrícola e Ambiental**, v. 16, p. 72-79, 2012.

CORDEIRO, S. A.; SOUZA, C. C.; MENDOZA, Z. M. S. H. Florestas brasileiras e as mudanças climáticas. **Revista Cientifica Eletrônica de Engenharia Florestal**, v. 11, p. 1-20, 2008.

COSTA, J. P. R.; MORAES, J. C. Médias mensais de variáveis metereológicas. In: LISBOA, P. L. B. (org.). **Caxiuanã**. Belém, Museu Paraense Emílio Goeldi, Belém, 2002. p. 225-232.

COSTA, R. F.; SILVA, V. P. R.; RUIVO, M. L. P.; MEIR, P.; COSTA, A. C. L.; MALHI, Y. S.; BRAGA, A. P.; GONÇALVES, P. H. L.; JÚNIOR, J. A. S.; GRACE, J. Transpiração em espécie de grande porte na Floresta Nacional de Caxiuanã, Pará. **Revista Brasileira de Engenharia Agrícola e Ambiental**. v.11, n. 2, p.180-189, 2007.

COLWELL, R. K. Statistical Estimation of species Richness and shared species from samples. 9.1.0, 2013. Available at: http://viceroy.colorado.edu/estimates/EstimateSPages/EstimateSRegistration.htm. Accessed in: 1 agosto. 2019.

DAVIDSON, E. A. et al. The Amazon basin in transition. **Nature**, v. 481, p. 321-328, 2012.

DOUGHTY, C. E.; METCALFE D. B.; GIRARDIN C. A. J. et al. Drought impact on forest carbon dynamics and fluxes in Amazonia. **Nature**, v. 519, p. 78-82, 2015.

FEELEY, K. J.; DAVIES, S. J.; PEREZ R.; HUBBELL S. P.; FOSTER R. B. Directional changes in the species composition of a tropical forest. **Ecology**, v. 92, n. 4, p. 871-882, 2011.

FELDPAUSCH, T. R.; PHILLIPS, O. L.; BRIENEN, R. J. W. et al. Amazon forest response to repeated droughts. **Global Biogeochemical Cycles**, v. 30, n. 7, p. 964-982, 2016.

FERREIRA, T. S.; HIGUCHI, P.; SILVA, A. C.; MANTOVANI, A.; MARCON, A. K.; SALAMI, B. et al. Distribuição e Riqueza de Espécies Arbóreas Raras em Fragmentos de Floresta Ombrófila Mista ao longo de um gradiente Altitudinal, em Santa Catarina. **Revista Árvore**, v. 39, n. 3, p. 447-455, 2015.

HAMMER, O. Paleontological Statistics Software Package for Education and Data Analysis, v.3.23, 2013. Disponível em: https://folk.uio.no/ohammer/past/. Accessed in: agosto 2019.

HEWITT, J. E; THRUSH, S. F; ELLINGSEN, K. E.The role of time and species identities in spatial patterns of species richness and conservation. **Conservation Biology**, v. 30, n. 5, p. 1080-1088. 2016.

HILL, M. O. Diversity and evenness: a unifying notation and its consequences. **Ecology**. v. 54, n. 2, p. 427-432, 1973.

HUNTINGFORD, C.; ZELAZOWSKI, P.; GALBRAITH, D.; MERCADO, L. M; SITCH, S.; FISHER, R. et al. Simulated resilience of tropical rain forests to CO_2-induced climate change. **Nature Geoscience**, v. 6, abr., 2013.

ICMBIO. Plano de Manejo da Floresta Nacional de Caxiuanã - PA, v.1, 2012. Available at:https://www.icmbio.gov.br/portal/unidadesdeconservação/biomas-brasileiros/amazonia/unidades-de-conservação-amazonia/1928-flona-de-caxiuanã. Accessed in: 1 agosto. 2019.

LISBOA, P. L. B.; SILVA, A. S. L; ALMEIDA, S. S. Florística e Estrutura dos Ambientes: A diversidade florística em Caxiuanã. In: LISBOA, P. L. B. **Caxiuanã**. Belém: Museu Paraense Emílio Goeldi, 1997. p. 163-193

MAGURRAN, A. E. **Medindo a Diversidade Biológica**. UFPR, 2013. 261p.

MARENGO, J. A.; TOMASELLA, J.; ALVES, L. M.; SOARES. W. R.; RODRIGUEZ, D. A. The drought of 2010 in the context of historical droughts in the Amazon region. **Geophysical Research Letters**, v. 38, p. 1-5, 2011.

MENDES, F. S.; JARDIM, F. C. S.; CARVALHO, J. O. P.; SOUZA, D. V.; ARAÚJO, C. B.; OLIVEIRA, M. G. et al. Dinâmica da Estrutura da Vegetação do Sub-bosque sob influência da Exploração em uma Floresta de Terra Firme no município de Moju-PA. **Ciência Florestal**, v. 23, n. 2, p. 379-391, 2013.

OKSANEN, J. et al. Vegan: Community Ecology Package. R package, 2018. v 2.5-3.

OLIVEIRA, A. A. R. **Estudo de respiração do solo na floresta nacional de Caxiuanã, projeto Esecaflor/Lba**. Santarém, 2014. 74f. Dissertação (Mestrado em Recursos Naturais da Amazônia) – Programa de Pós-Graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Santarém, 2014.

OLIVEIRA, A. N.; AMARAL I. L.; NOBRE, A. D.; COUTO, L. B.; SAHDO, R. M. Composition and floristic diversity in one hectare of a upland fores dense in Central Amazonia, Amazonas, Brazil. **Acta Amazônica**. v. 38, n. 4, p. 627-641, 2008.

PEREIRA, J. L. G.; RENNÓ, C. D.; SILVEIRA, O. T.; FERREIRA, L. V. Classificação da cobertura da terra na Amazônia com base em imagens de satélite e caracterização das classes com relação à superfície do terreno. **Geografia**, v. 21, n. 3, p.115-131, 2012.

R CORE TEAM. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2018. v.3.5.3.

SFB - SERVIÇO FLORESTAL BRASILEIRO. Florestas do Brasil em resumo - 2010: dados de 2005-2010. 2010. Available at: http://www.florestal.gov.br/documentos/publicacoes/1784-florestas-do-brasil-em-resumo-2010/file. Accessed in: maio 2019.

SILVA JÚNIOR, J. A. et al. Fluxos de CO_2 do Solo na Floresta Nacional de Caxiuanã, Pará, durante o Experimento ESECAFLOR/LBA. **Revista Brasileira de Meteorologia**, v.28, n.1, p. 85 - 94, 2013.

SALOMÃO, R. P.; JÚNIOR, S. B.; SANTANA, A. C. Análise da florística e estrutura de floresta primária visando a seleção de espécies-chave, através de análise multivariada, para a restauração de áreas mineradas em unidades de conservação. **Revista Árvore**. v. 36, n. 6, p. 989-1007, 2012.

STARK, S. C. et al. Amazon Forest carbon dynamics predicted by profiles of canopy leaf area and light environment. **Ecology Letters**, v. 15, n. 12, p. 1406-1414, 2012.

SWAINE, M. D.; LIEBERMAN, D.; PUTZ, F. E. The dynamics of tree populations in tropical forest: a review. **Journal of Tropical Ecology**. v. 3, n. 4, p. 359-366, 1987. TABARELLI, M.; C. F. D. ROCHA; H. P. ROMANOWSKI; O. ROCHA & L. D. LACERDA, L. D. PELD-CNPq: dez anos do Programa de Pesquisas Ecológicas de Longa Duração do Brasil: achados, lições e perspectivas. Universitária UFPE, 2013. 446p.

THE PLANT LIST VERSION 1.1 (ed.), 2010. Available at: http://www.theplantlist.org/. Accessed in: janeiro 2020.

TÓTHMÉRÉSZ, B. Comparison of different methods for diversity ordering. **Journal of Science**. v. 6, n. 2, p. 283-290, 1995.

WHITTAKER, R. H. Evolution and measurement of species diversity. **Taxon**. v. 21, n. 2/3, p. 213-251,1972.