



River damming affects seedling communities of a floodplain forest in the Central Amazon

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ABSTRACT

The flood pulse of black water rivers in the Amazon basin determines the composition of species along the flood gradient in igapó forests. The Balbina dam, built on the Uatumã River, has altered the flood pulse and caused changes in the floristic composition of adult trees throughout the downstream area. There is a lack of studies on how communities of seedlings in igapó forests respond to changes in the flood pulse. This study investigates the response of seedling communities in the igapó forest downstream the Balbina dam and compares it with two pristine areas. The areas were sampled with transects of 1x25 m within 36 plots (25x25 m) along the flood gradient. Richness and dominance were calculated by simple regression and ordination analyses. The pristine areas had the same pattern of richness, dominance and genera distribution along the flood gradient. However, the affected Uatumã area formed different groups of genera by NMDS analysis, which divided them along the flood gradient with significantly increased dominance of three genera. The insertion of the Balbina dam resulted a loss of lateral and longitudinal connectivity for the Uatumã River, and the alteration to seedling communities may alter the future landscape of downstream igapó forests.

Keywords: dams, environmental stress, flood gradient, floodplain, hydrologic cycle, seedlings, tropical rivers

Introduction

Plans to build hydroelectric power plants in the Amazon include dozens of large dams and more than a hundred smaller ones. If these plans take place, a large number of Brazilian pristine wetlands will be severely affected (Winemiller *et al.* 2016), as it occurs in rivers already dammed such as the Uatumã (Fearnside 2014), a black-water river bordered by seasonal floodplain or igapó forests (Prance 1980; Sioli 1985).

The Balbina hydroelectric power plant (HPP) was constructed more than thirty years ago on the Uatumã River and flooded about 240,000 ha of tropical forest (Fearnside

1990). Studies of the igapó forest along the course of the Uatumã River downstream of the dam indicated changes in richness and dominance of some species in the area. A study with juvenile trees in the igapó downstream of the dam showed that poorly flood-adapted species of the adjacent upland forest started to colonize the higher topographic levels, substituting the typical species of the flooded environments (Lobo *et al.* 2019). On the other hand, one of the tree species that dominates the low topographic levels, *Macrolobium acaciifolium* (Worbes *et al.* 1992), showed high mortality in the low levels of the igapó forest downstream the Balbina dam (Assahira *et al.* 2017). Moreover, the seedlings can be considered as the

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developmental stage most vulnerable to mortality in the face of an environmental disturbance (Fenner 1987; Pratt *et al.* 2014; Melo *et al.* 2015) even though this has not yet been directly addressed. Has the richness and floristic composition of seedling communities of the igapó forest downstream the Balbina dam changed throughout the entire topographic gradient?

Along large Amazonian rivers, the major force controlling the biota of river floodplains is the presence of a regular and predictable flood pulse, defined by Junk *et al.* (1989) as the annual shift between aquatic and terrestrial phases. However, more important than flood tolerance in adult individuals is seedling establishment, which is the critical phase determining the success of floodplains colonization is seedling establishment (Junk 1989). The investigation of floodplain forest seedlings helps to understand the mechanisms that determine the floristic composition and diversity, as well as the dispersal of species within the different flood levels (Zagt 1964; Ferreira 1997; Wittmann & Junk 2003; Ferreira *et al.* 2010). Floristic studies of adult individuals in Amazonian floodplain forests show that some species may present higher values of dominance at different flood levels of igapó forests, such as *Amanoa oblongifolia* (Phyllanthaceae) and *Aldina latifolia* (Fabaceae) (Ferreira 1997).

In response to alternation between aquatic and terrestrial phases, the seedlings from Amazonian floodplains have adaptations both to the stress of submersion and to drought (Parolin *et al.* 2003; 2010; Parolin 2010). During the dry period, many seedlings start colonizing low-lying areas, but are then eliminated during the following flood period. A successful establishment of a seedling at the lowest level of their habitats is only possible in prolonged low-water periods or in periods of several consecutive dry years, which allows seedlings to reach a size that enables them to survive (Junk 1989). However, the construction of the Balbina dam changed the regularity and predictability of the flood pulse downstream the Uatumã River; the flooding duration has risen up to 290 days per year with an increase of 105 cm in the lower topographies, while in the higher topographies of the igapó forest the flood height had a mean decrease of 95 cm (National Water Agency ANA 2018; Assahira *et al.* 2017).

There is still a lack of knowledge about the impacts caused in the seedling communities throughout the entire area after the Balbina dam construction; this type of study could serve to build basic information on the floristic composition of an igapó forest after a dam; besides, there are no studies of seedling communities under a regular flood pulse in a continuous topographic gradient. Despite the regularity of the flood pulse of large Amazonian rivers (Junk *et al.* 1989), the annual inundation of undisturbed floodplain forests presents variability between systems (Ward & Stanford 1995). Also, species composition may vary according to the position

along the flood gradient, along different river sections and between river basins (Wittmann *et al.* 2010a). Therefore, this study analyses patterns of richness, parameters of dominance and distribution of genera in the igapó forest seedling communities along a continuous flood gradient in two areas of different river basins with regular a flood pulse and compares it the disturbed flood regime as altered by the Balbina dam (Uatumã River). The following hypotheses were tested: i) The patterns of richness, dominance and distribution of genera in the pristine areas differ from the area affected by the dam due to alteration of the flood pulse; ii) Dominant genera distribute along the flood gradient both in pristine and altered areas, but dominance is higher in the affected area, since few genera can establish under the modified hydrological regime.

Materials and methods

Study area and flood gradient

The study was carried out during the terrestrial period of 2015 and 2016, in three central Amazonian igapó forests: (1) downstream of the Balbina dam, on the Uatumã River (Uatumã area), (2) on the Abacate River, an adjacent river to the Uatumã without the influence of a hydroelectric dam (Abacate area) and (3) on the Jaú River (Jaú area) (Tab. 1) (Fig. 1).

Table 1. Location of the three igapó forests sampled: Uatumã, Abacate and Jaú. Conservation units: “SDR” Sustainable Development Reserve and “PARNA” National Park.

igapó Forests	Conservation Units	Coordinates
Uatumã	Uatumã SDR	2°13'26.7"S 59°3'18.2"W
Abacate	Uatumã SDR	2°10'02.7"S 58°43'28.0"W
Jaú	PARNA Jaú	1°54'6.9"S 61°27'31.7"W

According to the hydrological data from 1974-2017 provided by the National Water Agency (ANA 2018), all selected areas presented a monomodal predictable flood pulse: long duration and high amplitude (Junk *et al.* 2014).

The flooding regime of the Uatumã River, and consequently that of the associated igapó forests, is under floodgate control of the Balbina hydroelectric power plant (Fearnside 1989; MME 2007). According to the data provided by ANA (2018), in the period after the dam construction the low water levels increased by 104 cm compared to pre-dam period, whereas the high-water levels declined by 95 cm.

The pristine area within the same watershed of the Uatumã River is located on the Abacate River, which is one of the main tributaries of the Uatumã and is located on the edge of the Uatumã SDR (IDESAM 2009a; b). The Jaú area is also pristine, however located outside the Uatumã River basin (Melack & Hess 2010).



Sampling of seedling communities

In the three sampled areas, cross transects were installed in 2015 (1x 25 m = 0.0625 ha) within plots of 25x25 m (Fig. 2A), along a continuous topographic gradient, totaling 36 plots ($N = 36$): 12 in the Uatumã area (0.75 ha); 12 in

the Abacate area (0.75 ha) and 12 in the Jaú area (0.75 ha). The total area sampled in the three forests was 2.25 ha. In the Uatumã and Abacate areas, the research team also utilized the permanent plots of the PELD-MAUA project (Long-Term Ecological Research Program of the Ecology, Monitoring and Sustainable use of Wetlands group).

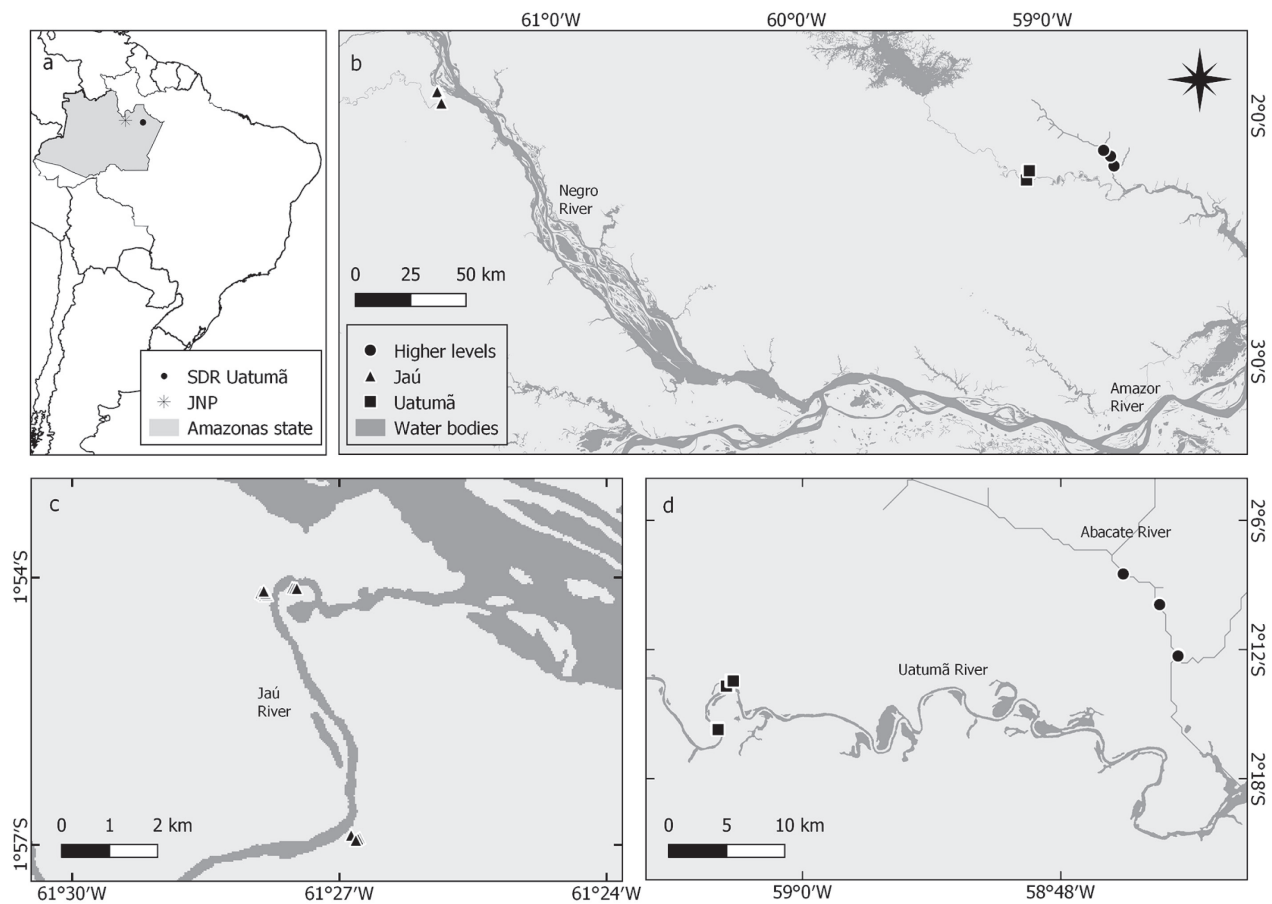


Figure 1. A. Brazil with Amazonas state highlighted. B. Study areas in shades of orange (gradient color refers to altitude, the darker - higher altitude); C. The plot's location in the igapó forest on the banks of the Jaú River in the PARNA Jaú (Jaú National Park - JNP) and d) Uatumã and Abacate Rivers in the Uatumã Sustainable Development Reserve (SDR) downstream of the Balbina hydroelectric dam. Images: SRTM satellite; waterbodies - earthexplorer.usgs.gov.

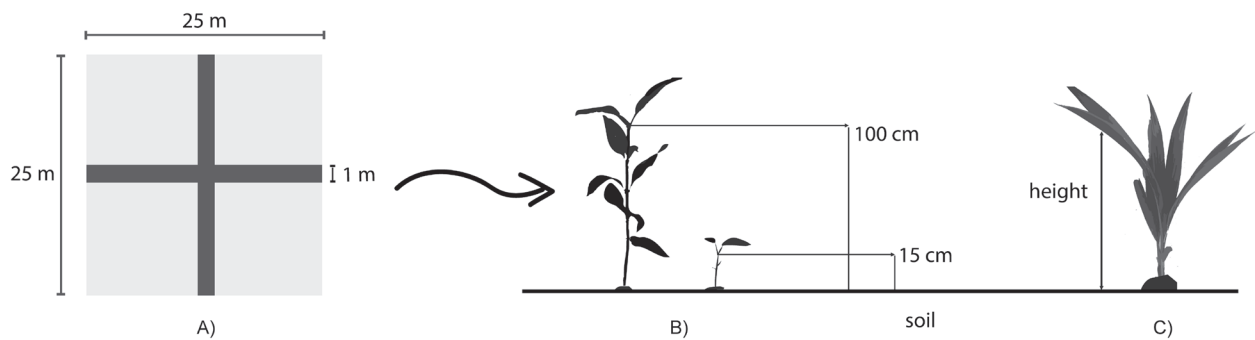


Figure 2. A. Plots of 25x25 meters with cross transects of 1x25 meters; B. Height measurement of the soil eudicotyledons up to the insertion of the leaf closest to the stem end - seedling from 15 to 100 cm high and C. Height measurement of palm trees - from the soil until the curvature of the highest and open leaf in the median region of the limbo.

Seedlings between 15-100 cm in height were measured from the ground to the apex of the last leaf (eudicotyledons; Mendes-Rodrigues *et al.* 2011) and, for palm trees, from the ground to the median region of the upper expanded leaf limbo (adapted from Mendes-Rodrigues *et al.* 2011 and Ewulo *et al.* 2015) (Fig. 2B, C).

The seedlings were identified by a parataxonomist *in loco*; and when the identification was not possible, they were photographed for further identification by the same parataxonomist in the INPA herbarium. All specimens were identified until the genus level. The names were confirmed on the websites: Tropicos (tropicos.org) and in the Flora of Brazil (floradobrasil.jbrj.gov.br). Botanical families were checked and listed according to the Angiosperm Phylogeny Group IV (APG IV 2016).

Flood gradients

The average flood in each sampled area was obtained by means of the flood marks printed on the tree trunk (four means per plot), referring to the maximum level of the river level during the last high-water period (in days per year). The values recorded in the field were correlated with the daily water levels (ANA 2018) of the Negro River scale (Manaus Harbor), to estimate the flooding days of the Uatumã in the period before the dam (1975 - 1986) and Jaú Rivers (1975-2017). The daily water levels of the Jatapu River were used to estimate the flood days of the Abacate River (2001-2017). Thus, the topographic levels of the three igapó forests sampled were classified according to the flood duration of each plot, forming a continuous gradient from 25 to 204 flood days per year.

According to the data provided by ANA, in the period before the dam (1975 - 1986), the amplitude of the Uatumã River reached a maximum of 35 cm and, in the period after the dam (1991 - 2017), presented an amplitude of up to 160 cm. This lack of predictability may have principally altered the intermediate topography (between high and low quotas), where flooding ceased to become a continuous event.

Data analysis

The parameters of genera richness, number of individuals, and the Berger-Parker dominance index, (d), were calculated for each plot. This index expresses the proportional relation of the most abundant species ($d = N_{\max} / N$), where N_{\max} in this study is the number of individuals in the most abundant genera (Berger & Parker 1970; Magurran 2004). Subsequently, a linear regression was performed to investigate how flooding and sampled areas affect floristic composition in the continuum gradient. To verify the significance of the flood on the number of individuals and richness, the Pearson correlation coefficient (r) was evaluated. Variance analysis (ANOVA) was used

for the comparison of species dominance between areas.

For structural analysis of the vegetation, we calculated the relative abundance (RA), relative frequency (RF), relative density (RD), relative dominance (DoR) and importance value index (VI) of the genera and families (Curtis & McIntosh 1951).

To analyze the floristic composition, a non-metric multidimensional scaling (NMDS) was performed based on genus abundance matrices, using the total number of individuals in each plot, topographic level, and area. The suitability of ordination for the interpretation was assessed by means of the STRESS value (Standard Residuals sum of squares). The Bray-Curtis dissimilarity index was also applied. An Analysis of Similarity (ANOSIM) was performed to examine significant differences in genera composition between the igapó forests.

Statistical calculations were processed in the software R (R Development Core Team 2018) with the Vegan package (Oksanen *et al.* 2018) and Betapart (Baselga *et al.* 2018).

Results

Richness and dominance patterns according to the flood gradient

A total of 3,654 individuals was sampled, belonging to 106 genera and 43 families. The sampled areas present richness of 69, 53 and 50 genera in the igapó forests of the Uatumã, Abacate and Jaú rivers, respectively. Richness was negatively correlated with flooding in all sampled areas: as flooding decreased, richness increased. Most plots at Uatumã area have low species richness, compared to the pristine areas (Fig. 3A). The Berger-Parker dominance index was positively correlated with flooding and the Uatumã area had higher dominance values (Fig. 3B).

The Pearson correlation coefficient (r) between the sampled areas was not significant between flood days and the number of individuals $r = -0.01$ ($p > 0.05$) but presented negative correlation between flood days and richness $r = -0.74$ ($p < 0.05$). The ANOVA test of the comparison of species dominance between the areas revealed no significant difference between the Jaú and Abacate areas ($p = 0.15$), as well as between the Uatumã and the Jaú ($p = 0.12$), but there was a highly significant difference between the Uatumã and the Abacate ($p = 0.001$). The similar value of RD in the pristine areas was presented for the genera *Elvasia* (38.16) and *Pouteria* (35.12), in the Abacate and Jaú areas respectively.

The total importance value (VI) for the 10 dominant genera of pristine areas was similar: 67.58 % for Abacate and 68.61 % for Jaú, while in the Uatumã area it was higher with 76.65 %. Furthermore, in the Uatumã area, the dominance values were discrepant with those from the pristine areas, with the *Astrocaryum* genus having a

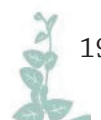


Table 2. Genera with higher importance value index (VI) in the forests along the Uatumã, Abacate and Jaú areas. RD = relative density; RF = relative frequency and DoR = relative dominance.

Uatumã	Family	Genera	RD	RF	DoR	VI
1.	Arecaceae	<i>Astrocaryum</i>	44.01	2.60	98.40	48.34
2.	Sapotaceae	<i>Pouteria</i>	25.68	6.49	0.07	10.75
3.	Euphorbiaceae	<i>Mabea</i>	4.89	4.55	0.82	3.42
4.	Myrtaceae	<i>Eugenia</i>	5.11	4.55	0.02	3.22
5.	Arecaceae	<i>Attalea</i>	6.50	2.60	0.08	3.06
6.	Fabaceae	<i>Inga</i>	3.32	5.19	0.26	2.92
7.	Lecythidaceae	<i>Eschweilera</i>	2.06	3.25	0.001	1.77
8.	Violaceae	<i>Rinorea</i>	0.72	2.60	0.02	1.11
9.	Piperaceae	<i>Piper</i>	0.58	2.60	0.02	1.07
10.	Moraceae	<i>Clarisia</i>	0.36	2.60	0.03	0.99
		Σ 11 - 69	6.77	62.97	0.28	23.35
	Total		100	100	100	100
Abacate	Family	Genera	RD	RF	DoR	VI
1.	Ochnaceae	<i>Elvasia</i>	38.16	6.45	25.57	23.39
2.	Fabaceae	<i>Swartzia</i>	6.79	4.84	13.01	8.22
3.	Clusiaceae	<i>Tovomita</i>	4.56	4.30	13.83	7.56
4.	Lecythidaceae	<i>Eschweilera</i>	7.18	5.91	5.16	6.09
5.	Chrysobalanaceae	<i>Licania</i>	6.02	5.91	5.31	5.75
6.	Apocynaceae	<i>Himatanthus</i>	4.08	4.84	4.78	4.57
7.	Annonaceae	<i>Unonopsis</i>	4.08	3.76	2.35	3.39
8.	Myrtaceae	<i>Eugenia</i>	2.33	4.84	2.82	3.33
9.	Melastomataceae	<i>Mouriri</i>	1.65	4.30	2.32	2.76
10.	Fabaceae	<i>Calliandra</i>	2.04	3.76	1.75	2.52
		Σ 11 - 53	23.11	51.08	23.09	32.42
	Total		100	100	100	100
Jaú	Family	Genera	RD	RF	DoR	VI
1.	Sapotaceae	<i>Pouteria</i>	35.12	8.59	24.15	22.62
2.	Clusiaceae	<i>Tovomita</i>	3.57	3.13	28.22	11.64
3.	Euphorbiaceae	<i>Mabea</i>	4.61	2.34	11.48	6.15
4.	Apocynaceae	<i>Aspidosperma</i>	5.50	2.34	9.33	5.73
5.	Fabaceae	<i>Tachigali</i>	7.44	5.47	2.53	5.15
6.	Fabaceae	<i>Swartzia</i>	5.51	5.47	1.44	4.14
7.	Lecythidaceae	<i>Eschweilera</i>	4.32	5.47	1.66	3.81
8.	Myrtaceae	<i>Eugenia</i>	3.27	4.69	2.85	3.60
9.	Arecaceae	<i>Astrocaryum</i>	3.57	3.13	2.12	2.94
10.	Melastomataceae	<i>Mouriri</i>	2.23	3.91	2.36	2.83
		Σ 11 - 50	24.85	55.47	13.85	31.39
	Total		100	100	100	100

high RD value (98.40 %) while the other genera (out of a total of 69) totaling 1.6 %; whereas in the Abacate and Jaú areas, *Astrocaryum* presented RD of 2.91 % and 3.57 %, respectively (Tab. 2).

Effect of the flood gradient and genera distribution

The distribution of the most dominant genera in the three areas shows that the majority are generalist, occurring all along the entire flood gradient, except for *Attalea* (Arecaceae), at higher topographic level and exclusively of the Uatumã area. The genera *Aspidosperma* (Apocynaceae), *Tovomita* (Clusiaceae) and *Elvasia* (Ochnaceae) were only recorded in pristine areas (Tab. 3, Fig. 4). Despite the difference in flood amplitude between the pristine areas,

the number of shared genera is higher than the number of shared genera to the Uatumã area (Figs. S1, S2; Tab. S1 in supplementary material).

Non-metric multidimensional scaling (NMDS) shows that the distance between the plots within each area had a genus change of the seedling community with the flood gradient. In pristine areas the zonation is gradual, and the plots are floristically close to the Uatumã area that is divided into different communities (Fig. 5). The ANOSIM test indicated significant dissimilarity between these groups ($p < 0.05$; $R = 0.4345$).

The agglomeration of the plots of all sampled areas ($N = 36$) in the NMDS formed three groups. The largest group, with the lowest floristic similarity, shows that the floristic composition of the Jaú area forms a grouping with



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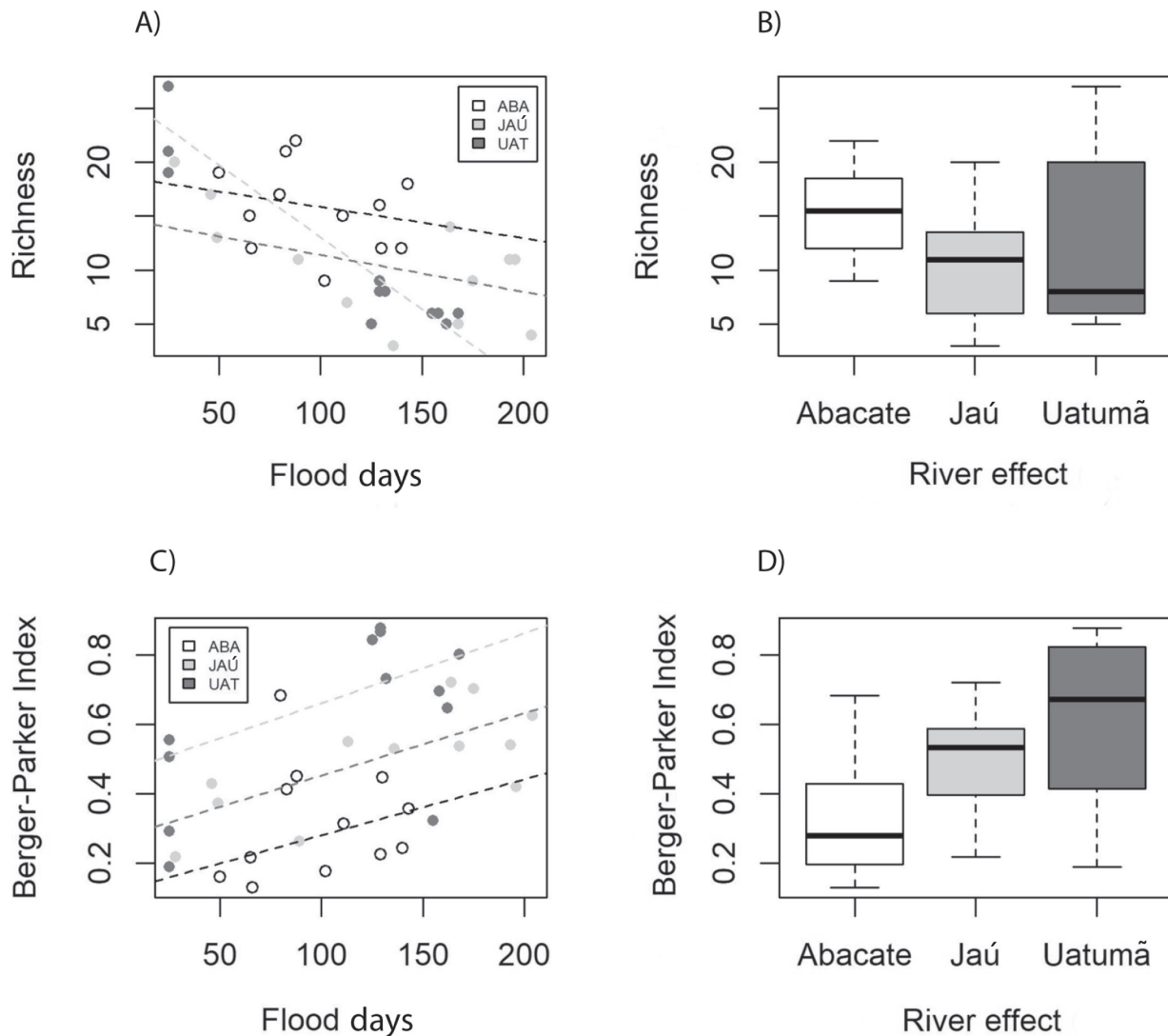


Figure 3. Regression of the parameters of richness (**A, B**) and dominance (**C, D**) of genera (Berger-Parker index) of the areas sampled according to the duration of the flooding in the plots.

floristic similarity between Abacate and Uatumã areas. Four plots of the Uatumã area was floristically similar with Jaú area, mainly due to the dominance of *Pouteria* in low topographies.

The NMDS also presented a smaller subgroup of plots within the Uatumã area, one of them being the grouping of the highest topographies, (25 flood days); this is mainly due to the dominance of the genus *Attalea*, neither found in the other plots of the Uatumã area, nor in the pristine areas.

The last subgroup, most floristically similar, show the highest similarity between plots within the Uatumã area, due to the dominance of the *Astrocaryum* genus. The plot with the longest flood time per year (204 days), located in the Jaú area, is floristically distant from the other plots (Fig. S3 in supplementary material). The STRESS value of the non-metric multidimensional scaling (NMDS) analysis was 0.2, allowing for interpretation of the results (Clarke 1993).

Table 3. Dominant genera (set of the five genera with greater relative dominance – DoR in the three forests of igapó), flood days and number of individuals in three igapó forests: Uatumã, with the flood pulse altered by the Balbina dam; Jaú and Abacate, pristine areas with a regular flood pulse.

Genera	Flood days	Number of Individuals		
		Uatumã	Abacate	Jaú
<i>Attalea</i>	25	145	0	0
<i>Swartzia</i>	25 to 196	1	57	37
<i>Eschweilera</i>	25 to 196	23	69	29
<i>Pouteria</i>	25 to 196	262	17	236
<i>Licania</i>	25 to 196	7	63	14
<i>Eugenia</i>	25 to 204	74	28	22
<i>Tachigali</i>	28 to 164	1	10	50
<i>Mabea</i>	25 to 193	108	8	31
<i>Aspidosperma</i>	28 to 111	0	11	37
<i>Tovomita</i>	28 to 196	0	56	24
<i>Astrocaryum</i>	46 to 196	1020	31	24
<i>Elvasia</i>	50 to 196	0	369	16

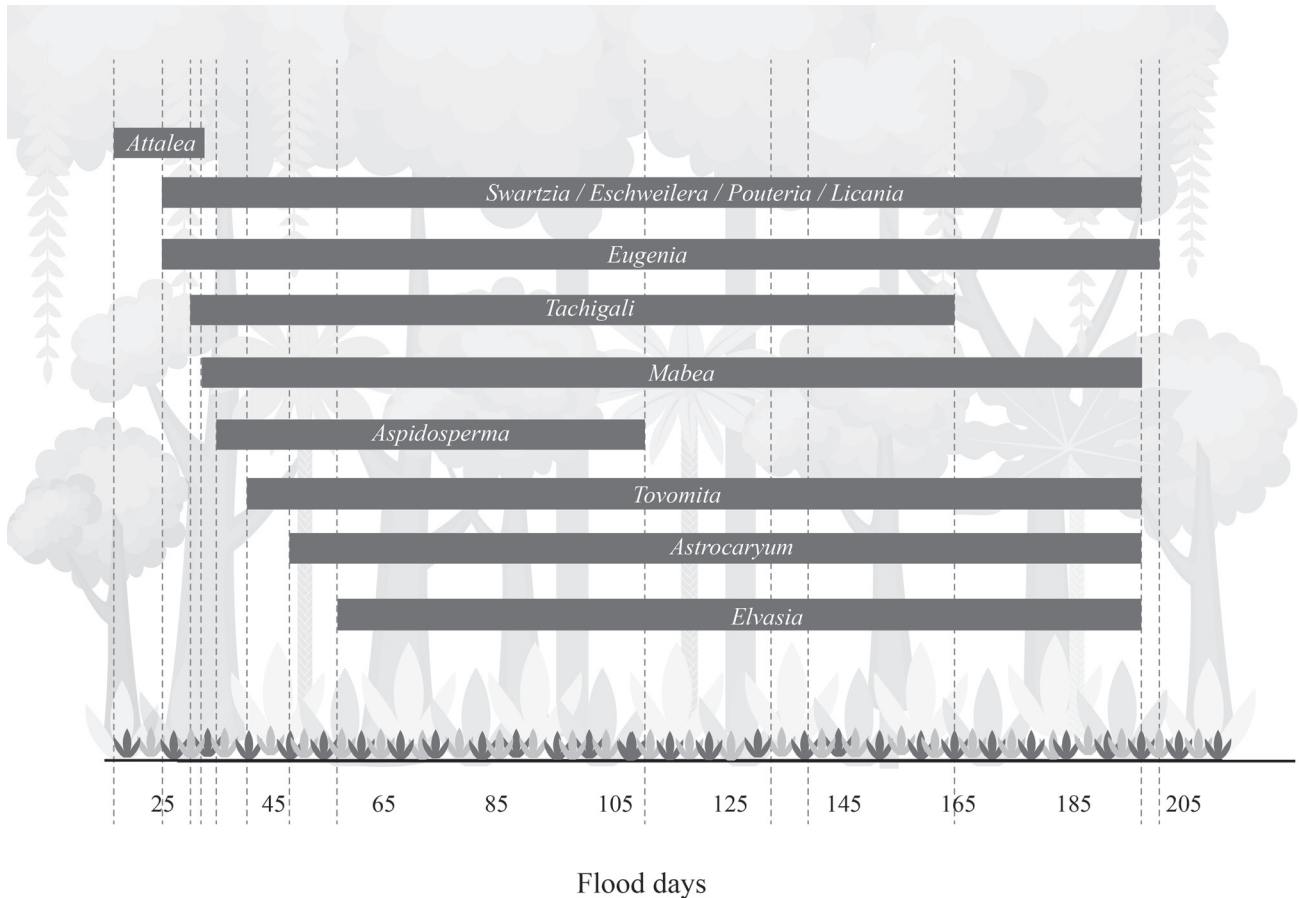


Figure 4. Distribution of the genera with a larger number of individuals in the seedling community along the flood gradient (topography) in three igapó forests of Uatumã, Abacate and Jaú rivers. The genus *Attalea* is exclusive to the Uatumã area, while *Aspidosperma*, *Tovomita* and *Elvasia* are genera exclusive to the Abacate and Jaú areas.

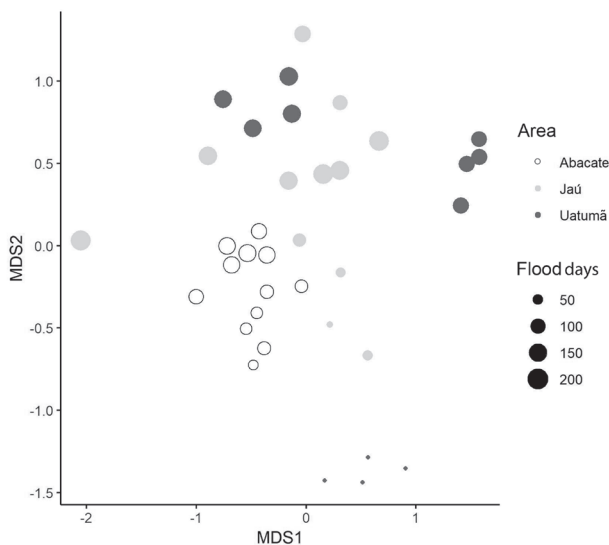


Figure 5. Non-metric multidimensional scaling (NMDS) relating flooding (50 to 200 days of annual flood) with the similarity of plots ($N = 36$) of the three igapó forests Uatumã, Abacate and Jaú. The NMDS shows three small groups referring to plots in the Uatumã area.

Discussion

Richness and dominance patterns according to the flood gradient

The genera richness in the seedling community in the three sampled areas, in general, increases as the flooding decreases, corroborating the results obtained for adult trees of flooded forests of the Brazilian Amazon by Ferreira (1997), Wittmann & Parolin (2005) and Assis *et al.* (2015). The increase in richness, as well as the distribution of genera along the gradient, is due to the different adaptations of the species in relation to fruiting, flowering, germination, establishment and survival of seedlings that are strongly synchronized to height and duration of the flood pulse (Parolin 2002; Haugaasen & Peres 2005; Ferreira *et al.* 2010; Oliveira-Wittmann *et al.* 2010).

On the other hand, the genera richness in the Uatumã area is less in the low and intermediate levels than in the pristine areas. Germination and survival of seedlings subjected to reduced levels of oxygen in the soil are factors that may have decreased the richness of genera

perceived in the lower levels. During germination in the community located within the low topographies of the floodplain forest, the seedling emergence period and cotyledon opening require a longer time in relation to the seedlings at topographic higher levels (Parolin 2002). Studies conducted by Melo *et al.* (2015) show that in a period of 20 to 115 days, some species of flooded forest are able to germinate and produce seedlings under water, but that others do not survive such prolonged floods. While the difference in tolerance to anoxia between species can be long or short-term, when an organic soil is flooded, the available oxygen is quickly exhausted through metabolism by organisms that use oxygen (Piedade *et al.* 2010; Parolin 2012). Thus, at the low levels, the seedling community was subjected to a decrease in the terrestrial phase and a longer period of flood days, presenting a lower richness of genera. This was also observed in the lower topographic dimension of the Jaú igapó forest, as demonstrated in the NMDS analysis.

In the intermediate levels of the Uatumã area, the genus *Astrocaryum* presented the highest dominance of the entire igapó forest under study, with the species *A. jauari*. Studies in floodplain forests on the Marchantaria island in the Solimões River accounted for a high number of seedlings, with some 940 individuals of *A. jauari* (Kubitzki & Ziburski 1994). The authors observed that the maturation of the fruits of the species is related to the peak of the flood period, as already demonstrated by Piedade *et al.* (2006) in the Anavilhanas archipelago of the Negro River, Amazonas. In this way, after the dam the increase in the daily amplitude of up to one meter in the flooding of the Uatumã River (Hidroweb-ANA 2018) may have favored *A. jauari*. According to Binotto *et al.* (2016) some species need a physiological recovery time after flooding and thus, in intermediate levels few genera could synchronize physiology and phenology with the irregularity of flooding after the construction of Balbina dam.

In the higher dimensions of the topography, where the flooding is lower, the richness of the seedling community was higher in the three studied areas, with the most diverse genera richness in the high level of the Uatumã area. The “terra firme” forest that surrounds the igapó forests of this study area contributes to the increase of genera richness. During the dry period, many seedlings start colonizing low-lying areas but then become eliminated during the following flood period (Junk 1989), but in the “high várzea”, where the flood is reduced, many species from the surrounding land can establish themselves (Wittmann *et al.* 2004), which was also observed for the igapó area of Uatumã by Lobo *et al.* (2019) with juvenile trees.

Therefore, the differences in the pattern of richness and dominance in the igapó forest of the Uatumã River downstream the dam throughout the entire topography reflect the loss of ecological processes within the drainage system (Philips 1989), and also highlight the fundamental

role of dispersion in the maintenance of local and regional diversity patterns (Wandrag *et al.* 2017).

Effect of the flood gradient and genera distribution

In general, within each pristine area, there is a similarity between the plots throughout the flood gradient, but the altered Uatumã area is divided into three different communities. The plots of all areas formed groups according to genera dominance. Among the pristine areas, the Abacate area presented the dominance pattern of the genus *Elvasia* (Ochnaceae), along the entire topography, with the same pattern occurring for the genus *Pouteria* (Sapotaceae) in the pristine Jaú area. This occurs because the flood travels through the igapó forest from the low levels to the highest topographies, corroborating the concept of lateral connectivity proposed by Ward (1989). However, in the Uatumã area, lateral connectivity was altered along the entire topography (Rocha *et al.* 2019). The suppression of flooding in the high quotas of the Uatumã area acted as a limiting factor for the establishment, for example, of *A. jauari*. This fact may be related to the dispersion of the species, carried out by gravity – barochory; by fishes – ichthyochory (Piedade *et al.* 2003) or vegetative by tillers (Miranda *et al.* 2001). Thus, the lack of record of the species in the high quotas indicates that the seeds are not dispersed by fish due to scarce flooding events.

In the pristine areas, several genera were generalists and were registered from the lowest topographic quotas to the highest, such as: *Himatanthus*, *Elvasia* and *Eugenia*, in the Abacate area; *Pouteria* and *Astrocaryum* in the Jaú area; and *Eschweilera*, *Licania* and *Tovomitia* in both areas. However, in general, the zonation of the seedling community was strongly related to the flood gradient in the three sampled areas, as observed by Wittmann *et al.* (2004; 2010b) in adult trees and in a community of seedlings by Piedade *et al.* (2005) in igapó forests of the Anavilhanas archipelago. For Ward & Stanford (1995), alluvial forest zonation patterns represent successional steps organized by the lateral migration of the river channel through the floodplain. Therefore, in areas with a regular flood pulse, such as the Abacate and Jaú areas, the regular zonation of genera distribution suggests that flooding interferes with dispersal strategies and the establishment of species.

However, the current composition of seedlings of the Uatumã area was altered, with different communities and dominant genera throughout the topographic gradient due to the irregularity of the flood pulse. Similar results were found in studies conducted by Turner & Karpiscak (1980) downstream of the hydroelectric dam “Glen Canyon”, on the Colorado River in the United States. There, likewise because of the decrease in maximum height of the river and daily variations in amplitude, the change in flooding patterns caused alterations in the composition, density and distribution of shrub and tree species. With the use of



photographs in the previous and posterior periods of the dam, the authors found that some plant species became more abundant within the range of their preexistence. Different areas of dominant plants were recorded along the topography with well-defined boundaries, which practically did not occur in the pre-dam period.

Even though they are different river basins, the low topographic dimension of the Uatumã area is floristically similar to the Jaú area, due to the dominance of *Pouteria*, indicating that the alteration of the flood pulse of the Uatumã River did not present itself as a factor stressful for this genus. Studies conducted by Armbrüster *et al.* (2004) compared the phenological and physiological reactions due to the water conditions of two species of adult trees in flooded forests of the Amazon, one of the genus *Laetia* (Flacourtiaceae) and another of the genus *Pouteria* (Sapotaceae). They verified that phenological differences cause different ecophysiological responses under the same environmental conditions in each species: during the sopping *Pouteria* sp. showed no differences in photosynthetic activity, but *Laetia* sp. had the reduced activity. Thus, seedlings of the genus *Pouteria* in the low quotas of the Uatumã area may have used morphophysiological adaptations during the increase of flooding, such as: decrease in gas exchange activity and growth rates, maintenance of leaves and rapid germination of 0 to 25 days, as found for the species *Pouteria glomerata* (Simone *et al.* 2002; Parolin *et al.* 2003; Maurenza *et al.* 2009). Thus, the genus *Pouteria* dominates the low quotas of the Uatumã, and some plots in the Jaú area along similar topographies. This genus is also frequently found with a high number of individuals in other floodplain forests of the Amazon under a regular flood pulse (Ferreira 1997; Hamaguchi & Scudeller 2011).

In the Jaú area, the genus *Astrocaryum* was found in the high and low quotas; in the Abacate area, only in the high quotas and in the Uatumã area only in the intermediate quotas. Arborescent palms are frequent in the Amazon, and generally constitute dense settlements in moist forests of drenched or flooded soils, such as the *A. macrocalyx* species representing 37.3% of the community of an alluvial forest in the Peruvian Amazon (Kahn & Mejia 1990). In the Brazilian Amazon, the species *A. jauari* forms almost homogeneous populations (Miranda & Rabelo 2008) and can be found along rivers of Amazonian white or black water (Kubitzki & Ziburski 1994). The species occurs in areas surrounding black water rivers with an amplitude ranging from 340 to 30 days of annual submersion, and a regular flood pulse (Piedade *et al.* 2005). In fact, it is more frequent with higher densities and greater growth in the Negro River trough and other environments of igapó forests (Piedade *et al.* 2016), as in studies of floristic composition in the Tarumã-Mirim River (Ferreira & Almeida 2005) and in the Mariuá archipelago (Junqueira *et al.* 2017). In the Uatumã area, intermediate topographic quotas are

dominated by *A. jauari*, and adult individuals dominate extensive areas of the igapó forest of the Uatumã River downstream the dam.

According to Connel & Lowmann (1989) a species can be considered monodominant, when the number of individuals equals 50% to 100% of canopy coverage. Monodominant species can cover hundreds of square kilometers and occur adjacent to significantly more diversified forest types (Hart *et al.* 1989), as the “terra firme” forest, which possesses a high diversity of species of trees (Gentry 1988) and occurs adjacent to the igapó forest in the Uatumã area. The dominance of *A. jauari* seedlings downstream the Balbina HPP probably occurred after the closure of the dam, because there is no record of this species in the pre-dam forest inventory of the upstream area (INPA/Eletronorte 1983), which includes adult individuals of palm trees in the igapó forests, as well as what was not recorded in the seedling community of the high and low quotas of the Uatumã area. Therefore, there are indications that *A. jauari* will eventually become a monodominant species in intermediate quotas.

Dominant palm formations were also reported in the Amazon on the Upper Negro River in Colombia and on the Amazon River in Peru with the species *Mauritia flexuosa* and *Copernicia alba* (Melack & Hess 2010), and still in South America, in the Pantanal, by the species *Attalea phalerata* and *A. speciosa* (Pott *et al.* 2011). In this context, in the high dimensions of the topography of the Uatumã area, the suppression of flooding due to the decrease of flood peaks (Assahira *et al.* 2017), seems to have favored the seedlings of the dominant genus *Attalea* (Arecaceae), registered exclusively in Uatumã area. However, the genus *Attalea* was found by Aguiar (2015) in the high dimensions of the topography in the igapó forest of the Jaú River. In the western Amazon, anthropic disturbances such as forest fragmentation also favor the dominance of the genus *Attalea* with the species *A. phalerata* (Carvalho *et al.* 2010) and in the eastern Amazon, cutting and burning of natural forests causes a disproportional increase of *A. maripa* (Araújo *et al.* 2012).

In addition to the increased selective pressure by the alteration of the flood pulse, the hydroelectric dam acts as a barrier for the propagules of some genera and can contribute to the change in the composition of species and genera between the upstream and downstream areas of the altered river (Andersson *et al.* 2000; Merritt & Wohl 2006; Shafroth 2016). The structure of the plant community of the floodplain depends on the migration of seeds and fruits of plant species by hydrochory and ichthyochory along the river (Kubitzki 1989; Ward & Stanford 1995; Hyslope & Trowsdale 2012). The species *Cassia leiandra* (Fabaceae), that possesses the seeds consumed by fish (Maia & Chalco 2002), has a high record of adult individuals in the igapó forest both upstream and downstream of the dam (Neves 2018; INPA/Eletronorte 1983). However, the genus *Cassia*, was not registered in the community of seedlings



of the Uatumã area. Thus, the longitudinal connectivity (Ward 1989) of the upstream region to the downstream region of the river, in forests with a regular flood pulse such as the Abacate and Jaú areas, allowed for a flow of propagules along the entire course of the river, favoring a wide distribution of species in the flooded plains of these rivers (Junk *et al.* 1989). This did not occur in the low and intermediate quotas of the altered Uatumã area.

Conclusions

The pristine areas present similar patterns of richness, dominance and distribution of genera along the flood gradient, either inside or outside the drainage basin of the Uatumã River. On the other hand, the Uatumã area affected by the Balbina hydroelectric plant does not follow the same patterns of the pristine areas and a change in the composition of the seedling communities was observed throughout the topographic gradient.

After the hydroelectric dam, the alteration of the community of seedlings in the Uatumã area was influenced by the loss of lateral and longitudinal connectivity that can change the floristic composition of adult trees in the future and, consequently, the landscape downstream the igapó forest. The loss of lateral connectivity along the entire flood gradient led to the establishment of seedlings of different genera, specifically within the three dimensions of the topography (low, intermediate and high quotas) where some of these genera became dominant. At the same time, the loss of longitudinal connectivity of the Uatumã River acted as a barrier to seed dispersal of species that depend on water.

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