

# Interannual hydrological variations and ecological phytoplankton patterns in Amazonian floodplain lakes

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**Abstract** Amazonian aquatic environments are complex, and their interaction promotes heterogeneous environments that in turn make it difficult to describe the development of patterns. Amazonian floodplain lakes have different environmental and biological responses in similar water periods due to the interannual variation. We evaluated if the interannual variations in the physical–chemical structure and the phytoplankton community promote environmentally and biologically contrasted conditions between similar hydrological periods. Phytoplankton community structure has differences between periods, but these differences do not necessarily promote dissimilarities. Most of the phytoplankton species belong to the same functional groups. The compositions of species and

functional groups between sample units inside lakes are variable and may or may not have significant differences in dissimilarity, but both periods are equally heterogeneous. Beta diversity has shown that the replacement of species and functional groups causes a high level of variation between sites, which maintain a high heterogeneity between periods. These variations have different responses for different scales turning the interpretation of patterns for these environments a problematic task. Hence, scale and interannual variability are factors that need to be carefully considered when setting standards to describe the ecological dynamics of floodplain lakes in the Amazonian system.

**Keywords** Amazonian wetlands · Biodiversity · Plankton · Freshwater · Ecology · Beta diversity

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## Introduction

Wetlands are essential continental components with fundamental hydrological and ecological functions such as water storage, water-quality improvement, and biodiversity conservation (Mitsch & Gosselink, 2007). They cover about 14% of the Amazon lowland basin, reaching to 800,000 km<sup>2</sup> during flooding season (Hess et al., 2015). The large floodplain lakes associated to the “white-water” main tributaries known as várzeas (Sioli, 1984) present distinct characteristics mainly resulting from contrasted morphology and degree of connectivity with the main Solimões/Amazon corridor (Prance, 1980; Sioli, 1984; Sippel et al., 1992). Along the main Solimões/Amazon corridor, floodplains have a predictable and monomodal flood pulse with four distinct periods (flooding, high water, flushing, and low water) commonly considered throughout the seasonal cycle (Prance, 1980; Bonnet et al., 2008; Rudorff et al., 2014a; Bonnet et al., 2017). The hydrological phases are closely linked to the ecological processes of the floodplain systems, and spatial and temporal changes in biodiversity are related to variations between the phases of the flood pulse (Tockner et al., 2000). The flooding process promotes water’s and nutrients’ renewal leading to a peak in primary productivity. The moving terrestrial/aquatic transition creates a great variety of environmental conditions conducive to biodiversity, whereas during high water period primary productivity is weaker because of dilution, shorter residence time, and increased depth (Ciarrocchi et al., 1976; Schöngart & Junk, 2007; Thomaz et al., 2007; Junk et al., 2012). During the flushing period, decreasing depth and degradation of the autogenic organic material promotes a second peak in primary productivity (Ciarrocchi et al., 1976; Alcântara et al., 2011). During low water, floodplains present a smaller water volume profoundly stirred and turbid and remain or not connected to the main channel (Tockner et al., 2000). Despite the predictability of the flood pulse, small increments in mainstream peak discharge may cause disproportionately large changes of the through-flow within the floodplains (Rudorff et al., 2014b; Bonnet et al., 2017). Floodplain lake biodiversity conservation is a crucial challenge as they are considered as among the most diversified environments in the world (Junk et al., 2010) but increasingly

threatened by land-use changes and dam proliferation in the basin (Forsberg et al., 2017).

On a general point of view, ecological systems exhibit heterogeneity on a wide range of scales, which is often a problem for ecologists (Levin, 1992; Merico et al., 2014). Larger scales tend to have greater environmental heterogeneity and may reveal different patterns from those that would be observed on a smaller scale (Lawton, 1999; Simberloff, 2004). These differences increase the difficulty in unraveling patterns that represent both scales (Huston, 1999; Stendera et al., 2012; Zagmajster et al., 2014; Saraiva et al., 2015). Throughout distribution, composition, and diversity of communities, it is possible to evaluate the organization of species in space along an environmental gradient (Howeth & Leibold, 2010; Massol et al., 2011; Chust et al., 2013; Gianuca et al., 2017). Since the work of Whittaker (1960), the beta diversity has aroused considerable interest, mainly for its application in evaluation of processes that generate and maintain biodiversity in ecosystems (Legendre & De Cáceres, 2013). There are several proposals to address and study beta diversity. The most common form is through similarity indices between sites (Whittaker, 1960; Anderson et al., 2006; Baselga, 2010; Carvalho et al., 2013; Baselga & Leprieur, 2015). Moreover, beta diversity can be divided into two components: (1) replacement, or directional change in the composition of the community; or (2) nondirectional change of community, concentrating on the variations in community compositions between the sampling units (Legendre, 2014).

The beta diversity can be used to analyze complex systems, such as the Amazonian floodplain lakes system, verifying if ecological factors (e.g., spatial distribution, environmental heterogeneity, hydrological connectivity, and morphology) influence the species composition of the community (Carvalho et al., 2013), thus giving some guiding rules for their protection. Phytoplanktonic organisms respond very rapidly to variations (Loverde-Oliveira & Huszar, 2007; Angeler & Drakare, 2013; Goes et al., 2014). Thus, studying the beta diversity of this community should help to understand the ecological processes of the Amazon floodplain lakes system better. In addition, functional approach makes community ecology more general and predictive, allowing the link between ecology of communities and ecosystems (McGill et al., 2006; Westoby & Wright, 2006; Webb

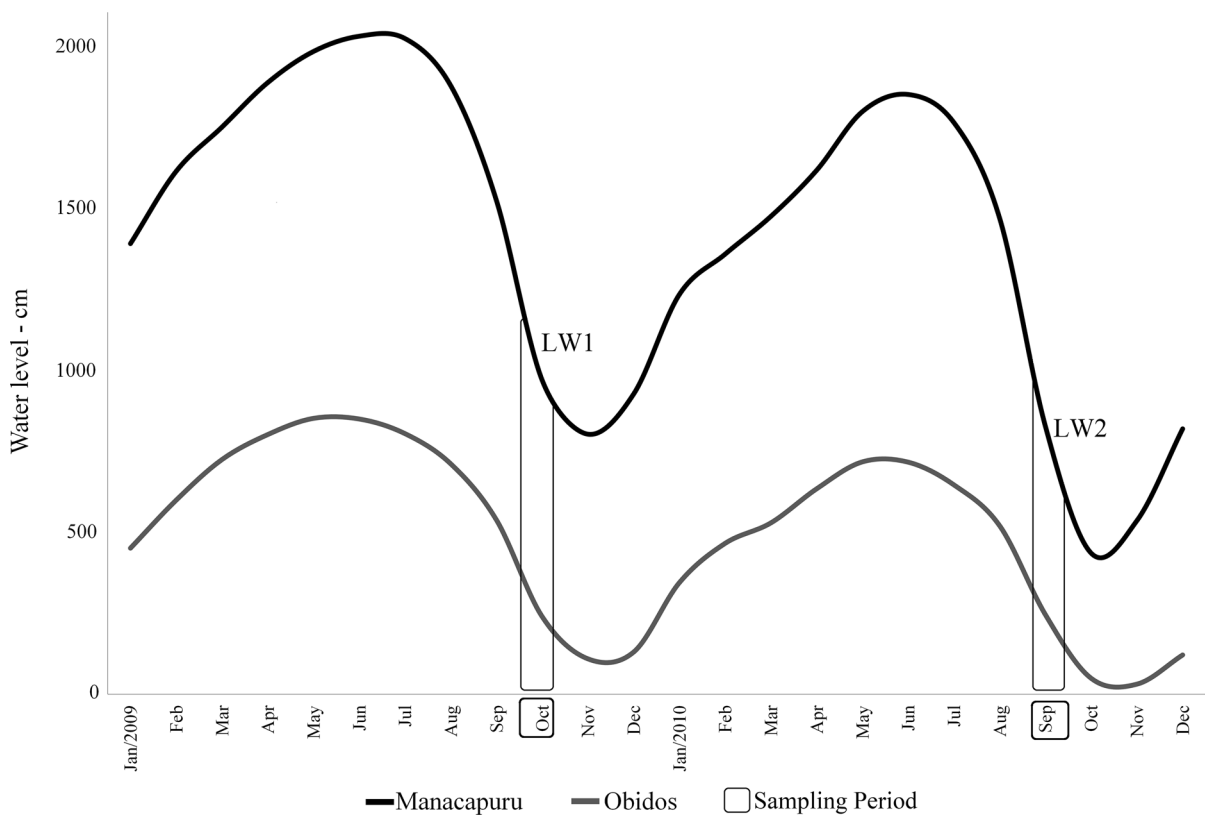
et al., 2010), and can be an alternative to overcome difficulty in unraveling patterns between ecological scales (Reynolds et al., 2002).

Interannual variation of flood pulse promotes changes that can affect the aquatic community and unravel these changes is an essential key for better understand the Amazonian floodplain lakes system and further promote right decision to ensure sustainable use and conservation for these crucial areas. In this work, we assessed the interannual variation in the physical–chemical structure and the phytoplankton community, at two low water periods at local and regional scales. Thus, we evaluated (1) if the variabilities under environmental and biological conditions between two similar periods exist, and if so at what scales, and (2) to what extent these differences have an influence upon the phytoplankton biodiversity structure.

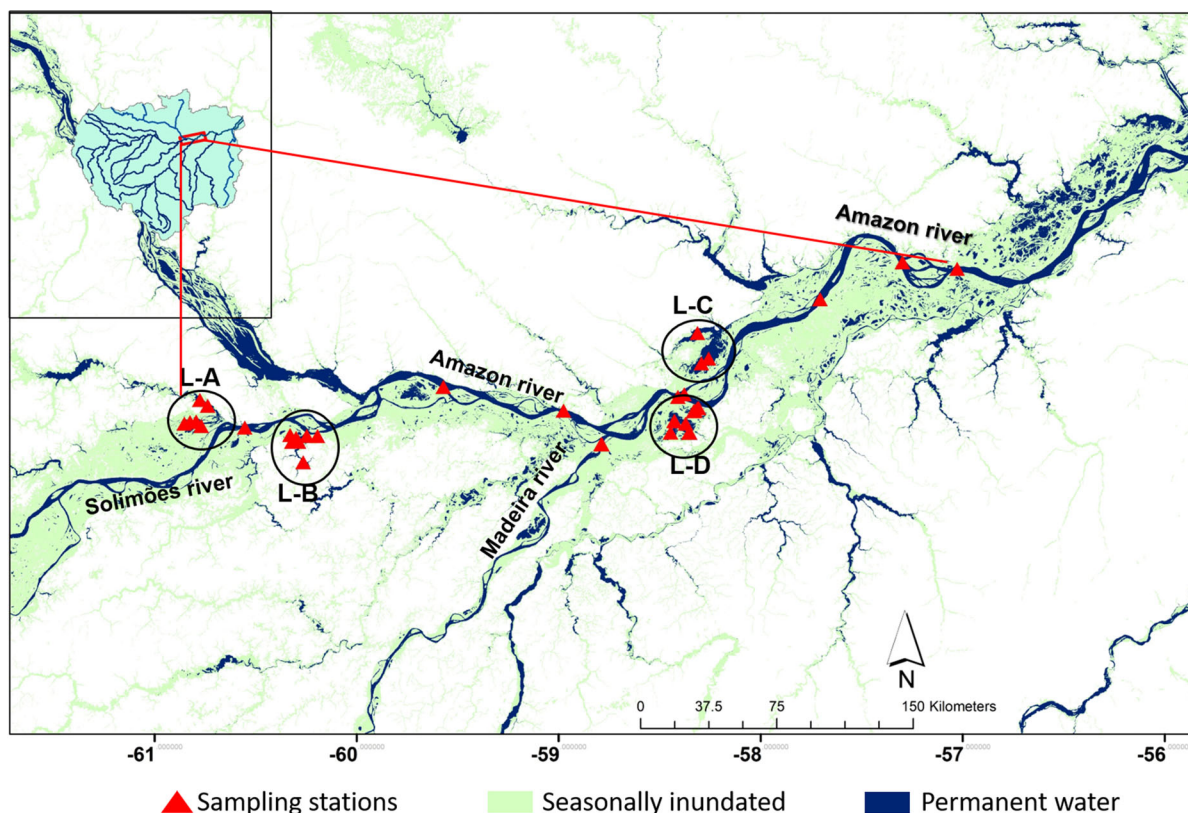
## Material and method

### Study area

The samples were collected during two low water (or very late flushing) periods: the first one (LW1) in October 2009 and the second one (LW2) in September 2010 (Fig. 1), during which the water level in the river was similar and less than 400 cm at the Óbidos gage. The study area (Fig. 2) was divided into five areas with points collected in the Solimões/Amazon mainstream and points collected in 4 floodplain lakes (L-A, L-B, L-C, and L-D). L-A is located on the left margin of the Solimões River. It is a fertile floodplain, widely used for both subsistence and commercial agriculture, receiving influence from both the Solimões River to the south and Manacapuru River to the north (Sampaio et al., 2012). L-B is located further downstream on the right margin of the Solimões River. It is composed of a lake with flooded forests and other wetlands linked to



**Fig. 1** Amazon river's monthly water levels at Manacapuru and Óbidos gages between 2009 and 2010. LW1 2009 period of collecting data; LW2 2010 period of collecting data. Built from data from the Brazilian National Water Agency (ANA)



**Fig. 2** Map of study area with locations of the lakes and sites of sampling units in the main channel of the Amazon River and in 4 floodplain lakes (L-A, L-B, L-C and L-D)

the river by a perennial channel on the northeast side of the floodplain. It receives influence from the mainstream mainly through overbank flow at high water level and from the Janauacá river located south (Bonnet et al., 2017). L-C is located along the left margin on the Amazon and near the confluence with the Madeira River. As L-D is located slightly downstream on the right margin of the Amazon River, it has a higher degree of connection with Amazon river. The fifth area is composed of samples collected in the main channel of the Amazon River and comprises sites between these four floodplain lakes (Fig. 2). Due to the hydrometric variation resulting from the flood pulse, 23 samples were collected during LW1 and 25 samples in LW2.

#### Environmental and biological variables

The environmental variables (temperature of water, electrical conductivity, pH and dissolved oxygen), were measured by a multiparameter probe (model YSI 6820-V2). The analysis of ammonium ( $\text{NH}_4$ ) was done according to Grasshoff (1983). The analysis of chlorophyll-a (Chl-a) was done by filtering three aliquots about 500 to 750 ml of water under pressure in the NALGENE filtration system and glass fiber filters (membrane 0.7  $\mu\text{m}$  porosity; Millipore Whatman GF/F), the membranes were wrapped in aluminum foil and frozen for subsequent chlorophyll-a analyses. In the laboratory, chlorophyll-a filters were extracted with buffered acetone (90% acetone + 10% saturated magnesium carbonate) (Jespersen & Christoffersen, 1987), the extracts were kept for 24 h in the refrigerator before colorimetry determination (APHA, 1998). The quantitative samples of

phytoplankton were collected and were stored in 10-mL amber vials and fixed with acetic Lugol solution. Phytoplankton was counted following the Utermöhl method (Utermöhl, 1958), at  $\times 400$  magnification. The counting was done randomly until 100 individuals of the most frequent species were obtained (cells, colonies, or filaments were counted as one individual), with an error being less than 20%, with a confidence coefficient of 95% (Lund et al., 1958). The adopted system for classifying phytoplankton was that of Hoek et al. (1995). The algal biovolume was calculated by multiplying the abundance of each species by the mean cell volume (Hillebrand et al., 1999), based on the measurement of at least 30 individuals and was expressed in  $\text{mm}^3 \text{ l}^{-1}$ . This biovolume was used to select the functional groups. The functional groups (FG) of phytoplankton were classified according to Reynolds et al. (2002), with the modifications made by Padisák et al. (2009). For the functional groups, specific biomass was estimated from the product of the population and mean unit volume and only those that contributed with at least 5% of the total biovolume per sample unit were considered Kruk et al. (2002).

#### Data analysis

We conducted the analyses at regional and local scales. The regional scale (Reg), includes all samples from lakes and the Solimões/Amazon River. At the local scale, we separately considered the lakes L-A, L-B, L-C, L-D, and the mainstream (River). Data analysis of similarity and heterogeneity was done considering environmental (ENV), phytoplankton species (SPP) and functional group (FG) approach. In order to evaluate the similarity between periods LW1 and LW2, all data were submitted to a permutational multivariate analysis of variance using distance matrices with the *adonis* function of the vegan package (Oksanen et al., 2013). The dissimilarity evaluates the variance of all sample units together in each period and evaluates also whether the differences between the periods are significant. As the inputs are linear predictors, and a response matrix of an arbitrary number of columns, this analysis describes how variation is attributed to different experimental treatments. For further details, see Mcardle and Anderson (2013). To assess heterogeneity for environmental and biological data, we used a distance-based dispersion

test for multivariate data with the *betadisper* function of the vegan package (Oksanen et al., 2013). The test is based on the individual variance of each of sample units measuring the dispersion with the mean distance of the sample units to a central point (Anderson, 2001, 2006). So that the larger the mean distance to centroid the greater heterogeneity of the group. In our case, LW1 and LW2 are the groups. To test the significance of variances between groups, we proceeded to analyze of variance (ANOVA). For further details, see Anderson (2006).

To assess the heterogeneity of biological data during each period, we evaluated the total beta diversity ( $\beta T$ ) and its components (replacement and nestedness) as described by Legendre & De Cáceres (2013). The analyses were performed using the package *adespatial* (Dray et al., 2016). We used the Baselga Family of Indices with the Sorensen's dissimilarity index (Baselga, 2010) that provides the multiple-site dissimilarities across all sites and the estimated distribution of those values. Phytoplankton abundance data were pretransformed with Hellinger transformation (Legendre & De Cáceres, 2013).

The maximum value of beta diversity ( $\beta T = 1$ ) occurs when all sites contain a different set of species with no species in common. Once the  $\beta T$  has a fixed range of values for any community, which does not depend on the total abundance in the community composition, it is possible to compare datasets which have the same or different numbers of sampling units, as long as the calculations have been done using the same index (Legendre & De Cáceres, 2013). Using beta-diversity matrices, two distance-based Redundancy Analyses (dbRDAs) were run for each period considering SPP and FG approaches. This technique allows analyzing if there is an ecologically relevant relationship between biological and environmental data in each period. Steps in the procedure include (i) calculating a matrix of distances among replicates using the beta-diversity distance matrix; (ii) determining the principal coordinates which preserve these distances (species data); (iii) creating a matrix of dummy variables (model); (iv) analyzing the relationship between species data and the model using RDA; and (v) implementing a test by permutation for particular statistics corresponding to the particular terms in the model (Legendre & Anderson, 1999; Mcardle & Anderson, 2013). The results are shown by graphs, two for each period considering the SPP and

FG approaches. This method is provided by function *dbrda* in the *vegan* package. All analyses were performed using the R program (Team, 2018).

## Results

The total of 219 phytoplankton species was identified with 192 species in LW1 and 153 species in the LW2 period (Supplementary Material 1 and 2). Cyanobacteria were the most representative in both scales and periods. The regional scale had the same classes between periods, but at local scales, the phytoplankton group's representativeness differs between periods (Table 1). In both periods and all sites, one or more species of cyanobacteria of the genus *Dolichospermum*, *Phormidium*, *Oscillatoria*, and *Cylindrospermopsis* always appear among the species with greater representativity (Fig. 3a and b). We identified 14 functional groups (FGs) in LW1 and 19 functional groups in LW2 periods (supplementary material 3). During LW1, we identified only 4 FGs in L-B, thus contrasting with the other lakes where we recognized 11 or 12 groups during the same period. During LW2, all sites had at least 11 FGs. However, whatever the periods or the scales considered, 4 FGs (**T<sub>C</sub>**, **MP**, **S1**, and **H1**), accounted for at least 80% of total biomass (Fig. 3c and d).

The codon **T<sub>C</sub>** is composed of cyanobacteria and is characteristic of eutrophic standing waters, or slow-flowing rivers (Padišák et al., 2009), and the most representative species recorded were *Phormidium* spp. The codon **MP** is composed of species of bacillariophytes and cyanobacteria, and frequently stirred up, inorganically turbid shallow lakes (Padišák et al., 2009); during the present study, *Oscillatoria cf. amoena* and *Pseudanabaena cf. catenata* were recorded in this codon. The codon **S1** is characteristic of turbid mixed environments and filamentous cyanoprokaryotes (Reynolds et al., 2002); this codon was represented by *Planktothrix isothrix* (Skuja) Komárek & Komárk.-Legn. and *Planktothrix cf. agardhii*. The codon **H1** comprises the genus of cyanobacteria *Anabaena*, updated to *Dolichospermum* (Wacklin et al., 2009), *Anabaenopsis* and *Aphanizomenon*, and is characteristic of eutrophic, both stratified and shallow lakes with low nitrogen content (Padišák et al., 2009). Besides these codons, we recognized two other functional groups, but less

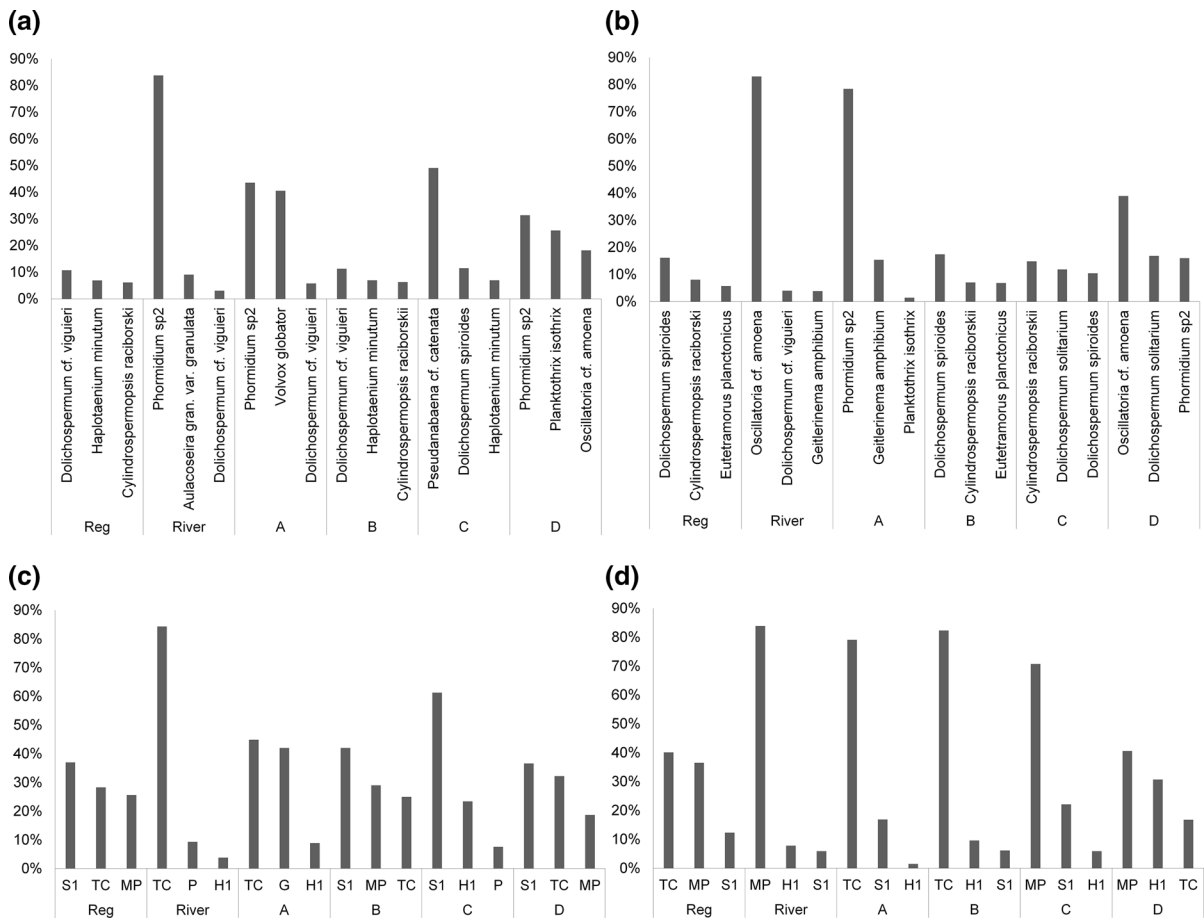
**Table 1** Most representative phytoplankton groups

LW1	%	LW2	%
<b>Reg</b>			
Cyanophyceae	60.5	Cyanophyceae	4.3
Chlorophyceae	15.5	Chlorophyceae	23.0
Conjugatophyceae	13.1	Conjugatophyceae	1.6
<b>River</b>			
Cyanophyceae	88.2	Cyanophyceae	97.7
Bacillariophyceae	10.9	Bacillariophyceae	1.6
Chlorophyceae	0.4	Dinophyceae	0.4
<b>A</b>			
Cyanophyceae	52.4	Cyanophyceae	97.1
Chlorophyceae	43.1	Bacillariophyceae	1.1
Bacillariophyceae	2.7	Dinophyceae	1.0
<b>B</b>			
Cyanophyceae	59.8	Cyanophyceae	46.1
Chlorophyceae	15.5	Chlorophyceae	25.0
Conjugatophyceae	13.4	Conjugatophyceae	10.0
<b>C</b>			
Cyanophyceae	74.3	Cyanophyceae	70.7
Chlorophyceae	15.0	Chlorophyceae	14.3
Conjugatophyceae	7.0	Conjugatophyceae	6.0
<b>D</b>			
Cyanophyceae	91.1	Cyanophyceae	94.5
Bacillariophyceae	5.3	Bacillariophyceae	4.6
Euglenophyceae	1.9	Chlorophyceae	0.3

LW1 2009; LW2 2010; Reg regional scale; River Amazon river; A, B, C and D lakes

representative than the above cited in each lake, the codons **P** and **G**. The codon **P** was present in L-C and in the river during the LW1 period. This codon is characteristic of high trophic shallow lakes where the mean depth is 2–3 m with continuous or semicontinuous mixed layer (Padišák et al., 2009) and was represented by *Aulacoseira granulate* (Ehrenb.) Simonsen. The codon **G** was only present in L-A during the LW1 period. This codon is usually associated with nutrient-rich habitats in stagnant water columns, small eutrophic lakes, and is composed of *Chlorophyceae* (Padišák et al., 2009) being represented in the studied system by *Volvox globator* Linnaeus.

Temperature and pH mean values were the most stable parameters throughout periods and scales (Table 2). The other environmental parameters



**Fig. 3** Bar graph of the most representative phytoplankton species and functional groups. LW1 2009; LW2 2010; **a** and **b** species graphs; **c** and **d** functional groups graphs; Reg regional

scale; River Amazon river; A, B, C and D lakes; S1, TC, MP, H1, G, P codon of phytoplankton functional groups

exhibited different variations between periods, as indicated by the coefficient of variation (CV) (Table 2). The environmental (ENV) differences between LW1 and LW2 analyzed on a regional scale, showed a significant dissimilarity (Adonis test,  $P < 0.05$ ) but no significant differences in heterogeneity (Betadisper test,  $P > 0.05$ ) between periods (Table 3). Moreover, the biological response (SPP and FG) had no significant differences at this scale. The environmental differences characterize the periods as distinct on a regional scale, although they are not so distinct regarding their biological condition (Table 3).

At the local scale, the analyses showed that only L-C and L-D had a significant dissimilarity ( $P < 0.05$ ) for ENV but did not have a significant difference ( $P > 0.05$ ) in heterogeneity. The L-C and L-D were

environmentally dissimilar between periods, although the heterogeneity inside the lake was not. Moreover, the heterogeneity of the phytoplankton abundance was not different between the periods for none of the lakes, except L-B which exhibited a significant dissimilarity between periods, for SPP and FG (Table 3).

The total biodiversity  $\beta T$  was greater during LW1 than during LW2 for both, SPP and FG approaches, at both scales (Table 4). Whatever the scale and the approach,  $\beta T$  is principally composed by replacement of species or functional groups (Table 4). This result means that there was considerable heterogeneity of SPP and FG among sampling sites. However, L-C and L-D presented the highest differences of SPP- $\beta T$  among periods, indicating a considerable dissimilarity in the composition of species between the periods in

**Table 2** Summary of environmental data

	LW1							LW2						
	Temp	Cond	O2	Alc	NH4	Chl-a	pH	Temp	Cond	O2	Alc	NH4	Chl-a	pH
<b>Reg</b>														
Min	30.1	10.0	1.3	0.1	0.5	2.7	5.0	30.1	10.0	1.3	0.1	0.5	2.7	5.0
Max	34.3	80.0	10.1	0.7	10.5	53.4	8.6	34.3	80.0	10.1	0.7	10.5	53.4	8.6
Median	31.5	61.0	6.3	0.4	1.5	18.3	6.8	31.5	61.0	6.3	0.4	1.5	18.3	6.8
Mean	31.7	57.5	6.4	0.4	2.6	19.3	6.9	31.7	57.5	6.4	0.4	2.6	19.3	6.9
SD	0.92	16.38	2.34	0.13	2.79	13.84	0.76	1.16	16.39	2.70	0.13	0.36	9.37	1.02
CV	0.029	0.285	0.364	0.310	1.085	0.716	0.109	0.037	0.285	0.421	0.304	0.139	0.485	0.147
<b>River</b>														
Min	30.9	63.0	5.6	0.4	0.8	2.9	6.7	30.2	48.3	5.3	0.3	0.7	1.3	6.7
Max	31.9	77.0	7.3	0.5	6.4	6.7	7.2	31.6	88.0	8.0	0.5	1.4	5.0	7.3
Median	31.0	65.0	5.6	0.5	1.5	3.2	6.8	30.6	53.5	5.8	0.4	0.8	1.7	6.8
Mean	31.2	67.0	5.7	0.5	3.1	3.7	6.8	31.0	62.5	6.7	0.5	1.0	3.8	6.9
SD	0.41	6.23	0.77	0.04	2.37	1.66	0.26	0.65	24.87	1.51	0.17	0.28	1.80	0.38
CV	0.013	0.093	0.137	0.085	0.762	0.443	0.038	0.021	0.398	0.225	0.361	0.276	0.471	0.055
<b>A</b>														
Min	31.3	10.0	1.3	0.1	1.2	9.9	5.0	30.5	10.0	1.3	0.0	0.6	3.6	5.4
Max	34.3	80.0	10.1	0.7	2.9	26.7	7.5	31.7	70.0	2.7	0.5	1.3	8.6	7.1
Median	31.8	75.0	4.0	0.6	2.6	21.8	6.6	30.8	68.0	2.4	0.5	1.0	7.0	6.9
Mean	32.3	60.0	4.9	0.5	2.3	20.1	6.4	30.9	54.0	2.2	0.4	1.0	6.5	6.6
SD	1.37	33.51	3.78	0.29	0.81	7.70	1.05	0.55	29.36	0.64	0.23	0.29	2.31	0.82
CV	0.042	0.558	0.780	0.600	0.353	0.384	0.164	0.018	0.544	0.290	0.600	0.299	0.354	0.125
<b>B</b>														
Min	30.9	33.0	3.0	0.2	0.5	20.7	6.2	30.6	40.0	2.6	0.3	0.6	7.2	6.5
Max	33.1	71.0	9.5	0.5	2.4	53.5	7.5	32.3	68.0	7.4	0.5	2.1	38.7	6.9
Median	32.0	58.8	8.0	0.4	1.1	32.6	6.6	30.9	60.0	4.6	0.4	1.1	15.6	6.7
Mean	32.0	57.0	7.0	0.4	1.2	33.5	6.8	31.1	56.8	4.9	0.4	1.1	17.1	6.7
SD	0.83	13.24	2.54	0.10	0.65	11.18	0.44	0.65	10.09	1.74	0.09	0.53	11.44	0.13
CV	0.026	0.232	0.363	0.254	0.541	0.333	0.065	0.021	0.178	0.354	0.230	0.472	0.669	0.019
<b>C</b>														
Min	31.5	39.2	7.9	0.3	0.7	7.3	7.9	33.6	53.0	10.3	0.3	0.6	10.7	9.4
Max	31.7	44.0	9.1	0.4	0.9	13.4	8.6	33.6	54.0	10.2	0.3	0.9	21.6	9.4
Median	31.7	39.5	9.1	0.4	0.7	13.4	8.6	33.6	54.0	10.2	0.3	0.6	21.6	9.4
Mean	31.6	40.9	8.7	0.3	0.8	11.4	8.3	33.6	53.7	10.3	0.3	0.7	18.0	9.4
SD	0.16	2.69	0.70	0.03	0.13	3.54	0.36	0.00	0.58	0.01	0.00	0.17	6.29	0.01
CV	0.005	0.066	0.080	0.092	0.168	0.312	0.043	0.000	0.011	0.001	0.002	0.236	0.350	0.001
<b>D</b>														
Min	30.1	53.0	4.7	0.3	2.6	6.1	6.7	30.9	58.0	5.4	0.4	0.7	12.0	6.9
Max	32.3	62.0	7.6	0.4	10.5	30.3	7.1	33.5	65.0	9.6	0.4	1.6	28.0	8.5
Median	30.8	56.5	5.7	0.4	6.8	19.9	7.0	32.0	61.0	7.0	0.4	1.1	17.0	7.5
Mean	31.0	57.0	5.9	0.4	6.7	19.1	6.9	32.0	61.0	7.6	0.4	1.1	18.1	7.6
SD	0.97	3.74	1.31	0.03	4.25	12.13	0.19	1.02	2.28	1.68	0.01	0.31	6.15	0.69
CV	0.031	0.066	0.222	0.087	0.639	0.636	0.028	0.032	0.037	0.222	0.036	0.282	0.340	0.090

LW1 2009; LW2 2010; Reg regional scale; River Amazon river; A, B, C and D = lakes; Min minimum; Max maximum; SD standard deviation; CV coefficient of variation; Temp temperature (°C); Cond conductivity (µS/cm); O2 dissolved oxygen (mg/L); Alc Alkalinity (µmol/L); NH4 Ammonium (µmol/L); Chl-a Chlorophyll-a (mg/m<sup>3</sup>)



**Table 3** Results of dissimilarity and heterogeneity tests

	Environmental					SPP					FG				
	ADONIS		Betadisper			ADONIS		Betadisper			ADONIS		Betadisper		
	<i>F</i>	<i>P</i>	LW1d	LW2d	<i>P</i>	<i>F</i>	<i>P</i>	LW1d	LW2d	<i>P</i>	<i>F</i>	<i>P</i>	LW1d	LW2d	<i>P</i>
Reg	2.262	<b>0.046</b>	2.999	2.654	0.318	1.170	0.299	0.645	0.638	0.538	0.620	0.615	0.617	0.585	0.230
River	1.502	0.177	1.657	2.454	0.247	0.772	0.672	0.483	0.562	0.488	0.702	0.753	0.399	0.522	0.429
A	2.318	0.137	2.817	1.556	0.161	1.050	0.433	0.594	0.536	0.473	1.181	0.383	0.579	0.520	0.487
B	1.473	0.207	2.528	2.008	0.160	2.525	<b>0.003</b>	0.420	0.460	0.622	3.429	<b>0.008</b>	0.417	0.552	0.225
C	6.070	<b>0.010</b>	1.733	1.774	0.930	1.287	0.200	0.562	0.438	0.483	4.790	0.100	0.319	0.185	0.733
D	3.894	<b>0.003</b>	2.841	2.140	0.076	1.648	0.136	0.541	0.440	0.491	2.593	0.060	0.392	0.468	0.854

SPP phytoplankton at species level; FG phytoplankton at functional groups level; Reg regional scale; River Amazon river; A, B, C and D lakes; DIS dissimilarity index, HTR heterogeneity index; F f-statistics; P significant value of test ( $\leq 0.05$  significative, bold values); LW1d mean distance to centroid in 2009; LW2d mean distance to centroid in 2010

**Table 4** Results of beta-diversity test

	SPP						FG					
	LW1			LW2			LW1			LW2		
	$\beta T$	%Rep	%Nes	$\beta T$	%Rep	%Nes	$\beta T$	%Rep	%Nes	$\beta T$	%Rep	%Nes
Reg	0.83	90.9	9.1	0.72	95.6	4.4	0.67	92.3	7.7	0.59	90.2	9.8
River	0.60	91.1	8.9	0.54	90.1	9.9	0.66	93.3	6.7	0.52	89.9	10.1
A	0.91	99.1	0.9	0.83	99.5	0.5	0.53	97.7	2.3	0.73	95.4	4.6
B	0.56	97.3	2.7	0.50	87.1	12.9	0.61	75.8	24.2	0.15	73.5	26.5
C	0.80	86.9	13.1	0.56	99.1	0.9	0.55	92.5	7.5	0.54	91.5	8.5
D	0.82	95.9	4.1	0.59	89.1	10.9	0.75	88.7	11.3	0.64	93.4	6.6

SPP phytoplankton at species level; FG phytoplankton at functional groups level; LW1 2009; LW2 2010; Reg regional scale; River Amazon river; A, B, C and D lakes;  $\beta T$  total beta diversity; %Rep proportion of  $\beta T$  due to replacement; %Nes proportion of  $\beta T$  due to nestedness

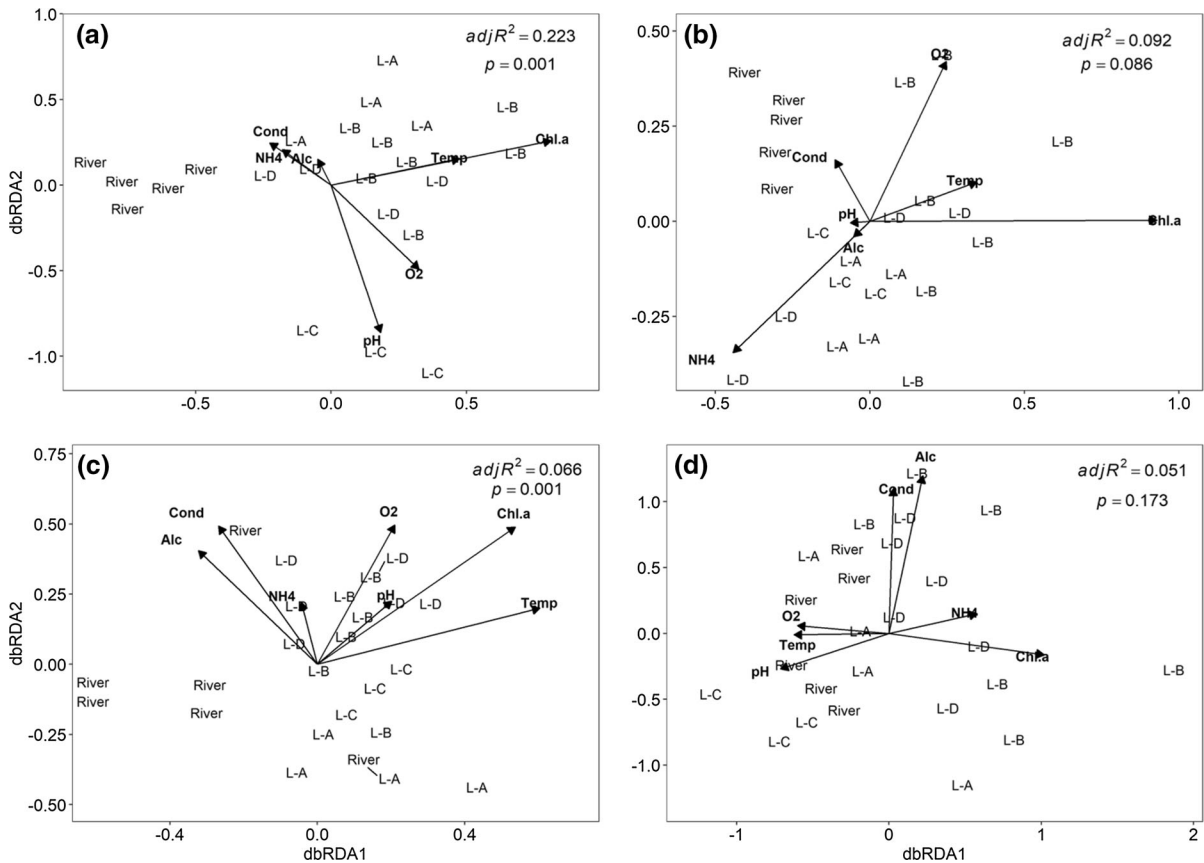
these two lakes. These results are summarized in Table 4.

The canonical analysis performed with dbRDA showed that variation of species composition was significantly related to environmental variables ( $P < 0.005$ ) at SPP level during both periods (Fig. 4a and c), but not for FG approach ( $P > 0.005$ ) (Fig. 4b and d). Although there is a significant result at SPP level, the strength of the relationship between species and environmental variables is only weak for both periods, once we have low  $\text{adj}R^2$  (Fig. 4a and c).

## Discussion

Studies about floodplains have sought to identify and understand the mechanisms responsible for generating structural, biological, and environmental patterns (De Oliveira & Calheiros, 2000; Panarelli et al., 2013; Bozelli et al., 2015). Our results suggest that although on a regional scale there is a pattern that repeats between two similar hydrologic periods, the same does not seem to be right on a local scale. As expected, between the periods on the regional scale, there is a significant environmental but not a biological difference.

The results show that cyanobacteria were the most abundant phytoplankton group found during both periods. Some genera of cyanobacteria can fix



**Fig. 4** Distance-based redundancy analysis (dbRDA). **a** and **c** = SPP  $\beta$ T explained by environmental variables at species level; **b** and **d** = FG  $\beta$ T explained by environmental variables at functional group level; *dbRDA1* Axis1; *dbRDA2* Axis2; *adjR*<sup>2</sup>

adjusted  $R^2$ ;  $P$  significant value ( $\leq 0.05$  significant); *Temp* temperature; *Cond* conductivity; *O<sub>2</sub>* dissolved oxygen; *Alc* alkalinity; *NH<sub>4</sub>* Ammonium; *Chl-a* Chlorophyll-a; *River* Amazon river; A, B, C, and D lakes

atmospheric nitrogen (Schindler et al., 2008; Thad Scott & McCarthys, 2010; Schindler, 2012), others may also store phosphorus (Lampert & Sommer, 2007). The nitrogen-fixing cyanobacteria belong to codon H1 and were found in all lakes in at least one period. Also, some genera of cyanobacteria can differentiate other specialized cells like the akinetes, spore-like cells, characterized by a thick cell wall and by a multilayered extracellular envelope (Adams & Duggan, 1999). These cells are produced in response to unfavorable environmental conditions, which probably result in a shortage of cellular energy when environmental conditions become suitable again, akinetes germinate into vegetative cells (Sciuto & Moro, 2015). All these skills give to cyanobacteria a competitive advantage and might explain why

environmental dissimilarity does not promote dissimilarity in phytoplankton community on a regional scale.

The Amazon aquatic environment exhibits a complex interaction, promoting heterogeneous environments (Bonnet et al., 2008, 2017), and this heterogeneity reflects in phytoplankton community. Our results showed that despite there are species differences between locals and periods, these species belong to same functional groups. In addition, the functional groups found on a regional scale in both periods are characteristic of stirred environments. This condition promotes environmental differences between the sample units and maintains the heterogeneity between periods.

Even though all sites were connected to the main channel of the river, the heterogeneity on the local

scale was significant. During LW1, in the Amazon River, the great representativity of codon  $T_C$  (characteristic of standing waters, or slow-flowing rivers), reflect the influence of tributaries in marginal areas that are small and have low-flux conditions. The results of the LW2 period also reflects an influence of marginal areas, once some species and functional groups exhibited during LW2 are ‘non-adapted’ to river conditions, as LW1. The interannual variation of environmental conditions affects the sites differently, and these differences affect the composition of phytoplankton in the river. The amplitude of the flood in each hydrological cycle is also a factor to be considered. During 2009, flood reached a very high water level (Fig. 1) and was recognized as exceptional (Chen et al., 2010), while 2010 was considered as dry when compared with the historical mean.

L-C and L-D lakes did not exhibit differences in environmental and biological approaches for both, dissimilarity and heterogeneity. In these lakes, the representativity of cyanobacteria was higher than in the others lakes, and probably for the same reasons than described for the regional scale (cyanobacteria skills), there was no biological dissimilarity. These floodplain lakes are closely located downstream the Madeira–Amazon rivers’ junction and tend to be influenced due to their proximity. The presence of FG **MP** supports this influence, once this codon includes organisms that could resist to dispersal process, due to their eco-physiological adaptations. It is generally associated with large rivers (Sharma et al., 2006; Christosomou et al., 2009).

L-A did not show dissimilarity or significant heterogeneity for both, environmental and biological approaches. The results obtained in L-A draw attention during the LW2 because this lake is widely used for both subsistence and commercial agriculture (Davidson et al., 2012; Sampaio et al., 2012), and almost 100% of biomass presented was composed by cyanobacteria in this period. In addition, L-A is influenced by Manacapurú river, a blackwater river rich in organic matter at the north. The cyanobacteria blooms are usually related to eutrophication and may represent risks to the ecological balance of ecosystems and public health due to the potential release of toxins, as evidenced by several studies (Paerl & Otten, 2013; Pimentel & Giani, 2014; Rastogi et al., 2015; Sukenik et al., 2015). Moreover, deforestation, agricultural and fisheries activities, such as those practiced in this lake,

may accelerate and intensified the eutrophication processes (Affonso et al., 2011; Rastogi et al., 2014). L-B lake was the only one where biological dissimilarity between periods for both, SPP and FG approach was exhibited. L-B is connected to Solimões River by one channel at the north. During low water and flushing periods, the water flows from L-B to the mainstream, so the influence during this period is from other water sources such rain, runoff from local watershed and seepage (Bonnet et al., 2017).

Considering the functional approach, we can note that the composition and structure of the phytoplankton community changed between the two periods. During LW1, the most representative codon is characterized by highly light-deficient conditions and by photo-adapting Cyanobacteria, but sensitive to flushing. During LW2, the most representative codon is also characteristic of a light-deficient condition and eutrophic standing waters, or slow-flowing rivers, but is sensitive to nutrient deficiency (Reynolds et al., 2002; Padisák et al., 2009). Thus, the changes that occurred between the two periods of low waters can lead to a change in the community present in this lake. The same explanation could be used to interpret the results from the other lakes, but none of them presented significant differences in the biological community.

The beta-diversity approach also demonstrates biological heterogeneity, and its components may indicate how it occurs. The comparison of beta-diversity data enables to highlight why there were differences in community composition among sites inside the lakes between the periods. High environmental heterogeneity favors high replacement rates of organisms with high dispersal capacity, specifically phytoplankton (Beisner et al., 2006; Lima-Mendez et al., 2015; Machado et al., 2015; Wojciechowski et al., 2017). Our  $\beta T$  results showed that species and functional groups replacement was more intense than nestedness in all analyses. The replacement of species and functional groups causes a high level of variation between sites, which is reflected in high heterogeneity. The results also help to understand the previous heterogeneity tests for biological data. Even though in L-A, L-C and L-D, the same species composition occurs in the two periods (no significant dissimilarity), the structure of species or functional groups composition between the sample units inside these lakes is variable (no significant differences in heterogeneity).

On the other hand, even though in L-B the different species composition promotes a significant dissimilarity, the structure of this composition in each site inside this lake is also variable as in the others lakes. In conclusion, we observe the same heterogeneity between periods.

Moreover, when  $\beta T$  of species is bigger than  $\beta T$  of functional groups, it means that the species belong to the same few FGs, despite the high variability at the species level. This occurs during LW1 on the regional scale and on a local scale in L-A, L-C, and L-D, and during LW2 on the regional scale and in most of the lakes. This means that the conditions were more selective and favored organisms with a specific ability. Contrarily, when  $\beta T$  of functional groups was bigger than  $\beta T$  of species, the conditions were less selective and more favorable to a broader range of phytoplankton. This occurred in the River and L-B during the LW1 period, and in L-C during LW2. Thus, there is not a defined pattern at the local scale, but at the regional scale, it exists. In addition, the detection of regional patterns depends on the strength of the environmental gradients (Ptacnik et al., 2010). Hence, factors such as water residence time, flux, the local contribution of streams, and other sources like subterranean water and rain, seem to be as important as environmental factors measured to structure the phytoplankton community. Indeed, the hydrological balance during the high water period plays a vital role in determining the magnitude of the river–floodplain exchanges and drives substantial interannual variability (Rudorff et al., 2014b). Our canonical analyses with a dbRDA, show that environmental conditions measured were significant for species in both periods, but not for functional groups. Even so, the environmental variables measured were not very explicative for the variance observed indicating again that there are others factors that play an essential role in the biological dynamics. Despite this, our results showed that there are interannual variations that can be observed in the phytoplankton community. A deepening of dispersion processes such as those promoted by connection with the main river channel, dispersion agents (e.g., air, birds) and the nondirectional processes that operate in the environments (Salmaso et al., 2015) are essential factors that can contribute to a better understanding of these systems.

## Conclusion

We identified a large number of phytoplankton species, but they belong to a relatively small number of functional groups. There exist significant interannual variations regarding environmental conditions but not regarding phytoplankton community structure at the regional scale. The ability of cyanobacteria to adapt to contrasted ecological conditions is a plausible explanation to account for the absence of biological dissimilarities. The same is observed at local scale except for one site where biological dissimilarity was evidenced between both periods and could be explained by contrasting inputs from the local drainage basin between the two periods. Beta-diversity analysis evidenced the high replacement rates and that there is no defined pattern at the local scale, although at the regional level, it exists. The strength of the environmental gradients is an essential factor to identify trends for the Amazonian floodplain system.

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