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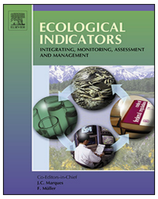

Morphology-based functional groups as the best tool to characterize shallow lake-dwelling phytoplankton on an Amazonian floodplain

Maria Tereza Morais Pereira Souza Lobo[a,b,*], Ina de Souza Nogueira[b], Luciano Fabris Sgarbi[c], Cleber Nunes Kraus[d], Eudes de Oliveira Bomfim[e], Jérémie Garnier[f,h], David da Motta Marques[g,i], Marie-Paule Bonnet[h,i]

[a] Programa de Pós-graduação em Biodiversidade Vegetal, Instituto de Ciências de Biológicas, Universidade Federal de Goiás, Goiânia GO 74690-900, Brazil
[b] Departamento de Botânica, Universidade Federal de Goiás, Goiânia GO 74690-900, Brazil
[c] Programa de Pós-gradução em Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia GO 74690-900, Brazil
[d] Programa de Pós-graduação em Ciências Ambientais, Universidade de Brasília, Planaltina DF 73.340-710, Brazil
[e] Programa de Pós-Graduação em Geociências Aplicadas, Universidade de Brasília, Instituto de Geociências, Brasília DF 70.910-900, Brazil
[f] Universidade de Brasília, Laboratório de Geoquímica, Instituto de Geociências, Brasília DF 70.910-900, Brazil
[g] Instituto de Pesquisas Hidráulicas, Universidade Federal do Rio Grande do Sul, Avenida Bento Gonçalves, Porto Alegre RS 91.501-970, Brazil
[h] Joint International Laboratory LMI OCE 'Observatory of Environmental Change', UnB/IRD, Brasília DF 70.910-900, Brazil
[i] Institut de Recherche pour le Développement, UMR Espace-DEV, Maison de la télédétection, 500 rue J.F. Breton, 34000 Montpellier, France

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ABSTRACT

River floodplains are subject to different inundation scenarios, mainly related to the flood pulse. Moreover, the ecology of floodplain lakes is modulated by exchanges of water with the main stream. On Amazonian floodplains, the water level fluctuates seasonally, with four distinct stages during the year: rising, high, falling, and low water. This study evaluated how/which three functional approaches to phytoplankton (FG, functional groups; MFG, morphofunctional groups; and MBFG, morphology-based functional groups) showed the largest relation to the environmental variations in response to rising and falling water periods, using data of the seven lakes sampled during rising and falling water periods, on the Curuaí Floodplain system, Pará state, Brazil. We used a Principal Coordinates Analysis to check for differences in phytoplankton species composition between the rising and falling water periods and a Redundancy Analysis to evaluate the relationship between functional approaches and environmental. Electrical conductivity, silica, and pH were the most important environmental variables to structuring the phytoplankton. The biological dissimilarity was computed using Bray-Curtis index for species biovolume and indicated greater similarity among the species compositions in the lakes during the falling water period. During rising water species is adapted in almost all lentic ecosystems (FG **Y**) and autotrophic organisms typical from the meroplanktonic that can be found in phytoplankton samples of the shallow lakes (FG **MP**); cryptomonads (MFG **2d**), large centrics (MFG **6a**), and large pennates (MFG **6b**); and non-flagellated organisms with siliceous exoskeletons (MBFG **VI**) and unicellular flagellates of medium to large size (MBFG **V**) were predominant. During falling water, species that tolerate eutrophic to hypertrophic environments with low nitrogen content predominated all shallow lakes (FGs **H1** and **M**; MFGs **5e** and **5b**; and MBFGs **III** and **VII)** and *Dolichospermum* spp. formed blooms. Morphology-based functional groups were the larger relation with the environmental variations than did functional groups and morphofunctional groups. MBFGs provides a relatively simple and objective classification and were the best in characterizing phytoplankton dynamics on the Curuaí floodplain. Therefore, we recommend using these groups to study phytoplankton ecology in shallow floodplain lakes.

1. Introduction

Biological classification systems allow study of the various relationships between living organisms, and in general, serve to categorize, group, and sometimes to form hierarchies of organisms (Linnaeus, 1758). The frequent use of functional classifications by

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[*] Corresponding author at: Laboratório de Análise e Gerenciamento Ambiental de Recursos Hídricos (LAMARH), Universidade Federal de Goiás, Campus Samambaia, Alameda Palmeiras – Quadra I – Lote i2, Goiânia GO 74690-900, Brazil.

E-mail address: mariate.morais@gmail.com (M.T.M.P.S. Lobo).

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ecologists is based on the evolutionary perspective that the functional criteria comprise biological processes and characteristics, and consequently generate ecological adaptations. Each functional association reflects the simultaneous responses of the individual species to environmental variations in an ecosystem (Reynolds et al., 2002).

Based on the assumption that species of different taxonomic groups can share ecological characteristics, different functional classifications of phytoplankton have been proposed: functional groups—FGs (Reynolds et al., 2002, Journal of Plant Research 24, updated by Padisák et al., 2009, Hydrobiologia 621); morphofunctional groups—MFGs, (Salmaso and Padisák, 2007, Hydrobiologia 578); and morphology-based functional groups—MBFGs (Kruk et al., 2010, Freshwater Biology 55). Phytoplankton functional approaches allow comparison of environmental studies and facilitate the assessment of biological responses to environmental conditions (Reynolds et al., 2002; Machado et al., 2015). Overall, phytoplankton classification uses morphological, physiological, and ecological traits, and when appropriate, taxonomic relationships (Salmaso et al., 2015). The classification of Reynolds et al. (2002) consists of a system comprising 31 functional groups whose species share ecological affinities based on tolerances and sensitivities under different environmental conditions. Padisák et al. (2009) consolidated the previous classification and updated the list to 40 functional groups (FGs). Salmaso and Padisák (2007), using taxonomic, morphometric, structural, and functional characteristics, developed another classification system, with 31 morphofunctional groups (MFGs). This system separates the cyanobacteria from other groups of algae, but left a classification gap by not including the large filamentous cyanobacteria (oscillatorialeans). Kruk et al. (2010) proposed a new functional approach for phytoplankton: morphology-based functional groups (MBFGs), which resulted in a dichotomous key based exclusively on the morphology of organisms. Although this approach could be considered simplistic, the morphology eventually expresses the physiology of the species (Reynolds, 1988; Naselli-Flores and Barone, 2007). The three approaches differ in the number of groups proposed, the main classification criteria, and the taxonomic and morphological and/or functional refinement used in each analysis (Brasil and Huszar, 2011).

Many studies have used phytoplankton functional groups in analyses of different systems around the world, such as reservoirs (e.g., Rangel et al., 2016; de Souza et al., 2016), rivers (e.g., Abonyi et al., 2012; Devercelli and O'Farrell, 2013), and floodplain lakes (e.g., Stanković et al., 2012a,b; Stević et al., 2013). Floodplain systems consist of flooded areas along the main river that periodically oscillate between the aquatic-terrestrial transition zone (ATTZ). The flood pulse is the structuring force of these ecosystems (Junk et al., 1989); on Amazonian floodplains, the flood pulse generates four distinct hydrological periods (rising, high water, falling. and low water), and leads to high spatio-temporal heterogeneity in the aquatic communities (Ward and Stanford, 1995; Ward et al., 1999). The physical and chemical properties of Amazonian floodplain lakes vary widely depending on the seasonal water level fluctuation (Affonso et al., 2015), soil type, vegetation cover, climate conditions (Junk, 2013; Junk et al., 2015), and human land use and occupation (Junk and Cunha, 2012) and can cause increased nutrients leading to high levels of phytoplankton blooms.

Studies using single functional group approach to analyze floodplain phytoplankton have used FGs, such as in Brazil for the Upper Paraná River (Bovo-Scomparin and Train, 2008; Bovo-Scomparin et al., 2013; Zanco et al., 2017), Pantanal (Loverde-Oliveira and Huszar, 2007), the Araguaia River (Nabout et al., 2006; Nabout and Nogueira, 2007), in the Amazon basin (Huszar and Reynolds, 1997). In other countries still using FGs, for the middle stretch of the Paraná River in Argentina (Devercelli, 2006), for northern Australia, in Mary River (Townsend, 2006) for Cross River in Nigeria (Okogwu and Ugwumba, 2012) and for the shallow lake Sakadaš, situated on the floodplain of the Danube River in Croatia (Mihaljević et al., 2009; Mihaljević et al., 2010; Stević et al., 2013). MFGs were used in Europe by Mihaljević et al. (2013) and in Argentina by Devercelli (2010), and MBFGs to study the spatial patterns of the Danube River (Mihaljević et al., 2015). Studies applying two functional approaches, FGs and MFGs, were used in the Mura, Drava, Danube, and Sava rivers in Croatia by Stanković et al. (2012a,b); and FGs and MBFGs were used as indicators of the environmental variation in the floodplain of the Upper Paraná River (Bortolini et al., 2014). Three functional approaches to understanding phytoplankton dynamics were used in human-impacted shallow lakes of the Argentine Pampas plain (Izaguirre et al., 2012), for phytoplankton changes in the Danube River (Mihaljević et al., 2014), and in deep karstic lakes (Žutinic et al., 2014).

This study evaluated which of three phytoplankton functional approaches (functional groups-FGs, morphofunctional groups-MFGs, and morphology-based functional groups-MBFGs) showed the largest relation to the environmental variations during of rising and falling water periods in Amazonian floodplain lakes. Our hypothesis was that different functional classifications (FGs, MFGs, and MBFGs) have different capacities to characterize phytoplankton dynamics; and we also evaluated if the disconnection of the lakes due to the falling water period led to greater heterogeneity of the functional groups. The research questions included: (i) Which of the functional approaches best characterize phytoplankton dynamics on this Amazonian floodplain, composed predominantly of shallow lakes?; (ii) Do the functional and morphological characteristics reflect the environmental variability during rising and falling water periods?; and (iii) Which environmental variables modified by the flood pulse are more influential in the structuring of the phytoplankton community in these environments?

2. Materials and methods

2.1. Study area

The study was conducted on the Curuaí Floodplain (01°50′16″S – 02°15′12″S and 055°00′51″W – 056°05′00″W), Pará state, Brazil (Fig. 1). It is located on the right bank of the Amazon River, 900 km upriver from the Atlantic Ocean. The floodplain extends approximately 130 Km along the main course of the Amazon River, and is composed of more than 30 lakes that are temporarily or permanently connected to each other and to the Amazon River by several channels (Maurice-Bourgoin et al., 2007; Bonnet et al., 2005, 2008). The largest lake, Lago Grande, is approximately 50 km long (Barbosa et al., 2006).

The maximum river level occurs between May and June, and the minimum is in November and December. The flooded area varies between 575 and 2090 km^2 for water levels between 3.0 and 9.6 m (Barbosa et al., 2006; Bonnet et al., 2008), and in years of extreme floods such as 2009, the flooded area can reach up to 2500 km^2 for a water level reaching 11 m. The main lakes have the characteristics of a white-water system (Lago Grande, Poção Grande, Salé, Poção, Santaninha, Piedade, and Piraquara) (Sioli, 1984; Junk et al., 2012).

According to the Köppen and Geiger (1928) classification, the climate is humid tropical (Af), marked by rainfall in all seasons and annual mean temperature between 24 and 26 °C (Fisch et al., 1998). The mean annual precipitation in the eastern Amazon basin is 2460 mm (Amanajás and Braga, 2012).

2.2. Environmental variables

Sampling data were taken on parallel transects in seven lakes along the length of the Curuaí Floodplain. We collected from 26 sampling points during the rising water period (March 2013) and 25 during the falling water period (September 2013).

Water temperature (WT), water depth (WD), pH and electrical conductivity (EC) were measured *in situ* using a YSI EXO 2 multiparameter probe. Turbidity (TB) was estimated by absorbance in a spectrophotometer (Varian Cary 1-E), considering a ratio between low- and high-molecular-weight compounds (Strome and Miller, 1978).

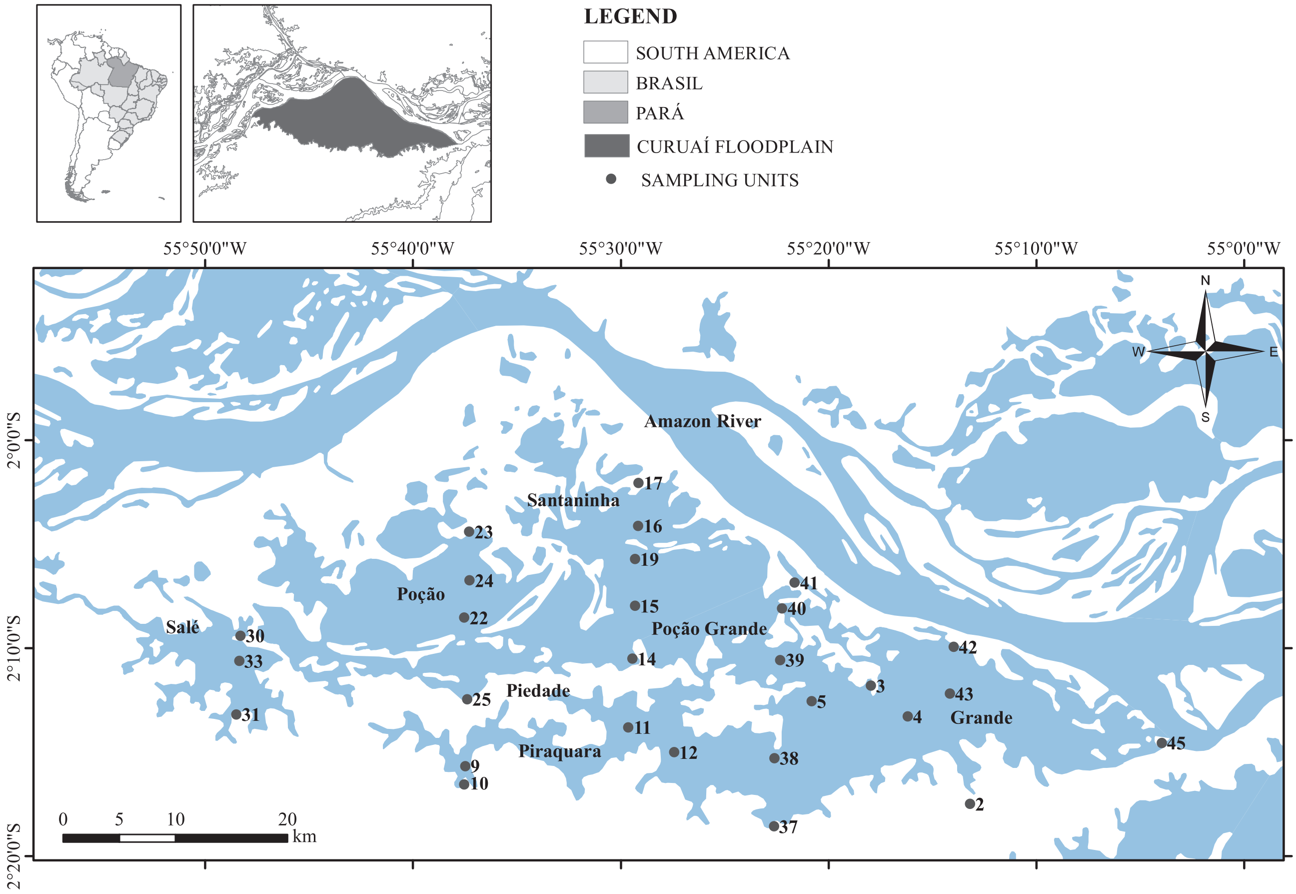

Fig. 1. Location of the Curuaí floodplain, Amazon basin, Brazil, showing the lakes and sampling points distributed in the parallel transects.

Silica (SI) was quantified by a photometric method using a specific kit (Si Merck Spectroquant® Kit for silicates – silicic acid). Total nitrogen (TN) and total phosphorus (TP) were colorimetrically determined following Mackereth et al. (1989).

2.3. *Biological sampling*

Phytoplankton and environmental variables in the floodplain lakes were sampled simultaneously, at the subsurface. Quantitative samples of phytoplankton were stored in 100-mL amber bottles and fixed with acetic Lugol's solution.

Phytoplankton population densities (ind mL^{-1}) were estimated by counts in random fields (Uehlinger, 1964) in an inverted Zeiss microscope, model Carl Zeiss Axiovert 25, at 400 × magnification, using the sedimentation technique (Utermöhl, 1958). The units (cells, colonies, and filaments) were enumerated for at least 100 specimens of the most frequent species (Lund et al., 1958). Phytoplankton biovolume (mm^3 L^{-1}) was estimated by multiplying the density of each species by the mean cell volume (Hillebrand et al., 1999), based on measurements of at least 20 individuals.

All phytoplankton taxa were grouped into functional groups (FGs) (Padisák et al., 2009), morphofunctional groups (MFGs) (Salmaso and Padisák, 2007), and morphology-based functional groups (MBFGs) (Kruk et al., 2010). To better include the filamentous cyanobacteria, the groups **5f** (large filaments without gas-vesicles or aerotopes) and **5g** (large filaments with gas-vesicles or aerotopes) were added to the morphofunctional groups.

Descriptors species were those that the biovolume sum of each representative was at least 51% of the total biovolume in each lake of the Curuaí floodplain.

2.4. *Data analysis*

We used a Principal Coordinates Analysis (PCoA; Legendre and Legendre, 2012) to check for differences in phytoplankton species composition between the rising and falling water periods. The biological dissimilarity was computed using Bray-Curtis index for species biovolume and environmental variables.

We performed a Detrended Correspondence Analysis (DCA) for each functional approach, to evaluate whether the linear (Redundancy Analysis-RDA) or unimodal ordination method (Canonical Correspondence Analysis-CCA) was more appropriate. All gradient lengths were short (< 3.0), indicating a linear distribution of the data, and therefore the Redundancy Analysis (RDA) was selected (Lepš and Šmilauer, 2003) to evaluate the relationship between functional approaches and environmental variables. The limnological and morphometric variables were divided into two groups: 1) Conditions (water temperature, water depth, pH, electrical conductivity, and turbidity) and; 2) Resources (silica, total nitrogen, and total phosphorus). These variables were selected according to their influence on the phytoplankton metabolism. Prior to the analyzes, all environmental variables were standardized to have mean equal to zero and standard deviation equal to one. To avoid multicollinearity between variables, we assessed the variance inflation factor (VIF), all these values were < 1.57, thus all variables were kept in the analysis (Ter Braak, 1986). The analysis of variance (ANOVA single factor; significance level of 0.05) was used to check significant differences between environmental and biological variables the two periods. These analyses were performed using the software R (R Core Team, 2015) with the vegan package (Oksanen et al., 2007).

3. Results

3.1. Environmental and biological characterization of the Curuaí floodplain

Water temperatures were higher in the falling water period, when the highest value (34.8 °C) in the study period was recorded. Water depth of the Curuaí lakes during rising was 3.7 m, and during falling period was 3.9 m, i.e., relatively shallow. Mean pH values were circumneutrals (7.2- rising and 7.1-falling). The electrical conductivity varied from 34 to 74 $\mu\text{S}\,\text{cm}^{-1}$ during rising water and was higher in this period. Water turbidity showed a mean of 21.0 NTU during rising and 21.9 NTU during falling water. Higher silica levels were recorded during falling water (2.2–3.7 $\text{mg SI}\,\text{L}^{-1}$). During rising water, total nitrogen varied from 222.4 to 629.6 $\mu\text{g N}\,\text{L}^{-1}$. In the same period, total phosphorus varied from 22.1 to 186.4 $\mu\text{g P}\,\text{L}^{-1}$. Mean phytoplankton biovolume per sampling unit was higher during falling water (6.6 $\text{mm}^3\,\text{L}^{-1}$). The mean levels of water temperature, pH, and water turbidity were higher during falling water, and followed the highest mean concentrations of algal biovolume. Electrical conductivity ($p < 0.001$), silica ($p < 0.001$), total nitrogen ($p = 0.012$), total phosphorus ($p < 0.001$), and phytoplankton biovolume ($p < 0.001$) showed significant differences between the values during rising and falling water (Table 1).

3.2. Phytoplankton functional groups

Main species from both hydrological periods represented distinct functional groups. Descriptors species of the rising water period belonged to several taxonomic classes, diatoms (10 taxa), cryptomonads (4), chlorophyceans (4), euglenoids (4), cyanobacteria (2), and zygnematophyceans (1). During falling water, the descriptors taxa were composed exclusively of cyanobacteria in Lago Grande (3), Piraquara (3), Santaninha (2), and Poção (2) lakes, and of cyanobacteria and diatoms in Poção Grande, Piedade, and Salé lakes (Table 2).

Functional groups (FGs) were represented by 26 functional groups during rising water and by 29 during falling water. The functional groups that best characterized the phytoplankton community in this period were **Y** (5.0 $\text{mm}^3\,\text{L}^{-1}$), **MP** (4.5 $\text{mm}^3\,\text{L}^{-1}$) and **P** (4.2 $\text{mm}^3\,\text{L}^{-1}$). Species that is adapted in almost all lentic ecosystems were represented of the FG **Y**, formed by *Cryptomonas* spp. FG **MP** composed by *Pinnularia neomajor, Ulnaria ulna, Eunotia deficiens*, *Oscillatoria pernornata, Pseudanabaena galeata* and *P. catenata* typical from the meroplanktonic that can be accidentally found in phytoplankton samples especially in shallow systems. FG **P** is composed of species adapted to shallow lakes that tolerate high trophic states and were formed by *Aulacoseira granulata*, *Closterium* sp., and *Fragilaria* sp. (Fig. 1a; Supplementary Material). During the falling water period, the most important functional groups were **H1** (112.0 $\text{mm}^3\,\text{L}^{-1}$), **M** (18.3 $\text{mm}^3\,\text{L}^{-1}$), and **MP** (13.7 $\text{mm}^3\,\text{L}^{-1}$). FG **H1** is formed by species that tolerate eutrophic environments, both stratified and shallow lakes with low nitrogen content, and was represented by heterocyted cyanobacteria, including *Dolichospermum circinale*, *D. flosaquae*, *D. solitarium*, and *D. planctonicum.* FG **M** is composed of species that tolerate eutrophic to hypertrophic environments, represented predominantly of *Microcystis* spp. (*M. aeruginosa, M. protocystis* and *M. wesenbergii)*. FG **MP** included mainly diatoms (*Surirella rorata, Aulacoseira herzogii, Surirella* cf. *splendida, S. braunii, U. ulna,* the desmid *Desmidium* sp., and the oscillatorialeans *O. limosa* and *O. perornata* (Fig. 1b; Supplementary Material).

Morphofunctional groups (MFGs) were represented by 24 groups during rising water and by 28 during falling water. During the rising water period, we observed the same proportion of cryptomonads (**2d**, 18% of total biovolume), represented by *C. erosa, C. marssonii,* and *C. curvata*; large centric diatoms (**6a**, 18%), composed of *A. granulata, A. distans, Melosira* sp., and *Urosolenia* sp.; and large pennate diatoms (**6b**, 16%), composed of *P. neomajor, U. ulna, E. flexuosa* and, *Synedra goulardii* (Fig. 1c; Supplementary Material). During the falling water period, nostocaleans (**5e**) accounted for 71% of the total biovolume *(Dolichospermum* spp.). Chroococcales (**5b**, 8%) were represented mainly by *M. aeruginosa, M. protocystis,* and *M. wesenbergii* (Fig. 1d; Supplementary Material). Although they were not important in all functional approaches, MFG **5f** (large filaments without gas-vesicles or aerotopes) such as *O. limosa* and *O. americana* and MFG **5g** (large filaments with gas-vesicles or aerotopes) such as *O. perornata* and *Planktothrix isothrix* were added (oscillatorialeans). This proposal created a clearer classification by not including the biovolumes of these species in favor of another morphofunctional group.

Morphology-based functional groups (MBFGs) observed during both hydrological periods were represented by seven groups, which varied in prevalence. During the rising water period, groups **VI** and **V** occurred in the same proportions. MBFG **VI** was composed of non-flagellated organisms with siliceous exoskeletons (*P. neomajor, A. granulata, A. distans, E. deficiens,* and *S. goulardii*); MBFG **V** comprised unicellular flagellates of medium to large size (cryptomonads, dinoflagellates, euglenoids, and chlorococcaleans) including *Cryptomonas* spp., *Trachelomonas* sp., *Euglena* sp., and *Peridinium* spp.; and MBFG **VII** was represented by large mucilaginous colonies (mainly *V. aureus*). These MBFGs comprised 9.7 $\text{mm}^3\,\text{L}^{-1}$ (34%), 9.4 $\text{mm}^3\,\text{L}^{-1}$ (33%), and 4.0 $\text{mm}^3\,\text{L}^{-1}$ (14%) of the total phytoplankton biovolume in this period, respectively (Fig. 1e; Supplementary Material). During the falling water period, MBFG **III** comprised 117.6 $\text{mm}^3\,\text{L}^{-1}$ (72%) of the total phytoplankton biovolume. Large filaments with aerotopes (nostocaleans) predominated in Lago Grande, Piraquara, Poção Grande,

Table 1
Minimum, maximum, median, mean, and standard deviation of the environmental and phytoplankton variables on the Curuaí Floodplain during rising and falling water periods. ANOVA analysis between the two periods.

Variables	Water temperature (°C)	Water depth (m)	pH	Electrical conductivity (μS cm^{-1})	Turbidity (NTU)	Silica (mg Si L^{-1})	Total nitrogen (μg N L^{-1})	Total phosphorus (μg P L^{-1})	Phytoplankton biovolume (mm^3 L^{-1})
(a) Rising water									
Min.	29.7	1.7	6.5	34.0	4.7	2.0	225.4	22.1	0.2
Max.	33.5	5.7	7.7	74.0	31.1	3.4	629.6	186.4	4.1
Mean	30.8	3.7	7.2	64.9	21.0	2.4	379.6	86.1	1.1
SD	0.8	1.5	0.3	10.0	6.34	0.4	89.2	37.9	0.9
(b) Falling water									
Min.	29.8	2.5	6.1	32.0	5.0	2.2	187.1	7.1	1.0
Max.	34.8	8.4	9.4	49.0	48.0	3.7	570.0	111.3	25.7
Mean	31.2	3.9	7.4	41.6	21.9	3.0	309.4	51.0	6.6
SD	1.1	1.2	0.9	4.3	10.1	0.3	102.6	25.9	5.7
(c) ANOVA									
F	1.79	0.43	1.74	115.80	0.14	34.58	6.81	14.79	23.70
p-value	0.187	0.513	0.194	< **0.001**	0.709	< **0.001**	**0.012**	< **0.001**	< **0.001**

Table 2
Relative proportion of the descriptors species and their respective functional groups of each lake on the Curuaí Floodplain during **(a)** rising and **(b)** falling water periods.

Lakes	Descriptors species	FG	MFG	MBFG	%
(a) Rising water					
Lago Grande	*Cryptomonas marssonii/ Aulacoseira granulata/ C. curvata /Oedogonium* sp./*A. distans/Dolichospermum* sp./*Euglena* sp.	Y/P/Y/Td/C/H1/W1	2d/6a/2d/10a/6a/5e/1c	V/VI/V/IV/VI/III/V	10/10/10/8/5/5/4
Piraquara	*Trachelomonas volvocina/A. granulata/A. distans/Chroococcus* sp.	W2/P/C/Lo	2c/6a/6a/5d	V/VI/VI/I	20/18/10/8
Poção Grande	*A. granulata /Euglena* sp.	P/W1	6a/1c	VI/V	32/30
Santaninha	*Volvox aureus/Ulnaria ulna/C. marssonii/Oedogonium* sp.	G/MP/Y/Td	3b/6b/2d/10a	VII/VI/V/IV	18/14/10/8
Poção	*Oedogonium* sp./*A. granulata/Closterium* sp./*A. distans/T. verrucosa*	Td/P/P/C/W2	10a/6a/8a/6a/2c	IV/VI/IV/VI/V	16/14/8/8/7
Piedade	*C. erosa/A. granulata*	Y/P	2d/6a	V/VI	43/20
Salé	*Pinnularia neomajor*	MP	6b	VI	57
(b) Falling water					
Lago Grande	*Dolichospermum circinale/D. flosaquae/D. spiroides*	H1/H1/H1	5e/5e/5e	III/III/III	29/16/13
Piraquara	*D. circinale/D. flosaquae/D. spiroides*	H1/H1/H1	5e/5e/5e	III/III/III	19/18/12
Poção Grande	*D. circinale/D. flosaquae/Surirella rorata*	H1/H1/MP	5e/5e/6b	III/III/VI	44/14/7
Santaninha	*D. circinale/D. flosaquae*	H1/H1	5e/5e	III/III	38/22
Poção	*D. circinale/D. flosaquae*	H1/H1	5e/5e	III/III	47/15
Piedade	*S. rorata/D. circinale/S. braunii*	MP/H1/MP	6b/5e/6b	VI /III/VI	33/12/8
Salé	*D. planctonicum/D. circinale/Surirella rorata*	H1/H1/MP	5e/5e/6b	III/III/VI	30/18/10

FG, functional groups; MFG, morphofunctional groups; and MBFG, morphology-based functional groups.

Santaninha, Poção, and Salé lakes. Large mucilaginous colonies (**VII**) comprised 25.1 $mm^3 L^{-1}$ (15%), composed mainly of *Microcystis* spp., *Botryococcus protuberans, Radiocystis fernandoi, V. aureus*, and *Microcrocis pulchella*; and diatoms (**VI**) comprised 11.7 $mm^3 L^{-1}$ (7%), composed of *S. rorata, A. herzogii, Surirella* cf. *splendida, S. goulardii, A. granulata*, and *S. braunii* (Fig. 1f; Supplementary Material).

Briefly, during the rising water period, the same proportions of FGs **Y** (17%) and **MP** (16%); of MFGs **2d** (18%) **6a** (18%) and **6b** (16%); and MBFGs **VI** (34%) and **V** (33%) were recorded. During the falling water period, there was a great prevalence of cyanobacteria of the genera *Dolichospermum* and *Microcystis,* represented by groups **H1** (68%) and **M** (11%) (FGs); **5e** (71%), and **5b** (8%) (MFGs); and **III** (72%), and **VII** (15%) (MBFGs) in all the lakes. *Dolichospermum* spp. formed blooms, and *D. circinale* comprised 30% of total biovolume in this period.

Morphology-based functional groups (MBFGs) during the rising water period showed a larger biovolume in the western area of the floodplain (Salé), where the lakes were less influenced by Foz North and South. *P. neomajor* (**VI**), *V. aureus* (**VII**), and *A. distans* (**VI**). However, *Oedogonium* sp. (**IV**), *A. granulata* (**VI**), and *Closterium* sp. (**IV**) were most important in Poção Lake (Fig. 2a). During the falling water period, the biovolume increased significantly. The largest biovolume concentrations occurred in the southeast area and coincided with increased numbers of *D. circinale* (**III**), *D. flosaquae* (**III**), *D. spiroides* (**III**), *D. planctonicum* (**III**), and *S. rorata* (**VI**), which contributed to the biovolume in lakes Piraquara, Lago Grande, Poção Grande, and Santaninha (Fig. 2b).

3.3. Phytoplankton composition

We observed that the samples from the rising period were more similar to each other than samples from the falling period. Moreover, we observed a greater similarity among the species compositions in the lakes during the falling water period, and a clear separation between species of different sampling periods (Fig. 3). The relationship of each functional group showed a clear separation between samples in the rising and/or falling water periods (Fig. 4a–f), thus phytoplankton composition on the Curuaí Floodplain was determined by the hydrological period.

3.4. Phytoplankton functional groups-environment relationship

The RDA for the functional groups (FGs) explained 35% of the total variability in the phytoplankton community composition, and the first two canonical axes together represented 84.8% of the variance of the community-environment relationship (axis 1: 77.8; axis 2: 7.0%). Axis 1 was positively correlated with EC (0.89) and TP (0.49) and negatively with SI (–0.68). Axis 2 was positively correlated with pH (0.74), WD

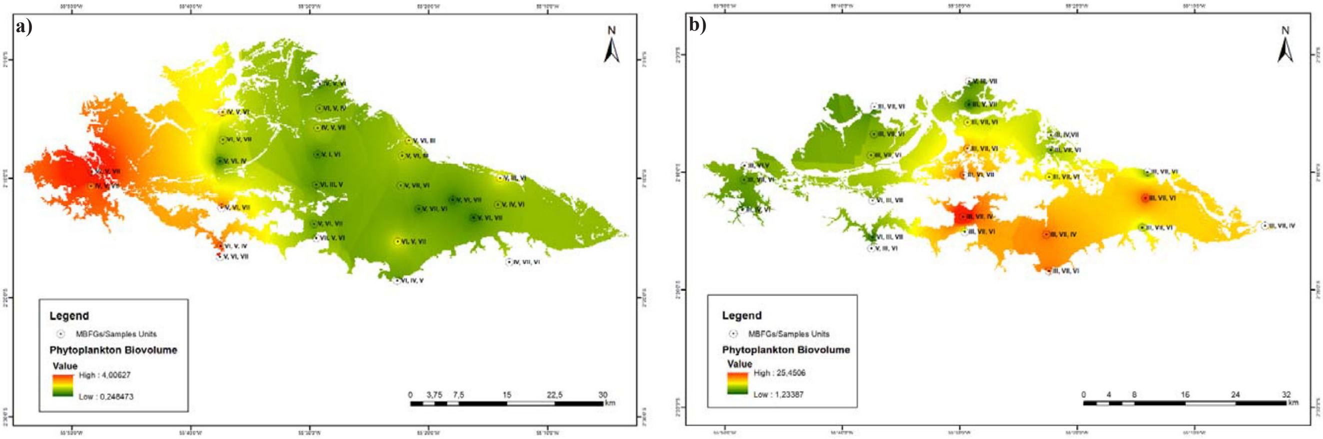

Fig. 2. Main morphology-based functional groups (MBFGs) distribution per sampling points on the Curuaí Floodplain during rising **(a)** and falling **(b)** water periods.

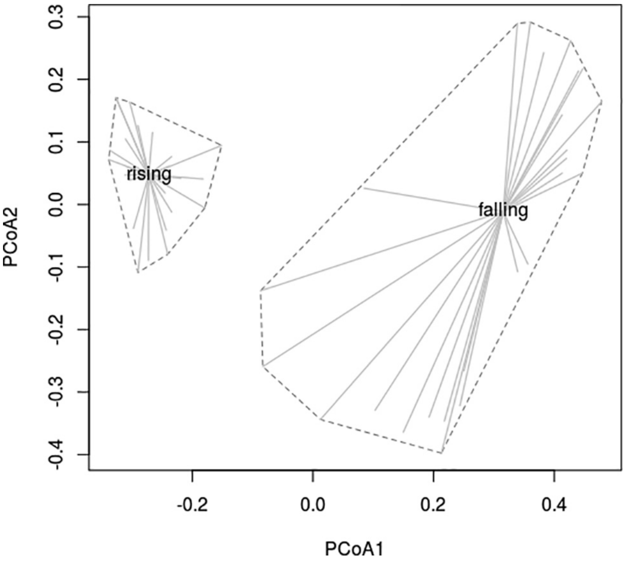

Fig. 3. Variation of phytoplankton species composition between rising water and falling water periods on the Curuaí floodplain. Each straight line within the polygons represents how far the composition of the community is from the centroid of each hydrological period.

(0.52), and SI (0.37). Higher levels of SI and, pH were associated with higher biovolumes **MP** (most of the diatoms and oscillatorialeans), and were prevalent during the falling water period. Higher values of EC were associated with the occurrence of FG **Y** (*Cryptomonas* spp.) during the rising water period (Fig. 4a and b).

The RDA for the morphofunctional groups (MFGs) explained 32% of the total variability in the phytoplankton community composition, and the first two canonical axes together represented 93.7% of the variance of the community-environment relationship (axis 1: 86.6; axis 2: 7.1%). Axis 1 was negatively with EC (−0.88) and TP (−0.43) and positively correlated with SI (0.67). Axis 2 was negatively correlated with pH (−0.59), SI (−0.52), and TB (−0.39). Higher levels of EC and TN were associated with a higher biovolume of MFGs **2d**, represented by the cryptomonads, and **6a**, formed by the large centrics diatoms during the rising water period (Fig. 4c and d).

The RDA for the morphology-based functional groups (MBFGs) explained 48% of the total variability in the phytoplankton community composition, and the first two canonical axes together represented 93.7% of the variance of the community-environment relationship (axis 1: 86.6; axis 2: 7.1%). Axis 1 was negatively correlated with EC (−0.87) and TP (−0.43) and positively with SI (0.66). Axis 2 was negatively correlated with pH (−0.59), SI (−0.51), and TB (−0.38). Higher levels of EC, TP, and TN were associated with higher biovolumes of MBFG **V** (cryptomonads, dinoflagellates, euglenoids, and chlorococcaleans) during the rising water period and MBFGs **III** (large filaments with aerotopes) and **VII** (large mucilaginous colonies) were associated with falling water period (Fig. 4e and f).

Electrical conductivity, silica, and pH were the most important environmental variables to structuring the phytoplankton functional groups on the Curuaí Floodplain (Fig. 4a–f).

4. Discussion

In evaluating capacities of different phytoplankton functional approach to characterize phytoplankton dynamics for Amazonian floodplain lakes, we found that morphology-based functional groups (MBFGs, Kruk et al., 2010, Freshwater Biology 55) were the largest related to the environmental variations during the rising and falling water periods on the Curuaí floodplain. In response to our research questions, the results showed that (i) MBFGs were the best in characterizing phytoplankton dynamics on the Curuaí Floodplain; (ii) the functional and morphological characteristics varied between the rising and falling water periods; and (iii) electrical conductivity, silica, and pH were the most important environmental variables in the structuring the phytoplankton functional groups on the Curuaí Floodplain. This finding is in agreement with studies of impacted shallow lakes (Izaguirre et al., 2012) and deep karstic lakes (Žutinic et al., 2014). The high explicability of this approach in such distinct environments suggests that this classification system can be used for long-term monitoring of aquatic systems and in studies comparing large numbers of lakes (Kruk et al., 2011). Additional advantages—such as the relative simplicity, objectivity, and lower taxonomic knowledge needed for its application—make this approach very promising.

Morphological traits were initially suggested to represent ecological characteristics because they were strongly related to the ability to acquire resources and to remain in the water column, and to be susceptible to predation (Litchman and Klausmeier, 2008; Naselli-Flores, 2014). However, the functional classification proposed by Reynolds et al. (2002) considers environmental information, which allows more detailed description of the phytoplankton assembly. Although the updated version proposed by Padisák et al. (2009) exchanged some taxa between groups and modified the original habitat template, facilitating its application, these last two classifications require extensive taxonomic knowledge regarding the autecology of the individual species or group of species. Furthermore, the classifications of Padisák et al. (2009) and Kruk et al. (2010) reinforce the idea of functionally equivalence species in which multiple species representing a variety of taxonomic groups can share similar, even identical, roles in ecosystem functionality (Loreau, 2004; Hubbell, 2005; Kruk et al., 2017).

Morphology-based functional groups (MBFGs) **III** and **VII** were important during the falling water period, while **VI** and **V** were predominant on rising water and were related to the highest values of electrical conductivity. These last three groups were also characteristic of La Limpia Lake, marked by high concentrations of inorganic suspended solids (Izaguirre et al., 2012).

The period of the greatest occurrence of diatoms (FG **MP**, MFGs **6a** and **6b**, and MBFG **VI**) during rising water was followed by lower levels of silica, which suggests that this chemical element was added to their frustules (Martin-Jézéquel et al., 2000).

Contrary to observations in a previous study (Nabout et al., 2006), our study recorded higher FG **Y** biovolumes during the rising water period. Similar results were observed in human-impacted environments in the Argentine Pampas, clear shallow lakes with macrophytes, and shallow lakes with high concentrations of suspended inorganic solids (Izaguirre et al., 2012). Limnological and morphometric conditions observed in the Curuaí Floodplain lakes stimulated the occurrence of cryptomonads with high surface:volume ratios, high growth rates, and efficient light usage and nutrient uptake (Reynolds et al., 2002; Reynolds, 2006).

We created two morphofunctional groups to comprise the phytoplankton composition of the Curuaí Floodplain. We added MFGs **5f** to include large filaments without gas-vesicles or aerotopes, such as *O. limosa* and *O. americana*, and **5g** to include large filaments with gas-vesicles or aerotopes, such as *O. perornata* and *Planktothrix isothrix* (oscillatorialeans). Although not important in all functional approaches, these filaments have high cell biovolume. This proposal aimed to clarify this classification by not grouping different functional traits in the same morphofunctional group. The closest existing group where we could attend these organisms would be **5a** thin filaments (oscillatorialeans) but this do not represent the organisms observed. Larger filaments may possess different adaptive strategies in turbid mixed environments (Reynolds et al., 2002). The presence of gas vacuoles or aerotopes is related to buoyancy (Walsby, 1972). The buoyancy of cyanobacteria is regulated by light, so they are more buoyant in low light intensities and less buoyant in high light intensities (Walsby, 1991, 1994).

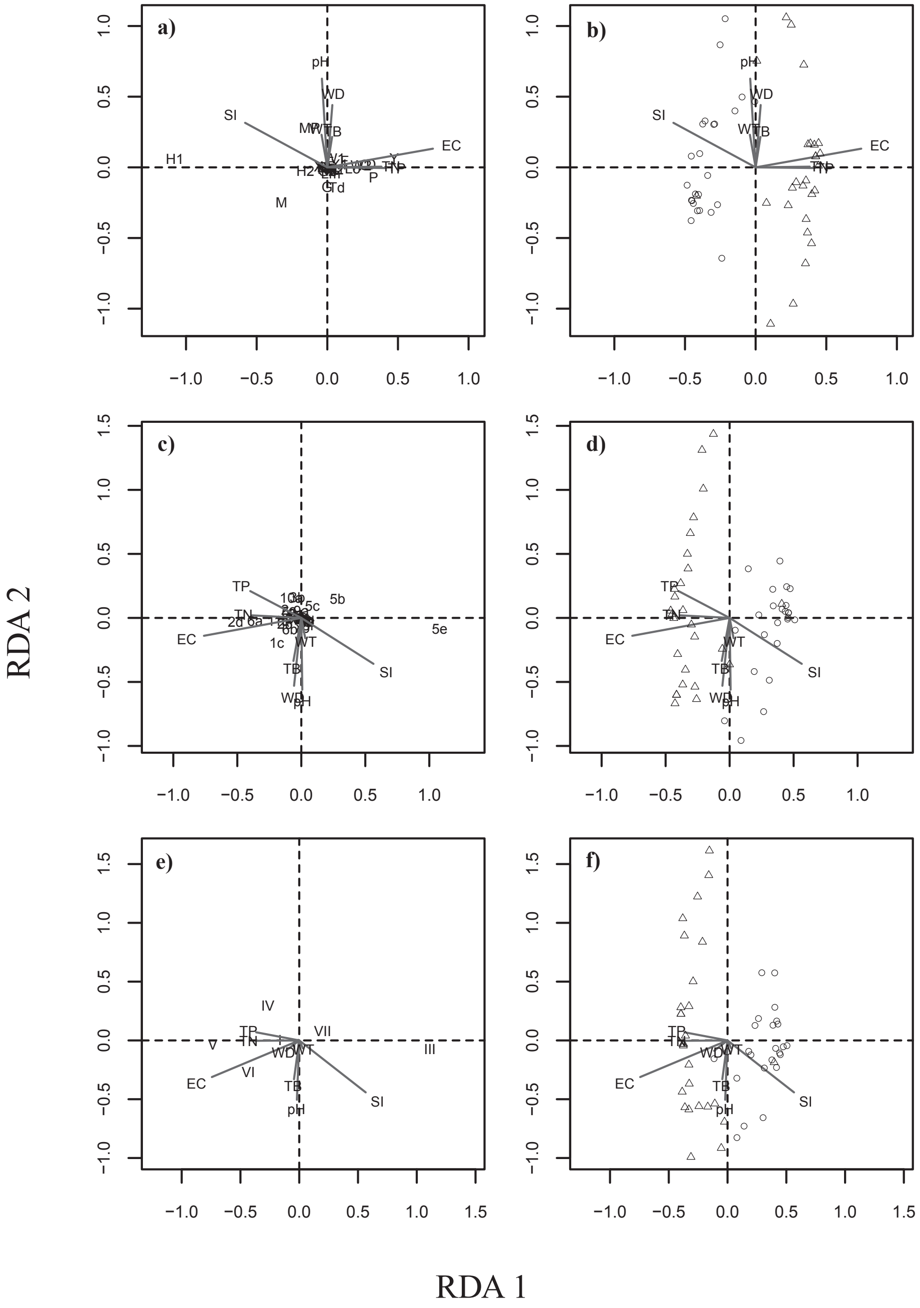

Fig. 4. First and second axes of the RDA based on the biovolume of the functional groups (FGs) **(a and b)**, morphofunctional groups (MFGs) **(c and d)** and morphology-based functional groups (MBFGs) **(e and f)** on the Curuaí floodplain. Left side, ordination of functional groups and environmental variables. Right side, ordination of sampling points and environmental variables (△ Rising, ○ Falling water period).

MFGs **2d** (cryptomonads) and **6a** (large centric diatoms) were related to the higher values of conductivity during rising water period when the lakes were more influenced by the main river channel, were also important in the Danube River (Mihaljević et al., 2013) during the summer-autumn transition in response to the higher water temperatures. Also during the rising water period, the same proportions of diatoms and cryptomonads were recorded in the Curuaí Floodplain. These MFGs were also noted in the Paraná River, Argentina (García de Emiliani, 1997; Devercelli, 2006). MFGs **6a** and **2d** tolerate highly turbulent environments (Salmaso and Padisák, 2007). The predominance of certain functional groups during rising water indicated that environmental conditions selected groups of species that share similar adaptive characteristics (Naselli-Flores and Barone, 2007). MFG **5e**, also numerous in shallow lakes with high turbidity (Izaguirre et al., 2012) was the main descriptor of the environment during the falling water period.

The highest levels of algal biovolume were recorded in the Curuaí Floodplain during the falling water period. The same pattern was observed in the limnophase of other tropical lowlands such as the Middle Araguaia River (Nabout et al., 2006) and the Upper Paraná River (Bortolini et al., 2014). In this period, the algal biovolume of our study—on average six times higher than during rising water.

The periodic connectivity between lakes typical of floodplain systems provides homogeneous aquatic communities (Lansac-Tôha et al., 2009; Hurd et al., 2016). However, in disagreement with our expectation, the composition of the phytoplankton communities of the lakes in the Curuaí Floodplain during the falling water period was more similar among each other than during the rising water period. Higher spatial contrasts between the samples observed during this period could be explained by the influence of the phytoplankton carried from the waters of the Solimões and Amazonas rivers, supplied by the runoff from the local drainage basin; this runoff may be significant only during the rising water period (Bonnet el al., 2008, 2017). During falling water, the environmental homogeneity was reflected in the occurrence of blooms of heterocyted cyanobacteria in all the lakes.

The blooms formed by *Dolichospermum* spp. (FG **H1**, MFG **5e**, and MBFG **III**) in periods of lower water volume were also recorded in floodplain lakes in other studies (Mihaljević and Stević, 2011; Mihaljević et al., 2013). In these studies, high biovolumes of these organisms were associated with higher water temperature, higher nutrient concentration, and greater water-column stability. In our study, high biovolumes of cyanobacteria were associated with higher water temperature and turbidity and more alkaline environment. According to Brasil et al. (2016), water-level reduction causes cyanobacterial blooms in shallow tropical lakes. Numerous species of cyanobacteria, such as *Dolichospermum* spp. and *Microcystis* spp., were described as potentially toxic by Sant'anna and Azevedo (2000), Sant'anna et al. (2008), and Jakubowska et al. (2013) and may be responsible for inhibiting the growth of other algae groups such as diatoms (Keating, 1978).

Cyanobacteria form a group of organisms that differ widely in functional characteristics (Salmaso and Padisák, 2007; Soares et al., 2013), and predominance of these organisms can occur throughout the year (Soares et al., 2009) or in certain periods, as occurs on the Curuaí Floodplain. In general, *Dolichospermum* spp. have a high surface:volume ratio, large cell biovolume, and low sedimentation rates because of their positive buoyancy (Reynolds, et al., 1987, Reynolds, 2006).

Most of the lakes remained relatively shallow in both periods. The dynamics of aquatic communities in tropical environments are more affected in shallow lakes than in deep lakes (Scheffer and van Nes, 2007; Janssen et al., 2014). Shallow lakes are strongly affected by the recurrent environmental changes in floodplains, such as eutrophication processes and increased nutrient load (Jeppesen et al., 2014) and release, discharge of agrochemicals, and interaction with different soil-use activities (Meerhoff and Jeppesen, 2010).

Heterocyted cyanobacteria occurred in all lakes during falling water period. FG **H1** is represented by species related to eutrophic environments, a stratified water column, and shallow lakes with low nitrogen availability (Padisák et al., 2009). Organisms of FG **MP** occur in frequently turbulent environments, and in shallow turbid lakes, due to the presence of inorganic compounds. FG **M** are characteristic of eutrophic to hypereutrophic environments and small to medium-size water bodies (Reynolds et al., 2002; Padisák et al., 2009). FGs **H1** and **M** were descriptors during the falling water period and reflected the conditions in the shallow eutrophic lakes on the Curuaí Floodplain (Bomfim et al., 2017; in submission).

5. Conclusions

Our study showed that the phytoplankton community composition varied between the rising and falling water periods. The occurrence of heterocyted cyanobacteria blooms in all the lakes during the falling water caused more similarity among the lakes than did in rising water period. MBFGs were the largest related to the environmental variations during the rising and falling water periods on the Curuaí floodplain influenced mainly by water electrical conductivity, silica, and pH. This approach provides a relatively simple and objective classification, thus we recommend using these groups to study phytoplankton ecology in shallow floodplain lakes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2018.07.038.

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