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ORIGINAL ARTICLE

Influence of niche and neutral processes on fish communities associated with changes in macrophyte rafts along the hydrological cycle

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Abstract

Aquatic macrophytes add structural complexity to the environment, which influences fish species. The structure of macrophytes rafts can vary depending on the hydrological cycle and space availability. Thus, the objective of the present study was to evaluate which predictors associated with environmental conditions, composition of macrophyte species and spatial factors can affect fish communities in different hydrological regimes. The study was carried out in oxbow lakes in the Amazon, in the middle Purus River, Amazonas, Brazil. Samples of fish and macrophytes were collected during the flood, receding and drought periods, and environmental variables were measured in all macrophytes rafts. Partial redundancy analysis was applied to quantify the relative contribution of environmental variables, macrophyte composition and spatial factors in the fish community. Our study revealed that environmental conditions and macrophyte species composition, and both spatially structured as well, were the main factors that explained changes in fish composition in floating meadows of oxbow lakes. Corroborating our predictions, the variations in the fish communities were explained mainly by niche-based processes, including environmental conditions and macrophyte species composition as an environmental component, which varied over the hydrological cycle. The spatial component was more important during flooding, environmental conditions during receding, and macrophyte species composition during the drought hydrological regime. However, the shared explanations that indicated a spatially structured environment, both for environmental conditions and for composition of macrophytes, were greater during all hydrological regimes, also supporting our prediction.

Keywords Fish fauna · Floodplain · Aquatic macrophytes · Complexity · Amazon Forest · Oxbow lakes

Introduction

Understanding species distribution is one of the main aims of ecology. Recently, it has been common to use niche and neutral processes to explain species distribution. In general, environmental heterogeneity relates to niche availability and spatial extent relates to dispersal rates of species. Aquatic plants are responsible for adding structural complexity to the environment (Savino and Stein 1982; Dibble et al. 1996; Padial et al. 2009), increasing environmental heterogeneity, niche dimensions, and consequently species richness (Agostinho et al. 2007). Several fish species use macrophyte rafts as sites for foraging (Pelicice and Agostinho 2006) on microorganisms (zooplanktons and macroinvertebrates) attached to submerged structures of macrophytes (Cyr and Downing 1988; Kurashov et al. 1996). Macrophyte rafts also provide shelter from predators (Dibble et al. 1996; Casatti et al. 2003; Pelicice et al. 2005; Pelicice and Agostinho 2006) and sites for

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spawning and larval development (Sazima and Zamprogno 1985; Agostinho et al. 2003; Agostinho et al. 2007).

Macrophytes provide many microhabitats for aquatic life and strongly affect nutrient cycling processes (Dibble and Thomaz 2006; Thomaz et al. 2008; Junk et al. 2012; Brito et al. 2020). Accordingly, they provide the basis for complex food chains and trophic interactions (Pott and Pott 2000; Meerhoff et al. 2007). Several ecological forms of aquatic macrophytes (submerged, emergent, amphibious, floating) usually colonize the same aquatic ecosystem simultaneously and can be affected in different ways by flood disturbances in a floodplain (Geest et al. 2005). For this reason, these life forms and their contribution to habitat complexity may directly influence the associated fish fauna.

Oxbow lakes are environments integrated ecologically with river-floodplain systems. The effects of flooding on the structure of oxbow lake communities depend on the intensity, duration and predictability of the floods, in addition to intrinsic habitat complexity and the availability of refuge (Junk et al. 1989, 2012). The macrophyte rafts in littoral areas may vary strongly depending on the hydrological cycle (Silva and Pinto-Silva 1989; Junk 1997), reflecting in a temporal dynamic under the influence of flood and drought conditions (Pott and Pott 2000; Röpke et al. 2016). Thus, variations in the aquatic vegetation along the hydrological cycle may determine the distribution of organisms associated with these habitats at both local and regional scales.

Several studies have recognized the importance of spatial processes in the distribution of species (Borcard et al. 1992; Legendre 1993; Viana and Chase 2019), allowing the identification of patterns and ecological processes (Tobin 2004). Accordingly, in addition to seeking to understand the influence of environmental structure on local communities, it is necessary to recognize the spatial relationships of communities and how they are distributed. The spatial distribution of biological communities may vary with increasing geographic distance, this pattern probably relates to random combinations of colonization and migration (Hubbell 2001). Alternatively, environmental factors that are spatially structured or environmental responses related to interactions between species can cause such patterns (Chase and Leibold 2003; Bell et al. 2006; Mertes and Jetz 2018).

Since the publication of the classic paper of MacArthur and MacArthur (1961), which placed the issue of habitat complexity in an ecological framework, many articles focusing on this topic have been published, especially for aquatic environments (Cunha et al. 2012). Nevertheless, information about the role of environmental and spatial factors on the distribution of fish species around macrophyte rafts is still inconsistent, especially when considering the influence of the intrinsic factors of each lake and variations along the hydrological cycle. In this context, we aimed to determine which predictors associated with environmental conditions, macrophyte species composition, and spatial factors may influence fish communities along different hydrological regimes in the oxbow lakes of an Amazonian floodplain. Specifically, we addressed the following questions. (i) Which environmental conditions, macrophyte species and spatial factors best explain variations in fish communities in oxbow lakes? (ii) Is the macrophyte species composition a good predictor of the variation in fish composition? (iii) Does the influence of environmental conditions, macrophyte species composition and spatial factors on fish communities vary according to the hydrological cycle? We expected that variations in the fish communities are explained mainly by niche-based processes, including macrophyte species composition as an environmental component, and that should vary according to each hydrological regime. In addition, because oxbow lakes may represent blocks of macrophyte rafts supported by environmental conditions intrinsic to each lake, we also predicted an influence of environmental factors that are spatially structured.

Material and methods

Study area

This study was conducted in eight oxbow lakes located in the middle reaches of the Purus River between the cities of Boca do Acre (8°42′39.75” S and 67°23′20.40” W) and Pauini (7°44′33.32” S and 67°1′20.35” W) (Fig. 1). The climate of the area is hot and wet and four hydrological periods determine the flood pulse in the region (flooding, flood, receding, and drought). Four of the eight oxbow lakes maintain hydrological connectivity during the four periods of the hydrological cycle, whereas three completely lose their connection with the main channel when the water level is low. Due to these variations in hydrological connectivity between periods, categories were created for the lake environments; four lakes were categorized parapotamon (backwater in permanent connection with the main channel, former side arm of braided channel) and the other four lakes formed from meandering curves that became disconnected were categorized as “Paleopotamon.” This terminology is associated with ecological differences between the water bodies of the floodplain and based on attributes such as connectivity, successional trajectory and structure of the communities (Ward and Stanford 1995; Rocha 2011); these categories were used as environmental variables in data analysis.

Data collection

We sampled five macrophyte rafts with different topologies, identified by the dominance of one or a few plant species and life forms, in each lake (Online Resource 1: Table 1S). The lake rafts ranged in area from 15 to 68 m^2. We collected

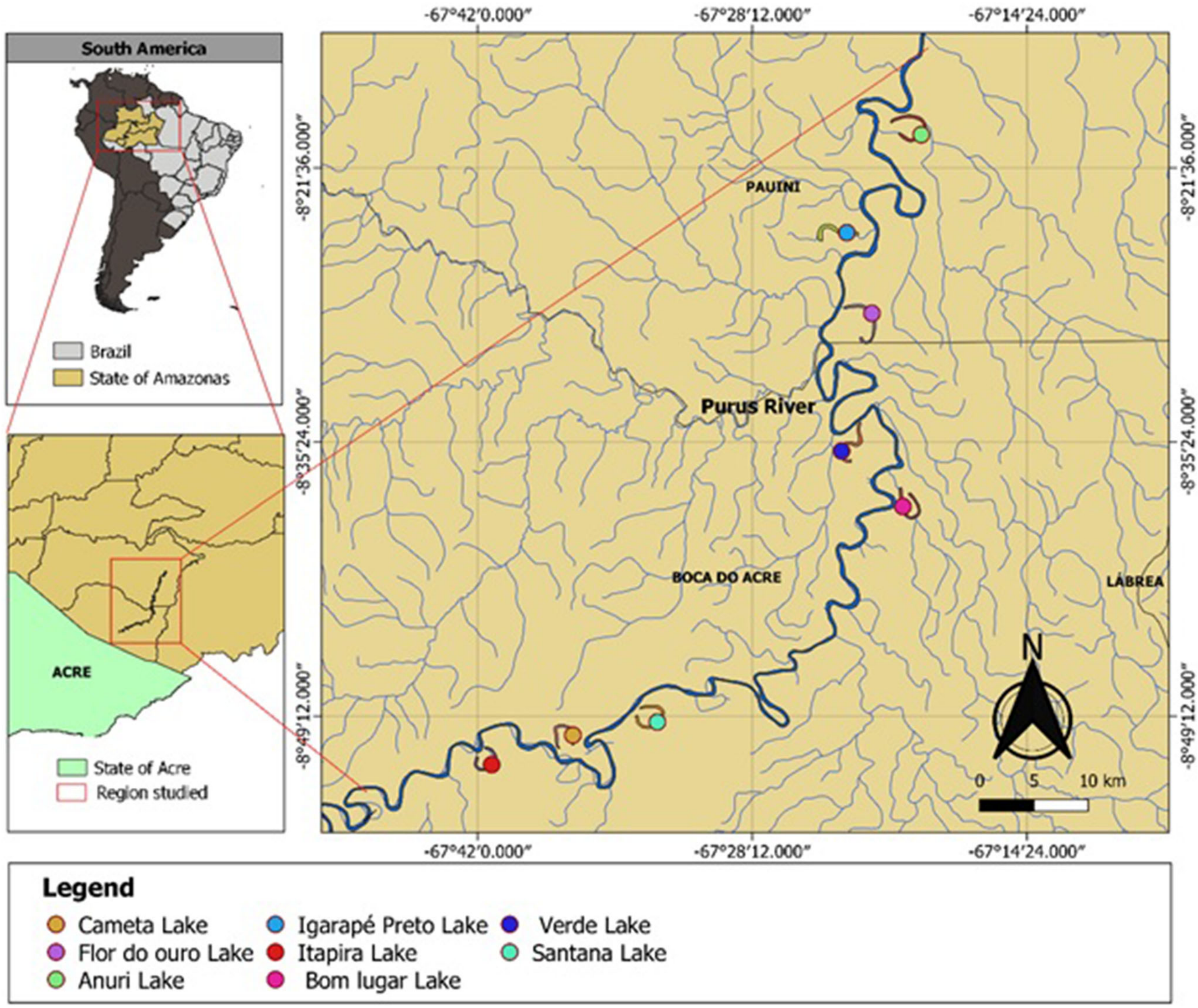

Fig. 1 Oxbow lakes located in the Middle Purus River in Western Amazonia, Boca do Acre AM, Brazil

samples during the flood, receding and drought periods in February, May and September 2012, respectively. Macrophyte rafts were sampled using a square frame that was haphazardly placed nine times on each stand. The relative abundance of macrophytes was visually estimated as the percent cover of each species within the 0.5 × 0.5 m floating square frame (Braun-Blanquet 1928), and species richness was determined as the number of species per sample. Species that could not be identified in the field were collected for further identification in the laboratory with specialized bibliography (Ferreira et al. 2011; Moura-Júnior et al. 2015).

We also quantified the total area (m^2) of macrophyte coverage by visiting all sections of the lake covered by aquatic vegetation and using a GPS to mark the locations of the macrophyte rafts, specifying the points corresponding to the edges of the banks. The data were plotted on a Landsat-5 image (path/row 005/062). After the identification of the lakes in the image, the limits of the environments were identified by vectoring. The area of macrophyte coverage was estimated to obtain the approximate total proportion of banks in each lake using ArcGIS® and ArcMap™. The distances between lakes (m) were measured following the watercourse connectivity obtained by Landsat/TM imagery with the aid of ArcGIS® and ArcMap™. These software packages were also used to measure the length of the hydrological connectivity between the main channel of the river and the lakes.

Fish were sampled in five rafts of aquatic macrophytes at each lake with the aid of a seine net 4 m^2 in area with 0.2 cm mesh. Samples were haphazardly collected with six consecutive throws of the net in each stand during the morning and again during the evening. The fish caught were identified, photographed, measured, weighed, and fixed in 10% formalin. A number of voucher specimens were deposited in the Ichthyological Collection of the Federal University of Acre with catalog numbers from MUFAC IC-936 to MUFAC IC-1020.

With the aid of a limnological probe, environmental variables were measured in all macrophyte rafts sampled at the surface, middle depth and bottom of the lakes. The probes measured the water temperature (°C), electrical conductivity (μS cm^{-1}), pH and dissolved oxygen (mg L^{-1}) every 2 h in a 24 h cycle. Water transparency (cm) and depth in the rafts were measured with a Secchi disk, and water level data for the Purus River were provided by the National Water Agency (NWA 2005) at two meteorological stations upstream from the sampling sites. Water samples for the analysis of chemical variables were collected at the surface and at the bottom of the lakes with a Van Dorn bottle and stored for analysis of total phosphorus and nitrogen according to Valderrama (1981).

Data analysis

To quantify the relative contribution of environmental conditions, macrophyte species composition and spatial factors (geographical distance) to the fish species composition in floating meadows of oxbow lakes we applied a partial redundancy analysis (pRDA) followed by variance partitioning to estimate pure and shared fractions of variance explained. Three matrices of explanatory variables were utilized: a matrix of environmental conditions (lake-river connectivity, pH, dissolved oxygen, water transparency, water level, lake depth, macrophyte species richness and area coverage by floating meadows), a matrix with percentage of each macrophyte species, and a matrix with spatial variables. The environmental variables were log-transformed (except pH) and the percentages of macrophyte species were standardized using the root squared transformation.

The spatial predictors were calculated from the geographical distance matrix using the principal coordinates of neighbor matrices technique (PCNM). The resulting PCNM eigenvectors were used to describe the spatial structures, which commonly represented patterns ranging from broad to fine scales. Due to the large number of predictors of the environmental conditions, as well as macrophyte species composition and spatial variables, a forward selection procedure (Blanchet et al. 2008) was used to avoid over-fitting. This procedure retains subsets of variables that contributed significantly to explain the variation in fish species composition. Only selected variables were used in pRDA and variance partitioning analysis. Variance partitioning splits the total variance, which is explained by pure and shared fractions, as well as the unexplained variation. The amount of variance explained by each component was estimated using adjusted R^2 values, and the significance of the components was evaluated with permutation tests (Peres-Neto et al. 2006). The species abundance data was Hellinger-transformed prior to pRDA and variance partitioning (Legendre and Gallagher 2001).

PCNM analyses, variance partitioning and significance tests of the components were performed with the vegan package (Oksanen et al. 2012), and the forward selection was performed with the packfor package (Dray et al. 2011), both available for R language (R Core Team 2012). Environmental, macrophyte species and spatial variables that explained more than 5% in the forward selection procedure were utilized to construct RDA ordination plots for each hydrological regime separately.

Results

Fish and macrophyte species richness

We collected 2293 specimens of fish, distributed in seven orders, 25 families, 66 genera and 84 species. Characiformes was the richest order with 37 species, followed by Siluriformes with 17 species, and Cichliformes with 8 species. The most abundant species were *Ctenobrycon hauxwellianus* Cope, 1870 ($n = 870$), *Hemigrammus neptunus* Zarske and Géry, 2002 ($n = 253$), *Mylossoma duriventre* Cuvier, 1818 ($n = 185$), *Leporinus friderici* Bloch, 1794 ($n = 93$), *Aphyocharax alburnus* Günther, 1869 ($n = 63$), *Leporinus obtusidens* Valenciennes, 1847 ($n = 57$), and *Schizodon fasciatus* Spix and Agassiz, 1829 ($n = 48$) (Online Resource 2: Table 2S). With a total of eight species, floating macrophytes comprised the most abundant group of plants during sampling. *Pistia stratiotes*, *Salvinia auriculata*, and *Eichhornia crassipes* were the most frequent species. The most abundant emergent species was *Paspalum repens*, which occurred in association with floating macrophytes in most oxbow lakes (Online Resource 1: Table 1S).

Environmental, macrophyte composition and spatial effects on fish composition

All environmental, macrophyte species composition and spatial models were significant ($p < 0.05$) and changed along the hydrological cycle. During flooding, the spatial component explained 27% of the variation which was more than that for the environmental and macrophyte components (21 and 14%, respectively; Fig. 2). Seven spatial variables were retained for the pRDA model. The environmental variables related to fish distribution were depth, connectivity, transparency, water level and macrophyte rafts area; and the macrophyte species selected were *Paspalum repens, Callitriche stagnalis* and *Lemna minor* (Table 1). The pure explanations of spatial, environmental and macrophyte components were 8, 2 and 1%, respectively. The shared explanation was 24% by macrophyte species and environmental variables, 30% by macrophyte species spatially structured, and 31% by environmental variables spatially structured. The three models combined explained

Table 1 Mean and standard deviation of abiotic variables that influenced the fish community of macrophyte banks of abandoned meander lakes

Lake	Period	Temp.	DO	Transp.	W_Level	Depth	Riq_Macro	Area_Macro	Connect.
Anuri	Flood	25.82 ± 0.69	4.02 ± 1.13	20 ± 0.1	1690.8 ± 232	426.2 ± 117	2 ± 1	2351 ± 576	Parapotamon
	Receding	22.81 ± 5.83	4.61 ± 0.57	53.33 ± 5.55	1256 ± 89	812 ± 274	2.6 ± 0.93	3270 ± 731	
	Drought	33.14 ± 6.74	4.27 ± 2.5	53.2 ± 5.12	702 ± 307.2	182.7 ± 71.28	108.2 ± 169.1	1096.86 ± 667	
Born Lugar	Flood	27.47 ± 2.29	4.36 ± 0.43	50 ± 0.01	1968.8 ± 39.52	1076 ± 219.2	7.8 ± 1.76	2685 ± 1.2	Parapotamon
	Receding	28.5 ± 0.76	6.44 ± 0.28	37 ± 0.01	1011 ± 38.4	1320 ± 104	3.2 ± 1.04	1217 ± 0.1	
	Drought	29.66 ± 3.62	2.74 ± 0.76	30 ± 0.01	513,4 ± 38.72	150 ± 46.8	3.4 ± 1.12	2203,2 ± 0.96	
Cameta	Flood	28.1 ± 0.57	7.31 ± 1.7	65 ± 0	2023.8 ± 7.44	1040 ± 248	6.81 ± 1.04	2207 ± 1.2	Paleopotamon
	Receding	31.18 ± 1.4	6.96 ± 0.25	65 ± 0.1	1322.2 ± 100.5	940 ± 384	4.4 ± 1.68	2508 ± 1.2	
	Drought	32.26 ± 2.55	3.56 ± 1.10	60 ± 0.3	513.4 ± 38.7	114.8 ± 5.52	3.8 ± 0.32	2308 ± 1.2	
Flor do ouro	Flood	28.54 ± 1.19	4.40 ± 0.25	30 ± 0.0	1857.4 ± 142.4	1200 ± 184	5 ± 0.8	3904 ± 1.2	Parapotamon
	Receding	27.95 ± 0.76	2.90 ± 0.44	70 ± 0.2	1011 ± 34.1	910 ± 176	3.6 ± 0.32	5465 ± 50.8	
	Drought	28.76 ± 0.94	3.416 ± 1.24	60 ± 0.1	614 ± 40.8	309.2 ± 104	4.6 ± 0.48	4685 ± 1.2	
Igarapé Preto	Flood	27.98 ± 2.26	4.41 ± 0.35	10 ± 0.1	1968.8 ± 39.5	229.4 ± 48.7	2.2 ± 0.64	110.2 ± 19.36	Parapotamon
	Receding	29.9 ± 0.83	6.04 ± 0.42	55 ± 0.1	1330 ± 44.9	1190 ± 168	4 ± 0.32	700 ± 48.9	
	Drought	34.36 ± 1.71	1.56 ± 0.09	40 ± 0.23	724 ± 8	17.4 ± 4.72	2.8 ± 0.64	621.6 ± 301.1	
Itapira	Flood	27.4 ± 1.35	5.30 ± 1.14	70.0 ± 0.1	2023.8 ± 7.44	1040.0 ± 248	3.0 ± 0	1427.0 ± 1.20	Paleopotamon
	Receding	30 ± 0.2	6.6 ± 0.1	30 ± 0.2	1282 ± 0.1	940 ± 0.2	1.6 ± 0.48	477 ± 1.2	
	Drought	32.56 ± 1.95	5.66 ± 0.69	20 ± 0.1	513.4 ± 38.7	229.6 ± 35.52	3 ± 0.1	952 ± 1.2	
Verde	Flood	25.4 ± 0.36	4.58 ± 0.18	18 ± 12.8	1934 ± 68.8	1200 ± 184	3.6 ± 0.48	2093 ± 1.2	Paleopotamon
	Receding	29.5 ± 0.75	3.5 ± 1.09	65 ± 0.1	1398.8 ± 44.96	1420 ± 168	3.8 ± 1.44	3809 ± 1.2	
	Drought	31.1 ± 1.92	3.16 ± 1.13	33 ± 15	830 ± 206.5	106.8 ± 31.5	3.6 ± 0.37	3401 ± 1	
Santana	Flood	29.7 ± 0.89	6,8 ± 2	38 ± 0.1	1913.8 ± 131	1076 ± 219	3.2 ± 0.96	2721 ± 1.2	Paleopotamon
	Receding	31.1 ± 0.80	4.86 ± 0.82	70 ± 0.1	1337.6 ± 78.08	1320 ± 104	3 ± 0.1	2790 ± 1.2	
	Drought	29.76 ± 3.39	3.61 ± 2.19	40 ± 0.01	513.4 ± 38.72	209 ± 34.4	3.8 ± 0.32	2372 ± 1.21	

Temp. – temperature; DO – dissolved oxygen; Transp. – transparency; W_Level water level; Macro_Ric – macrophyte richness; Macro_Area – macrophyte area; Connect. – hydrological connectivity

32% of the variation in fish communities during the flood hydrological regime (Fig. 2).

The environmental component explained 18% of the variation, which was more than that for the spatial and macrophyte species components (17 and 14%, respectively; Fig. 2) during the receding hydrological regime. The environmental variables selected were connectivity, transparency, macrophyte rafts area, depth, water level and dissolved oxygen (Fig. 3). The macrophyte species retained in explaining fish composition were *Phyllanthus fluitans, Paspalum repens, Salvinia auriculata* and *Cyperus helferi*. Six spatial variables were retained (Table 2). The pure explanations of spatial, environmental and macrophyte species components were 5, 4 and 4%, respectively. The shared explanation was 25% by macrophyte species and environmental variables, 26% by macrophyte species spatially structured, and 26% by environmental variables spatially structured. The three models combined explained 30% of the variation in fish communities during the receding hydrological regime (Fig. 2).

The macrophyte species composition component explained 51% of the variation, which was more than that for spatial and environmental components (42 and 37%, respectively; Fig. 2)

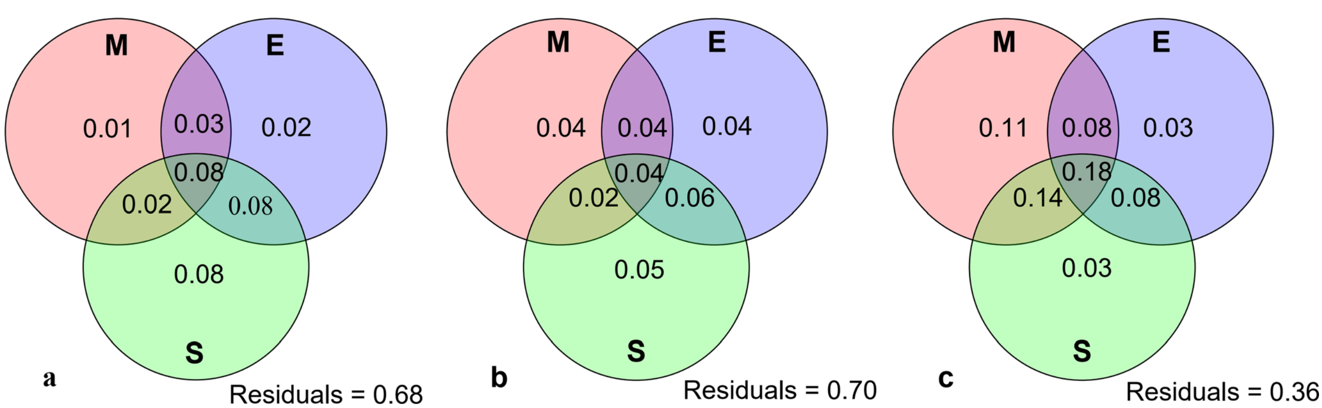

Fig. 2 Variation partitioning results for fish metacommunities associated with macrophyte rafts during the hydrological regimes of **a** flood, **b** receding, and **c** drought. Results based in a partial redundancy analysis. Values shown are adjusted R^2. M - Macrophyte species composition; E - environmental; S - spatial

Table 2 Explanatory variables retained in forward selection procedure and variation partitioning (adjusted R^2) resulting from partial redundancy analysis (pRDA)

RDA model	Variables retained in forward selection	Adj R^2
Flood		
Macrophyte	*Paspalum repens, Callitriche stagnalis, Lemna minor*	0.14*
Environmental	Depth, connectivity, transparency, water level, macrophyte raft area	0.21*
Spatial	1, 2, 10, 8, 7, 6, 4	0.27*
Full model		0.32*
Receding		
Macrophyte	*Phyllanthus fluitans, Paspalum repens, Salvnia auriculata, Cyperus helferi*	0.14*
Environmental	Connectivity, transparency, macrophyte raft area, depth, water level, dissolved oxygen	0.17*
Spatial	1, 2, 6, 8, 7, 9	0.17*
Full model		0.30*
Drought		
Macrophyte	*Eichhornia crassipes, Ammannia* sp., *Montrichardia linifera linifera, Lemna minor, Callitriche stagnalis, Pistia stratiotes, Salvinia auriculata, Cyperus helferi, Phyllanthus fluitans*	0.50*
Environmental	Connectivity, depth, transparency, macrophyte raft area, macrophyte richness, water level	0.37*
Spatial	1, 8, 7, 6, 2, 3, 10, 9	0.42*
Full model		0.64*

*$p < 0.05$

during the drought. The macrophyte species selected to explain fish composition were *E. crassipes, Ammannia* sp., *Montrichardia linifera, L. minor, Callitriche stagnalis, Pistia stratiotes, Salvinia auriculata, Cyperus helferi* and *Phyllanthus fluitans*. Eight spatial variables were retained, and the environmental variables selected were connectivity, depth, transparency, macrophyte rafts area, macrophyte species richness, and water level (Table 2). The pure explanations of macrophyte, spatial and environmental components were 11, 3 and 3%, respectively. The shared explanation was 61% by macrophyte species and environmental variables, 61% by macrophyte species spatially structured, and 53% by environmental variables spatially structured. The three models combined explained 64% of the variation in fish communities during the drought hydrological regime (Fig. 2).

Discussion

Our study reveals that environmental conditions and macrophyte species composition, and both spatially structured as well, are the main factors that explain changes in fish composition in floating meadows of oxbow lakes. Corroborating our predictions, the variations in the fish communities were explained mainly by niche-based processes, including environmental conditions and macrophyte species composition as an environmental component, which showed variation in explaining over the hydrological cycle. The spatial component was more important during the flood hydrological regime, environmental conditions during receding, and macrophyte species composition during drought. However, the shared explanations that indicate an environment spatially structured, both for environmental conditions and for composition of macrophytes, were greater during all hydrological regimes, also corroborating our prediction.

During the flood period, the fact that spatial variables are of greater importance in the composition of fish species associated with macrophytes, is probably because the flood pulse facilitates the dispersion of species both between banks and between lakes (the selected PCNMs were both short- and large-scale). This is because during the flood period, the hydrological connection between environments influences the dispersion and migration of fish species between habitats (Junk et al. 1989; Thomaz et al. 2008; Gomes et al. 2012).

During receding, environmental conditions were more important, as such result may be associated with changes in the conditions of each lake environment during this period. In these floodplain lakes, during this period, it was possible to observe the decrease in the water level of the river and, consequently, the retraction and disconnection of the lake environments. As the water level decreases, the lakes become shallower, some are isolated and smaller, so that they are influenced by local environmental characteristics, and consequently by local biotic forces, including density-dependent interactions, such as competition and predation (Rodríguez and Lewis 1997; Winemiller and Jepsen 1998; Thomé-

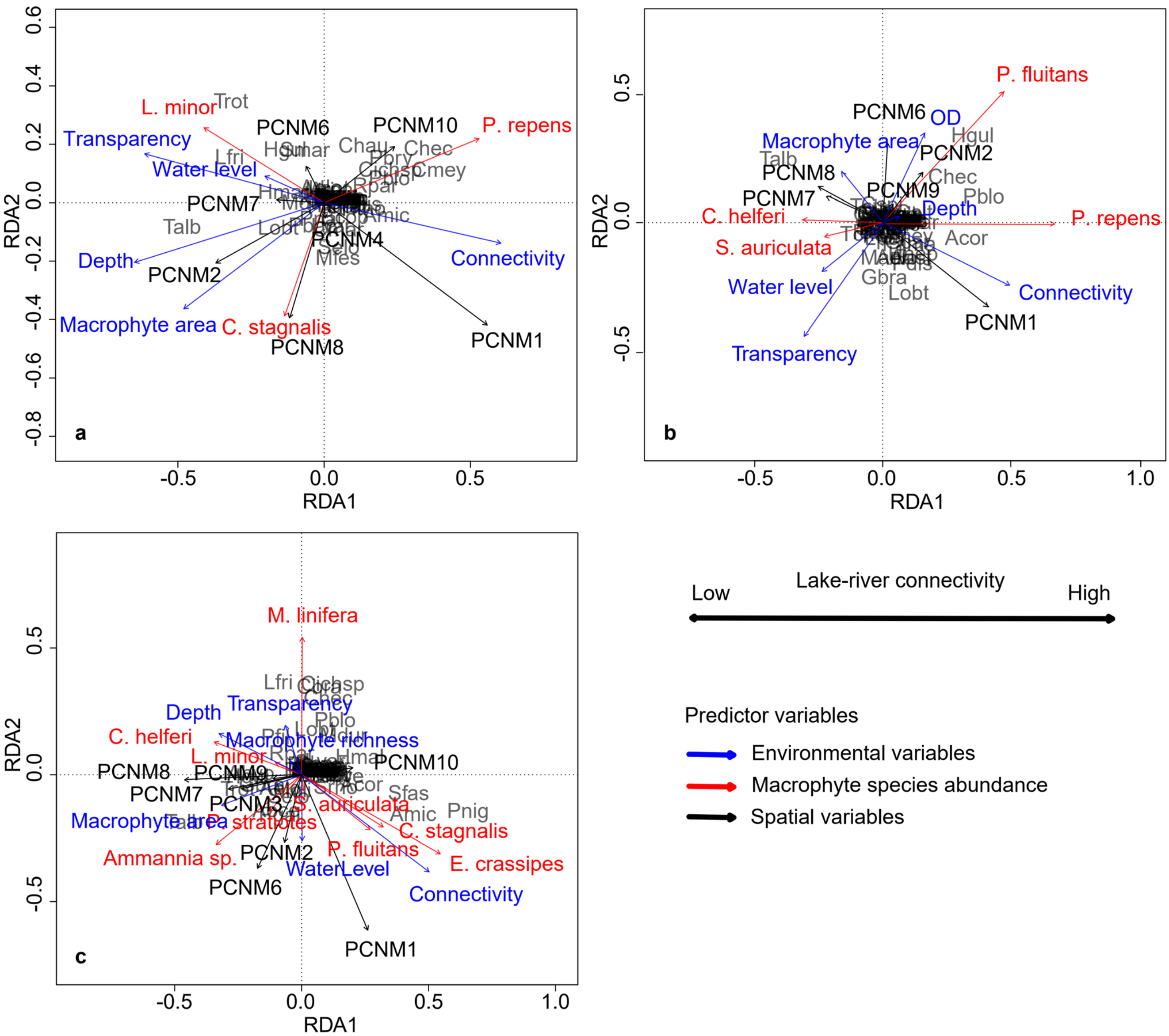

Fig. 3 Redundancy analysis (RDA) indicating the relationship between fish species composition and spatial, environmental and macrophyte factors in lake environments. **a** Flood; **b** receding; **c** drought

Souza and Chao 2004). Thus, we assume that fish communities in these environments tend to adjust by choosing macrophyte rafts with specific environmental conditions.

The variables hydrological connectivity, transparency, macrophyte rafts area, depth, water level and dissolved oxygen were extremely important for the variation of the fish community in this low-water period. The influence of the depth of the lakes on the fish community during receding waters reflects the importance of a local component in the distribution of the species, since it directly regulates several environmental factors, such as the dissolved oxygen and transparency of the water (Winemiller et al. 2000; Miranda 2011; Miranda and Hodges 2000). Water transparency can promote some fish species to seek hiding places among the roots of the macrophyte rafts. Because this local environmental component can favor predators visually capable of finding their prey, some species of fish may seek shelter in these environments as a way to avoid predation (Feyrer et al. 2004; Scarabotti et al. 2011).

Dissolved oxygen, on the other hand, may be a determining factor in the distribution of fish species among microhabitats, and may have been an important limiting factor in the occurrence of some species associated with macrophyte rafts, especially in paleopotamon lakes, where oxygen decreased during this period of receding waters. According to Jedicke et al. (1989), vegetation banks composed of species of floating macrophytes, such as *Pistia stratiotes* and *E. crassipes*, which also predominated in the present study, can release oxygen through their roots and thus benefit the fish in the period of hydrological disconnection. According to Saint-Paul and Soares (1987), certain species of fish also remain immobile under macrophytes to conserve energy during periods when the oxygen level in the lake is low. The macrophyte rafts area was also an environmental factor that influenced the fish community, and it is also responsible for the oxygenation of the water; many species of fish seek areas with medium vegetation cover, so that there are adequate levels of oxygen and, consequently, an area for shelter and foraging (Granzotti et al. 2019).

During the drought period, the composition of macrophytes was what most influenced the fish community in the lakes. This is a period in which the fish are somewhat isolated in the lakes, some reproduce in the banks, and that is when competition increases. Thus, the choice of macrophyte rafts with certain species of macrophytes (e.g., *E. crassipes*, *Ammannia* sp., *M. linifera*, *Callitriche stagnalis*, *L. minor*, *Pistia stratiotes*, *Salvinia auriculata*, *Cyperus helferi* and *Phyllanthus fluitans*) can reduce competition and increase fitness. In all hydrological cycles studied, both spatially structured environmental conditions and spatially structured macrophyte rafts were also important in explaining the variation in fish composition, in which spatial variables at various scales were also included. This may be due to the fact that macrophyte rafts form aggregates of macrophyte species that create specific conditions, and this occurs both within the same lake and between lakes. Thus, aquatic macrophytes can create different components of heterogeneity, as well as different habitats for aquatic organisms (Dibble and Thomaz 2006; Dibble and Pelicice 2010; Dias et al. 2017; Lusardi et al. 2018). Many species of macrophytes may have dense roots, submerged stems and leaves, thus providing structural complexity, availability of food and shelter in the fish community (Grenouillet et al. 2002; Padial et al. 2009).

Thus, it is possible to conclude from the results presented that the complexity of macrophytes combined with environmental and spatial variation, caused by the flood pulse, are capable of influencing the fish community in the lakes. Accordingly, due to the great importance of the relationship between macrophytes and fish, it is essential that the conservation of these macrophyte communities becomes a priority in management and conservation projects to maintain a high diversity of fish species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11756-021-00747-4.

Author contributions Lucena Rocha Virgilio and Lisandro J S. Vieira conceptualized and designed the study and assembled and organized the data. Lucena Rocha Virgilio and João C. B. Silva analyzed and interpreted the data and drafted the article. Monik Oliveira da Suçuarana was involved in critical revision of the article for important intellectual content.

Declarations

Conflict of interest The authors declare no conflict of interest.

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