

# Fish assemblage dynamics in a Neotropical floodplain relative to aquatic macrophytes and the homogenizing effect of a flood pulse

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**Abstract** The presence of aquatic macrophytes is a key factor in the selection of habitats by fish in floodplain lakes because these plants enhance the physical and biological complexities of aquatic habitats. The seasonal flood pulse may influence this interaction, but there is no information in the literature about the effects that flood events may have on macrophytes assemblages and its associated effects on fish assemblages. Thus, this article

aimed to investigate whether species richness, evenness and similarities in fish assemblage composition differed between littoral areas vegetated with macrophytes and unvegetated areas, before and after a flood. We sampled three lakes in the floodplain of the upper Paraná River basin. Sampling was conducted before (December 2004 and January 2005) and after (early March, late March and May 2005) a flood event. Overall, species richness and evenness were higher in macrophytes-covered areas. Before the flood, the composition of fish assemblages was distinct when comparing vegetated and unvegetated areas. After the flood, the similarity in fish assemblage composition was higher, indicating a homogenization effect of floods for fish inhabiting littoral areas of floodplain lakes. After the flood, opportunistic species dominated the fish assemblages in aquatic macrophytes, apparently restructuring assemblages in the littoral, restarting a succession process. Thus, the observed homogenization effect of the flood could minimize biological interactions and could induce fish assemblages to begin a new process of structurization.

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## Introduction

Aquatic vegetation leads to a more complex habitat physical structure and more patchy littoral areas

(Savino & Stein, 1989; Dibble et al., 1996; Petr, 2000; Dibble & Thomaz, 2009). Diverse macrophytes stands create a mosaic of littoral microhabitats that can sustain diverse biotic assemblages (Benson & Magnuson, 1992; Weaver et al., 1997; Grenouillet et al., 2000; Petry et al., 2003), especially on river-floodplain systems (Thomaz et al., 2004, 2009). In tropical and subtropical floodplain lakes, the complexity provided by free-floating macrophytes appears to be as important as submersed ones (Bonetto et al., 1969; Meerhoff et al., 2003).

The presence of aquatic macrophytes is a key factor in the selection of habitats by fish (Chick & McIvor, 1994, 1997; Grenouillet et al., 2000). Several studies identify three main mechanisms to explain fish-plant interactions in aquatic environments. First, forage fish species and juveniles (including those of large migratory species) use macrophytes as refuge to avoid predators (Savino & Stein, 1989; Chick & McIvor, 1994, 1997; Warfe & Barmuta, 2004). Second, macrophytes are used directly as food or indirectly as a source for periphyton and associated invertebrate prey (Rozas & Odum, 1988; Grenouillet & Pont, 2001; Casatti et al., 2003; Padial et al., 2009a). Third, macrophytes are used as spawning habitat, a place where nests are constructed, and as nurseries for initial life stages and juveniles (Dibble et al., 1996; Grenouillet & Pont, 2001; Sánchez-Botero & Araújo-Lima, 2001; Crampton & Hopkins, 2005; Bulla et al., 2011).

Despite the importance of vegetated areas in floodplain ecosystems, they are often not included in fish surveys, which usually give emphasis to unvegetated littoral areas. The main reason for this exclusion appears to be that non-vegetated sites are easier to sample with most gears. However, information on the interaction between fish and aquatic macrophytes is necessary for management of both assemblages (Thomaz & Bini, 2003), and this information is particularly scarce in the Neotropical realm (Agostinho et al., 2003; Pelicice et al., 2005; Agostinho et al., 2007; Thomaz et al., 2009). In Neotropical floodplains, several studies have addressed fish-plant interactions (Junk, 1973; Sazima & Zamprogno, 1985; Araújo-Lima et al., 1986; Delariva et al., 1994; Henderson & Hamilton, 1995; Meschiatti et al., 2000; Sánchez-Botero & Araújo-Lima, 2001; Agostinho et al., 2003; Petry et al., 2003; Pelicice et al., 2005; Agostinho et al., 2007). However, there is no information in the literature about the effects that flood

events may have on macrophytes assemblages and the associated effects on fish assemblages.

Although the Paraná River is intensely regulated by dams, the flood pulse is still the main force function structuring biological assemblages (Agostinho et al., 2000, 2009). In this study, we compared the ichthyofauna of littoral areas (unvegetated and vegetated with macrophytes) of lakes in the upper Paraná River floodplain in relation to the seasonal flood pulse. We hypothesized that the structural complexity afforded by aquatic macrophytes produces substantial differences in fish assemblages along a hydrological cycle, but that these differences would be blurred by the homogenizing effect of a flood pulse (*sensu* Thomaz et al., 2007). Specifically, we investigated whether fish species richness, evenness, and assemblage composition of unvegetated and vegetated littoral areas became more similar after a flood.

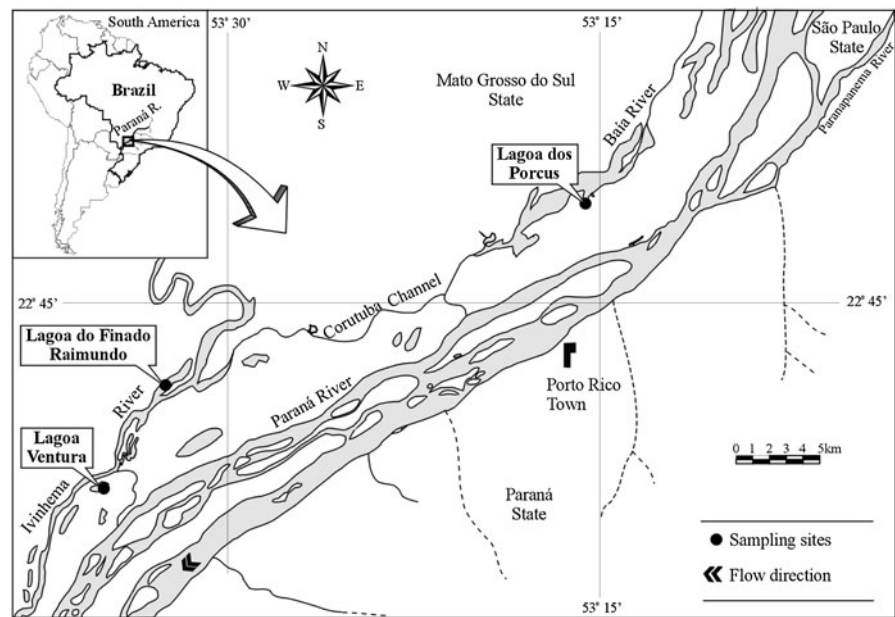
## Materials and methods

### Area of study

The Paraná River is the tenth largest river in discharge and the fourth in drainage area in the world ( $5.0 \times 10^8 \text{ m}^3 \text{ year}^{-1}$ ;  $2.8 \times 10^6 \text{ km}^2$ , respectively). It drains most of the central-south region of South America; from the Andes to the Serra do Mar near the Atlantic Ocean. Despite being highly regulated, the upper Paraná (above the Itaipu Dam) still sustains a great biological diversity, specially on its west (right) margin (Agostinho et al., 2007), between Porto Primavera Dam and Itaipu Reservoir, which represents the last lotic stretch of this river and where the upper Paraná floodplain is located. In this 230-km stretch, the upper Paraná floodplain may reach 20 km in width, with numerous secondary channels, lakes, and several tributaries including the Baía River and the lower reaches of the Ivaí and Ivinhema rivers (Fig. 1).

In this region, the Paraná River channel is anastomized, with low slope and several longitudinal and transversal bars, big islands, and the associated floodplains. There are numerous lakes (temporary and permanent) in the floodplain, filled by groundwater or by over spill of the Paraná or its tributaries. For this study, we selected three upper Paraná floodplain lakes; two located near the Ivinhema River (Ventura and Finado Raimundo lakes) and the other near the

**Fig. 1** Map of the upper Paraná River floodplain showing the sample sites (floodplain lakes) in the Ivinhema and Baía rivers, Mato Grosso do Sul State, Brazil



Baía River (Porcos Lake), all of them partly covered with macrophytes (over 30% of the area of each lake). These lakes were targeted because they were accessible and represented a broad spectrum of physical characteristics observed in the floodplain.

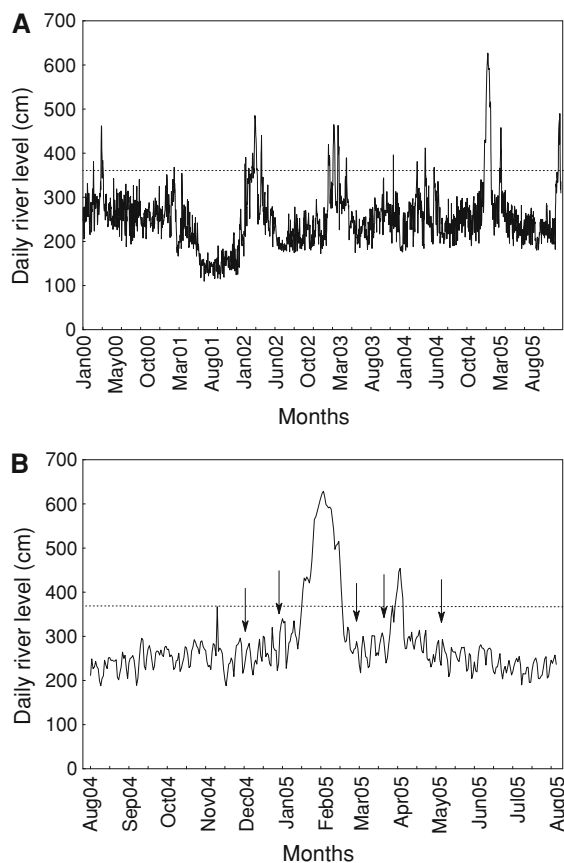
Ventura Lake ( $22^{\circ}51'23.7''\text{S}$ ;  $53^{\circ}36'1.02''\text{W}$ ) is located 200 m from the Ivinhema River (in its eastern, left, margin), separated only by a short (around 30 m long) 3-m high natural levee, and connects periodically to the river. The shape of the lake is elongated, extending 2085 m in length, with an area of 89.8 ha, a perimeter of 4697 m, and mean depth of 2.16 m. Finado Raimundo Lake ( $22^{\circ}47'57.6''\text{S}$ ;  $53^{\circ}32'29.16''\text{W}$ ) is permanently connected to the Ivinhema River (western, right, margin) by a 50-m long and 20-m wide channel. The natural levee near this lake is 1-m high. The lake is also elongated, extending 2919 m in length, with an area of 84.9 ha, a perimeter of 7151 m, and mean depth of 3.2 m. Porcos Lake ( $22^{\circ}42'4.44''\text{S}$ ;  $53^{\circ}14'40.08''\text{W}$ ) is permanently connected to the Baía River through a 60-m wide opening. It is also elongated, extending 781 m in length, with an area of 6.2 ha, a perimeter of 1283 m, and mean depth of 2.3 m. Its margins are 1 m above river level.

The region is affected by annual flood pulses associated with the wet season that may extend for several months. Flooding usually starts in early December and may last until June. During this period,

there may be 2–3 flood peaks. However, intensity of floods varies annually. The flood pulse investigated in this study occurred in February 2005, was the largest in a 6-year period between 2000 and 2005 (Fig. 2A), represented an increase in water level that reached 628.5 cm (measured near the city of Porto Rico, Paraná State, Brazil), and stayed above 400 cm for over 1 month (Fig. 2B). This flood inundated the entire floodplain, completely covering the study lakes and producing flow through them. Floods of this magnitude or higher have been rare in the region since the completion of Porto Primavera Dam in 1998, and have occurred only in 1999 and 2007 (Souza-Filho, 2009).

### Sampling

The three lakes were sampled in December, 2004 and January (before the flood), early March, late March, and May, 2005 (after the flood), between 0730 and 1130 h, over 4-d periods. The ichthyofaunas in macrophytes mats (dominated by  $\geq 80\%$  water hyacinth *Eichhornia crassipes*, with low percentages of *Limnobium laevigatum*, *Pistia stratiotes*, *Ricciocarpus natans*, *Salvinia auriculata*, *Salvinia herzogii*, *Salvinia minima*, all free floating; *Eichhornia azurea*, *Hydrocotyle ranunculoides*, *Oxycaryum cubense*, *Polygonum* spp, all emergent; *Cabomba furcata*,



**Fig. 2** Daily water levels of the Paraná River measured near the city of Porto Rico, Paraná State, Brazil, from 2000 to 2005 (A) and details of the studied flood (B). Dotted line indicate Paraná River bank overflow (from Agostinho et al., 2004). Arrows indicate date of sampling

*Egeria* spp., rooted and submersed; *Nymphaea amazonum* which is rooted with floating leaves and *Utricularia* spp., a free submersed; Thomaz et al., 2004) were sampled with a sieve and those of littoral areas devoid of macrophytes with a seine. The sieve had a rectangular metal frame (1.5 × 1.0 m) with a 500- $\mu$ m mesh net, following Nakatani et al. (2001). It was pushed under macrophytes and swiftly lifted to the surface to trap fish and macrophytes. Once the sieve was lifted above the water surface, aquatic plants were identified to species and discarded. The seine was 10-m long, 3-m high, with 500- $\mu$ m mesh. This gear was operated by sweeping a semi-circle next to shore. For every lake and month, we sampled three unvegetated and three vegetated areas, except in early March at Ventura Lake where only two unvegetated areas were sampled. At each sampling location we recorded

water temperature ( $^{\circ}$ C), pH, dissolved oxygen ( $\text{mg l}^{-1}$ ), and specific conductance ( $\mu\text{S cm}^{-1}$ ) using portable meters (in vegetated areas, abiotic variables were measured at the edge of the macrophytes mat). All fish were preserved in 4% formalin buffered with calcium carbonate. At the laboratory juveniles and adults were identified based on Graça & Pavanelli (2007) and larvae according to Nakatani et al. (2001).

The sieve and seine used in our study have potentially distinct catch efficiencies, to the extent that total catches are not directly comparable. Considering this limitation, our comparisons focused on percentage composition of species instead of absolute abundance, and on change in similarity rather than on change in absolute composition. Because our hypothesis was that fish assemblages in unvegetated and vegetated littoral areas became more similar after the flood, detection of a statistically significant increase in similarity can logically be construed as an effect of the flood as the selectivities of the gears are likely to stay constant before and after the flood.

#### Data analyses

The percentage composition matrices of the species (one before and another after the flood; controlling lakes and samples) were used to calculate species richness and evenness using PC-ORD v.4.01 (McCune & Mefford, 1999). Differences among the factors (Area: vegetated and unvegetated; Lake—Porcos, Finado Raimundo and Ventura) and their interaction were determined using permutational multivariate analyses of variance (PERMANOVA), applied on Euclidean resemblance matrices (Anderson, 2008).

Nonmetric multidimensional scaling (NMS) was applied to summarize patterns in similarities of the fish assemblage relative to study areas (vegetated, unvegetated) and lakes (Porcos, Finado Raimundo, Ventura), separated in relation to the flood (before, after). The NMS was applied to species abundance data relativized by the total count of fish collected in the sample (percentage composition), and using the Bray-Curtis coefficient as the resemblance measure. PERMANOVA was applied to test differences in fish assemblages relative to the factors Area and Lake, as well as their interaction. The PERMANOVA considered the samples of each lake, before the flood (December 2004 and January 2005) as replicates (six for each lake and sampled area; total of 36 samples).

**Table 1** Mean monthly values ( $n = 3$ ) and standard deviations (between parentheses) of the abiotic variables measured in the vegetated (VEG) and unvegetated (UNV) areas of the three studied floodplain lakes

Lake sample (month)	Water temperature (°C)		pH		Specific conductance ( $\mu\text{S cm}^{-1}$ )		Dissolved oxygen ( $\text{mg l}^{-1}$ )	
	VEG	UNV	VEG	UNV	VEG	UNV	VEG	UNV
<b>Ventura</b>								
December	27.0 (0.0)	26.8 (0.1)	6.3 (0.0)	6.8 (0.1)	36.0 (0.0)	34.1 (0.2)	5.7 (0.0)	5.7 (0.0)
January	28.4 (0.2)	28.6 (0.1)	5.8 (0.2)	5.9 (0.1)	34.9 (0.6)	34.7 (0.6)	6.2 (0.2)	6.1 (0.1)
March 1	29.7 (0.1)	29.7 (0.0)	6.8 (0.0)	6.9 (0.0)	55.3 (0.4)	54.9 (0.1)	4.4 (0.1)	4.2 (0.1)
March 2	26.7 (0.2)	27.6 (0.2)	6.9 (0.3)	7.2 (0.0)	33.2 (2.9)	32.9 (3.0)	6.2 (0.1)	6.5 (0.0)
May	22.9 (0.1)	23.1 (0.1)	6.5 (0.1)	6.9 (0.2)	50.4 (0.8)	48.8 (0.4)	6.5 (0.5)	7.3 (0.0)
Mean	26.9	27.2	6.5	6.7	42.0	41.1	5.8	6.0
<b>Finado Raimundo</b>								
December	27.5 (0.1)	27.4 (0.0)	6.8 (0.1)	6.8 (0.0)	32.5 (0.4)	33.4 (0.4)	4.8 (0.4)	4.7 (0.2)
January	27.7 (0.0)	27.7 (0.1)	5.7 (0.1)	5.6 (0.0)	34.8 (0.3)	34.6 (0.4)	3.9 (0.0)	3.8 (0.2)
March 1	29.5 (0.1)	29.8 (0.1)	7.0 (0.1)	7.3 (0.0)	57.4 (2.3)	60.8 (0.7)	4.9 (0.6)	5.5 (0.1)
March 2	28.2 (0.2)	28.1 (0.1)	7.2 (0.1)	7.2 (0.0)	32.4 (1.1)	32.4 (0.7)	6.0 (0.1)	6.0 (0.0)
May	24.7 (0.1)	24.2 (0.1)	6.3 (0.1)	6.3 (0.2)	44.6 (0.5)	45.2 (1.7)	6.7 (0.0)	6.7 (0.2)
Mean	27.5	27.4	6.6	6.6	40.3	41.3	5.3	5.3
<b>Porcos</b>								
December	27.3 (0.1)	27.3 (0.1)	6.1 (0.1)	6.1 (0.0)	29.8 (0.8)	29.4 (0.5)	4.1 (0.2)	4.1 (0.1)
January	28.0 (0.5)	28.2 (0.3)	5.3 (0.1)	5.4 (0.3)	25.5 (1.1)	26.4 (3.0)	2.6 (0.0)	2.5 (0.5)
March 1	28.4 (0.1)	28.4 (0.1)	6.5 (0.0)	6.4 (0.0)	46.1 (1.2)	45.5 (0.8)	2.8 (0.3)	2.7 (0.3)
March 2	28.2 (0.1)	27.8 (0.2)	8.5 (0.2)	8.7 (0.1)	33.9 (5.4)	32.8 (0.4)	8.1 (0.2)	8.8 (0.1)
May	23.7 (0.2)	23.9 (0.2)	5.5 (0.1)	5.5 (0.0)	30.0 (2.3)	28.8 (0.3)	4.3 (1.2)	4.8 (0.3)
Mean	27.1	27.1	6.4	6.4	33.1	32.6	4.4	4.6
Grand mean	27.2	27.2	6.5	6.6	38.5	38.3	5.1	5.3

After the flood (early and late March and May 2005), number of samples was 53. We used Monte Carlo permutations ( $N = 999$ ) of the similarity matrix to test for statistical significance at  $P \leq 0.05$ . We used the Type III error of PERMANOVA to determine significance (Anderson, 2008), due to the imbalance on our sampling design (only two samples in Ventura Lake in early March). The most influential species associated with each ordination axis were identified by examining the correlation (Spearman rank correlation,  $\rho$ ; STATISTICA 7.1) between species relative abundance and axes scores. We also determined the average similarity between unvegetated and vegetated areas for each lake (to evaluate possible distinct trends between them) and the distance between the centroids for unvegetated and vegetated areas before and after the flood, separately. The NMS, PERMANOVA, average similarities and distance between centroids procedures were implemented using PRIMER version

6 with the PERMANOVA+ add-on package (Clarke & Gorley, 2006; Anderson, 2008).

## Results

### Abiotic variables

Mean water temperature and pH were similar among the lakes during all sampling periods. However, mean specific conductance and dissolved oxygen were lower in Porcos Lake when compared to Ventura and Finado Raimundo lakes (Table 1). These two latter lakes belong to the Ivinhema River, which typically has greater specific conductance than the Baía River, where Porcos Lake is located (Roberto et al., 2009). However, the physicochemical conditions recorded were not restrictive to most fish species, except dissolved oxygen in Porcos (January and March 1)



and Finado Raimundo (January; average values  $< 4.0 \text{ mg l}^{-1}$ ; Table 1) lakes; values  $< 4.0 \text{ mg l}^{-1}$  may influence fish assemblages (Matthews, 1998).

### Ichthyofauna survey

We collected 15,426 fish, belonging to seven orders, 23 families, 47 genera and at least 59 fish species (some with taxonomic status still unresolved; Appendix 1—Electronic supplementary material). In vegetated areas, we collected 4,095 individuals of seven orders, belonging to at least 21 families, 40 genera and at least 51 species. In unvegetated areas, we collected 11,331 individuals of five orders, 15 families, 31 genera and at least 40 species.

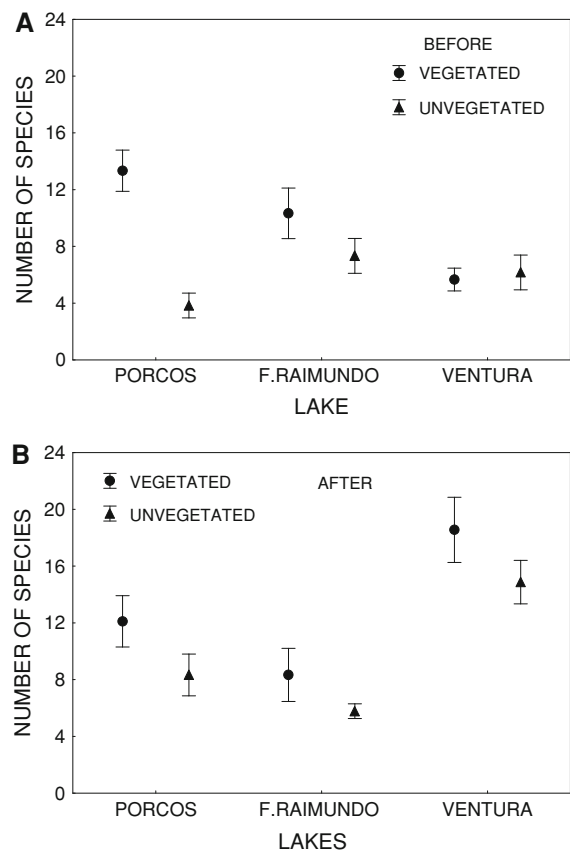
The most commonly collected taxa in vegetation samples were *Serrasalmus* spp. and *Serrapinus notomelas*, whereas in unvegetated samples, the most commonly collected species were *Cichla kelberi* (peacock bass, introduced from the Amazon basin) and *Astyanax altiparanae*. Species only captured before the flood were *Catathyridium jenynsii* (vegetated and unvegetated), *Hoplias* spp. (vegetated), and *Sternopygus macrurus* (vegetated). However, several species were captured only after the flood; for vegetated areas, we registered *Characidium* sp., *Cichlasoma paranaense*, *Hypostomus ancistroides*, *Hoplosternum littorale*, *Hoplias* sp2, *Oxydoras eigenmanni*, *Pseudoplatystoma corruscans*, *Schizodon* sp., *Serrapinus* sp2, and *Trachydoras paraguayensis*. For unvegetated areas, we captured *Hoplias* sp3, *Leporellus vittatus*, and *Odontostilbe* sp. In both habitat types, we captured *Characidium zebra*, *Leporinus lacustris*, *Leporinus obtusidens*, *Metynnis maculatus*, *Pimelodella avanhandavae*, *Pimelodella gracilis*, *Prochilodus lineatus*, *Schizodon borellii*, and *Leporinus* sp.

Several other species were captured before and after the flood, but only in one of the habitats sampled. This indicates that several species may have preferences for either vegetated or unvegetated areas. For unvegetated areas, these species included *Apareiodon affinis*, *Acestrorhynchus lacustris*, *Bryconamericus stramineus*, *C. kelberi*, *L. vittatus* and *Satanoperca papaterra*. For vegetated areas, they included *Brachyhypopomus pinnicaudatus*, *Crenicichla britskii*, *Gymnotus inaequilabiatus*, *Gymnotus* sp., *Hoplerythrinus unitaeniatus*, *Hyphessobrycon* spp., *Laetacara* sp., *Rivulus apiamici*, *Rhamphichthys hahni*, *Rhamdia quelen* and *Synbranchus marmoratus*. In all, nine taxa

were captured only in unvegetated areas whereas 23 taxa were captured only in vegetated areas (Appendix 1—Electronic supplementary material).

### Variations in species richness and evenness

Overall, mean species richness per sample was greater for vegetated areas, except for Ventura Lake before the flood (Fig. 3). The PERMANOVA identified a significant interaction for species richness before the flood (Pseudo  $F = 7.93$ ;  $P = 0.03$ ), indicating distinct trends among sites. A post-hoc comparison of the interaction showed differences between unvegetated and vegetated areas only for Porcos Lake ( $P = 0.007$ ; Fig. 3A). However, after the flood, the interaction was not significant (Pseudo  $F = 0.08$ ;  $P = 0.91$ ) and the factors Lake (Porcos, Finado Raimundo, Ventura) and Area (vegetated, unvegetated) were statistically significant (Pseudo  $F > 5.8$ ;  $P < 0.03$ ). A post-hoc



**Fig. 3** Variations in mean species richness ( $\pm$ standard error) for vegetated and unvegetated areas of the studied lakes before (A) and after (B) the flood ( $N = 6$  before;  $N = 9$  after)

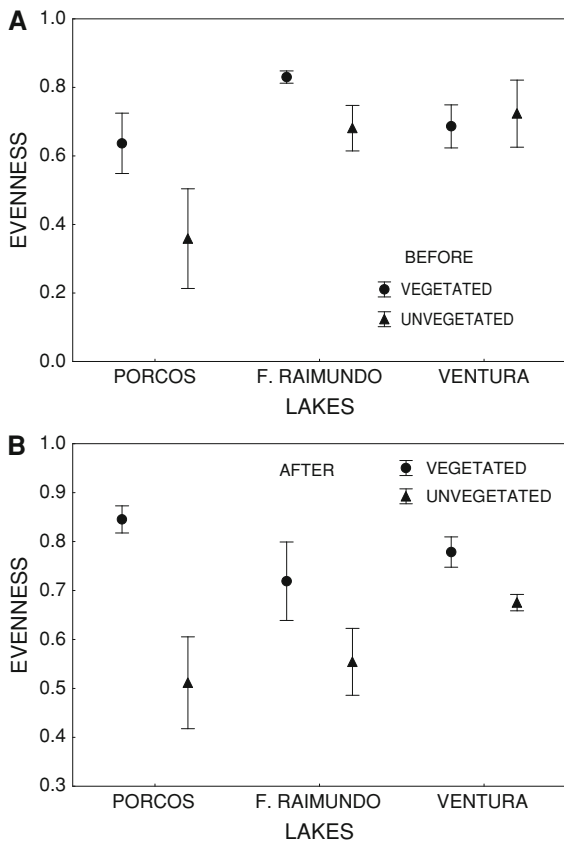
comparison also identified differences between the three lakes ( $P < 0.04$ ; Fig. 3B).

Evenness presented distinct trends before and after the flood, with lower values in the unvegetated areas before the flood in Porcos Lake and after the flood in all lakes (Fig. 4). The PERMANOVA identified significant differences for the Lake factor before the flood (Pseudo  $F = 4.75$ ;  $P = 0.01$ ), whereas the Area factor (Pseudo  $F = 3.23$ ;  $P = 0.09$ ) and the Lake X Area interaction (Pseudo  $F < 1.60$ ;  $P > 0.20$ ) were not significant. Porcos Lake differed from Finado Raimundo (Post-hoc;  $P = 0.01$ ; Fig. 4A) and the other comparisons were not significant (Porcos  $\times$  Ventura:  $P = 0.06$ ; Finado Raimundo  $\times$  Ventura:  $P = 0.46$ ). After the flood, the effect of area was significant (Pseudo  $F = 15.90$ ;  $P = 0.01$ ), with higher values of evenness in the vegetated sites. Lakes (Pseudo  $F = 1.06$ ;  $P = 0.34$ ) and the Lake X Area

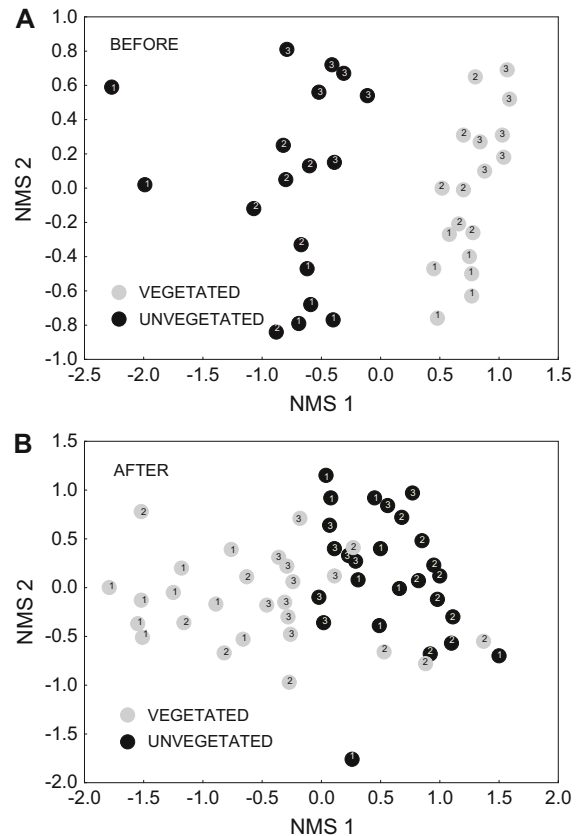
interaction (Pseudo  $F = 1.88$ ;  $P = 0.15$ ) were not significant.

Similarities in assemblage composition

Before the flood, there was a clear separation of the fish assemblages in vegetated and unvegetated areas (Fig. 5A). The PERMANOVA identified significant differences for both factors (Lake: Pseudo  $F = 5.14$ ;  $P = 0.01$ ; Area: Pseudo  $F = 16.69$ ;  $P = 0.01$ ) and their interaction (Pseudo  $F = 4.78$ ;  $P = 0.001$ ). A post-hoc comparison in the interaction revealed significant differences for all lakes for vegetated ( $P < 0.02$ ) and unvegetated ( $P < 0.02$ ) areas. Average similarities between unvegetated and vegetated areas, before the flood, were 2.55% for Porcos Lake,



**Fig. 4** Variations in mean evenness (±standard error) for the vegetated and unvegetated areas of the studied lakes before (A) and after (B) the flood ( $N = 6$  before—December 04, January 05;  $N = 9$  after—early and late March 05, May 05)



**Fig. 5** Ordination of the two axis generated by the nonmetric multidimensional scaling (NMS) applied to the fish relative abundance data matrix of vegetated and unvegetated areas, collected before (A: December 04 and January 05) and after (B: early and late March 05, May 05) the flood. The numbers inside circles identify lakes (1 Porcos, 2 Finado Raimundo, 3 Ventura)

2.17% for Finado Raimundo, and 4.50% for Ventura. The distance between centroids for unvegetated and vegetated areas before the flood was 61.80.

Species positively correlated with axis 1 (*Pterygoplichthys anisitsi* (Spearman  $\rho = 0.81$ ), Gymnotidae ( $\rho = 0.65$ ), *S. marmoratus* ( $\rho = 0.49$ ), *Eigenmannia trilineata* ( $\rho = 0.48$ ), *Hoplias* spp. ( $\rho = 0.45$ ), and *Serrasalmus* spp. ( $\rho = 0.45$ )) were proportionally better represented in vegetated areas (samples in the right side of Fig. 5A), whereas those with negative correlations (*Astyanax altiparanae* ( $\rho = -0.59$ ), *Aphyocharax dentatus* ( $\rho = -0.48$ ), *Bryconamericus stramineus* ( $\rho = -0.44$ ), *C. kelberi* ( $\rho = -0.42$ ), and *Hyphessobrycon* sp. ( $\rho = -0.40$ )) were more common in unvegetated areas (samples in the left side of Fig. 5A; Appendix 1—Electronic supplementary material). For axis 2, species positively correlated (*Hyphessobrycon* sp. ( $\rho = 0.42$ ), *Serrasalmus marginatus* ( $\rho = 0.42$ )) were more prominently represented in Ventura Lake (upper part of Fig. 5A), whereas those negatively correlated (*Moenkhausia sanctaefilomenae* ( $\rho = -0.58$ ), *A. altiparanae* ( $\rho = -0.43$ ), *Hoplias* sp1 ( $\rho = -0.42$ ), *R. apiamici* ( $\rho = -0.45$ ), and *Serrasalmus* spp. ( $\rho = -0.40$ )) were more prominently represented in Porcos Lake and some samples at Finado Raimundo Lake (lower part of Fig. 5A; Appendix 1—Electronic supplementary material).

After the flood, ordination showed that there was a separation of the fish assemblage in vegetated and unvegetated areas of the floodplain lakes, but with some overlap (Fig. 5B). The PERMANOVA identified significant differences for both factors (Lake: Pseudo  $F = 6.92$ ;  $P = 0.001$ ; Area: Pseudo  $F = 12.48$ ;  $P = 0.001$ ) and their interaction (Pseudo  $F = 2.82$ ;  $P = 0.001$ ). A post-hoc comparison revealed significant differences for all lakes for vegetated ( $P < 0.01$ ) and unvegetated ( $P < 0.03$ ) areas. After the floods, mean similarity between unvegetated and vegetated areas for the lakes increased. For Porcos Lake mean similarity was 6.67%, for Finado Raimundo was 23.21%, and for Ventura Lake was 31.80%. The distance between centroids between unvegetated and vegetated areas after the flood was 45.33.

Species positively correlated with axis 1 (*A. anisitsi* (Spearman  $\rho = 0.76$ ), *A. altiparanae* ( $\rho = 0.42$ )) were more abundant in unvegetated areas (right side of Fig. 5B; Appendix 1—Electronic supplementary

material), whereas those with negative correlation (*B. pinnicaudatus* ( $\rho = -0.76$ ), *Laetacara* sp. ( $\rho = -0.75$ ), *P. australis* ( $\rho = -0.70$ ), *G. inaequilabiatus* ( $\rho = -0.64$ ), *Parauchenipterus galeatus* ( $\rho = -0.59$ ), *S. marmoratus* ( $\rho = -0.53$ ), *E. trilineata* ( $\rho = -0.51$ ), *R. apiamici* ( $\rho = -0.48$ ), *Hoplias* sp1 ( $\rho = -0.44$ ), and *P. anisitsi* ( $\rho = -0.41$ )) were more abundant in vegetated areas (left side of Fig. 5B; Appendix 1—Electronic supplementary material). For axis 2, species positively correlated (*A. altiparanae* ( $\rho = 0.72$ ), *Steindachnerina brevipinna* ( $\rho = 0.44$ ), and *S. insculpta* ( $\rho = 0.44$ )) were more prominently represented in samples of Porcos Lake (upper part of Fig. 5B; Appendix 1—Electronic supplementary material), whereas the one negatively correlated (*A. anisitsi* ( $\rho = -0.40$ )) was more prominently in Finado Raimundo Lake (lower part of Fig. 5B; Appendix 1—Electronic supplementary material).

## Discussion

The upper Paraná River basin sustains a high diversity of aquatic fauna and flora, both in number of species and functional groups (Agostinho et al., 2000). However, little is known about the ecological aspects of the interaction between macrophytes and fish in this region (Agostinho et al., 2003, 2007; Pelicice et al., 2005; Padial et al., 2009b), or how this interaction is moderated by floods, possibly the principal environmental driver in this ecosystem. According to Rossi & Parma de Croux (1992), the limited attention given to the interplay between aquatic vegetation and fish in the Paraná River basin does not match the ecological importance of this interaction. Some studies conducted in lakes of the upper Paraná River floodplain have reported that macrophytes cover is an important factor explaining the structure of fish assemblages (Delariva et al., 1994; Okada et al., 2003; Agostinho et al., 2004). Suárez et al. (2001, 2004) confirmed that macrophytes cover was one of the main factors structuring the fish fauna, determining the abundance of the main fish species in lakes of the Pantanal floodplain (Brazil).

Stands of macrophytes and areas without these plants shared in common 54% of the species captured in the study lakes. A mechanism for this commonality could be the movements of fish between macrophytes stands and open waters (including unvegetated areas)



in these lakes, and the fact that many of these fish species are habitat generalists. A daily cycle in the use of these habitats by prey species suggest that they may avoid diurnal predation by seeking shelter in macrophytes (Petry et al., 2003; Agostinho et al., 2007). Alternatively, ontogenetic variation may explain their occurrence in both habitats, with immature fish (larvae and juveniles) potentially found more frequently in macrophytes stands and adults found more frequently in open waters. Immature and adult stages of small-sized fish species and immature stages of medium and large-sized species in general, make up the fish assemblages associated with macrophytes. In this habitat, fish encounter a variety of food items and benefit from shelter against predators (Junk, 1973; Araújo-Lima et al., 1986; Delariva et al., 1994; Meschiatti et al., 2000; Sánchez-Botero & Araújo-Lima 2001; Agostinho et al., 2003; Pelicice et al., 2005).

Before the flood, we registered a higher representation by species that develop parental care (equilibrium strategy, sensu Winemiller, 2005), including the introduced *C. kelberi*. However, after the flood we registered greater representation by opportunistic species, especially in vegetated areas (such as *A. anisitsi*, *A. dentatus*, *A. altiparanae* and *S. notomelas*) all small Characiformes with short life cycles. These species are considered efficient colonizers of habitats immediately after a disturbance. In this sense, the flood pulse is considered the main natural seasonal forcing function responsible for maintaining the dynamics of aquatic communities in river–floodplain systems (Junk et al., 1989; Lowe-McConnell, 1999).

Thomaz et al. (2007) and Roberto et al. (2009) reported reduced limnological variability after floods in several environments of the upper Paraná River floodplain, suggesting that flood pulses homogenize aquatic environments. Like Thomaz et al. (2007), we found reduced variability among the assemblages captured in macrophytes stands after the flood, corroborating the homogenization factor. Therefore, with a flood, fish assemblages tend to undergo homogenization even if habitat structure may not change, which could minimize biological interactions and could induce an assemblage to begin a new process of structurization (Mouquet et al., 2003).

Another explanation for the temporal variation of the reproductive strategies in the fish assemblages is

the reduced availability of substrate (macrophytes) available for shelter. Floating macrophytes exhibit intense growth when water level is increasing, and during floods and when water is receding from the floodplain, they drift (sometimes as huge islands) following the water flow to main river corridors (Lowe-McConnell, 1999; Bulla et al., 2011). Sometimes these islands become stuck on the margins of lakes or rivers. The drift of floating macrophytes may result in a considerable reduction in biomass of these plants locally (Padial et al., 2009b) and, consequently, may decrease the structural complexity at local scales.

Our study confirmed the homogenization effect of floods, described by Thomaz et al. (2007), but this time on the species composition of fish inhabiting macrophytes stands in floodplain lakes. Several of the species found in macrophytes stands have complex life strategies, with parental care and nest construction. After the flood, however, we identified a restart of succession, as the representation of species with complex life strategies declined and that of opportunistic species increased. We also found high catches of larvae and juveniles of several fish species in macrophytes stands. This finding confirms that the shallow, macrophytes-covered, littoral areas of floodplain lakes are important spawning and nursery habitats for many species that inhabit the floodplain. In addition, considering distinct spatial (micro-scale: macrophytes stands) and temporal (before and after floods) scales, further understanding of the dynamics of fish assemblages in floodplain lakes of the upper Paraná River must also consider the complex relationships between these scales and the ontogeny of the fish; the identification of nursery areas (preferred lakes) in the floodplain; and the role of introduced species on the dynamics of fish assemblages in macrophytes stands. All these aspects appear to be important themes for further studies.

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