Espínola Luis A. (Orcid ID: 0000-0003-2479-3079)

Abrial Elie (Orcid ID: 0000-0003-4563-5512)

Rabuffetti Ana P. (Orcid ID: 0000-0003-0106-0876)

Blettler Martin C. (Orcid ID: 0000-0001-5837-5241)

Discrimination of hydrologic variations for spatial distribution of fish

assemblage in a large subtropical temperate river.

Authors: Luis A. Espínola[1], Elie Abrial[1], Ana P. Rabuffetti[1], Nadson R. Simões[2], Mario

L. Amsler[1], Martin C. M. Blettler[1], Maria F. Eurich[1], Aldo R. Paira[1]

Authors addresses:

[1]Instituto Nacional de Limnología (INALI, CONICET/UNL), Ciudad Universitaria,

Paraje El Pozo Santa Fe, Argentina.

[2]Centro de Formação em Ciências Ambientais, Universidade Federal do Sul da

Bahia, Brasil.

Abstract:

This study examines the effects of the flow and flood pulses on spatial dispersion of fish assemblages in the floodplain of the Paraná River in Argentina. We tested the hypothesis that high water levels and greater lateral connectivity promote fish dispersal and spatial homogenization of assemblage structure. We sampled four sites during different phases of the annual hydrologic cycle from 2010 to 2016. Water surface in the area was estimated during each phase. We computed multivariate statistics and estimates of ß-diversity to analyze assemblage variations in relation to hydrological phases. Three hydrological phases were defined: low flow pulses (water levels between 2.3 and 3.2, approximately 10% of the floodplain covered by water), high flow pulses(between 3.2 and 4.5, from 11 to 84%), and floods (> 4.5 m, more than 84%). Although difference between high flow pulses and flood was not significant, ß-diversity values for these stages were higher than for low flow pulses. This suggests that floods and high flow pulses increase the spatial variability of fish assemblages, whereas homogenization processes occur later during low flow periods. This work provides further knowledge about the flood homogenization effect in a large unregulated floodplain where lateral connectivity still plays a significant role on ecological structuring processes.

Introduction

Hydrological pulsing of tropical and subtropical rivers is a major ecological driver that can be characterized by three components: spatial and temporal variation of attributes (amplitude, frequency, time, duration, intensity), degree of induced hydrologic connectivity (between floodplain and main channel), and seasonality (alternations between sustained high and low water phases) (Poff & Ward, 1990; Neiff, 1990). Variations in these elements affect processes that influence the temporality of habitats and the spatial distribution of aquatic flora and fauna (Junk et al.,1989; Poff & Allan, 1995; Arrington et al., 2005; Espínola et al., 2016). So these processes require an analysis and understanding, not only of local influences but also the dispersal processes (Holyoak et al., 2005). These events have motivated fluvial ecologist, proposing different conceptual models to interpret patterns and dynamics of river-floodplain systems and its biota (See review by Humphries et al., 2014).

The Flow Pulse Concept (FPC) stresses the importance of periodic floods as the driving force in river-floodplain ecosystems because floods not only expand aquatic habitat, but also increase interactions between aquatic and terrestrial compartments with strong effects on processes such as nutrient cycling, primary and secondary production, and population dynamics of aquatic organisms (Junk et al.,1989). The Hydro-Sedimentological Pulse (HSP) model extends the FPC by highlighting the effect of the dry phase (limnophase) in promoting homeostasis in river-floodplain systems (Neiff, 1990). The Homogenizing Force of Flood Pulse model (HFFP) emphasizes how floods increase connectivity of aquatic habitats and thereby function as a regional driving force that homogenizes the aquatic assemblages (Thomaz et al., 2007). The River Wave Concept (RWC, Humphries et

al., 2014) characterizes the hydrological fluctuations as a series of water waves with varying intensity, amplitude, length and frequency that pass over fluvial landscapes both longitudinally and laterally. The timing of ascending or descending components of these waves is a major determinant of inter-annual hydrological variation. This variation affects the degree of connectivity and increases the water surface between the main channel and lentic environments of the floodplain, changing the spatial distributions and densities of fishes and other aquatic organisms (Amoros & Roux, 1988; Poff & Ward, 1989; Neiff, 1990; Tockner et al., 2000; Agostinho et al., 2004; Miranda, 2005; Espínola et al., 2016).

All of these conceptual models highlight the importance of the seasonal hydrological variation (high and low water) for ecological processes (Simões et al., 2013), and these relationships have been investigated in studies of fish assemblages throughout the world (eg Junk et al., 1989; Neiff, 1990; Wootton et al., 1996; Matthews & Marsh-Matthews, 2003, Bêche, et al., 2009, Röpke et al., 2015). However, the ecological processes occurring between high and low water variations (flow pulses; Puckridge et al., 1998 and Tockner et al., 2000) have been less well studied (e.g. processes related to fish assemblages; Espínola et al., 2016).

With focus on spatial variations of the fish community, the flood effect has been well studied in the literature, with particular emphasis on the flood or dry period (e.g. Penha et al. 2017; Cruz et al. 2018). However, as mentioned above for ecological processes, it is notable that a few information exists about the mechanisms taking place in the transition phases. Spatial variations can be assessed through ß-diversity, which is a measure of variation in species composition among habitat patches (Vellend 2001; Koleff et al. 2003). Moreover, ß-diversity can be used as a subsidiary to biodiversity conservation (Legendre et al. 2005; Symons

and Arnott 2013), because it quantifies biodiversity loss and may inform the placement of protected areas for management of biological resources (Socolar et al. 2016).

This paper deals with the effects of increasing water levels on the spatial distribution of fish assemblages inhabiting the floodplain of the Paraná River. It is the world's ninth largest river according to its mean annual discharge (18,000 m3 s-1; Latrubesse, 2008), and has a seasonal regimen (Neiff, 1990; Giacosa et al., 2000). The main channel, in Argentina, has built a large undammed floodplain over nearly 2,000 km (Hammerly, 2011). Our analyses focus on the spatial structuring of fish assemblages during the gradual rising and falling stages occurring between the two extremes (high and low waters). We examined the relationships between water levels, available flooded areas and fish assemblages in view of a better understanding of dispersion and homogenization processes into the floodplain. This study is an extension of the HFFP model, providing further knowledge about fish assemblage dynamics in large floodplains such as in the middle reach of the Paraná River.

Materials and methods

Study area

This study was conducted on a free course of the Paraná River known as the Middle Paraná River, whose plant configuration is typically an anabranch (Latrubesse 2008). The main channel presents a succession of narrowing and widening where it is divided into two or more arms separated by islands and/or banks formed by continuous erosive and deposition processes of varying intensity (Amsler and Drago 2009). This reach of the free flowing river has an alluvial plain of ≈20.000 km2, composed by a heterogeneous mosaic of lotic and lentic bodies that

vary in shapes and surfaces according to the variations of long and short term hydrology (Iriondo, 1988). Its wide is 10 km in Corrientes and is gradually increasing to 40 km at the apex of the delta located near Diamante (Entre Ríos State). The difference in height is 38 m from Resistencia (Chaco) to Diamante resulting in a very low slope of 6.33 x 10-5 (Paira, 2017).This immense floodplain consists of a mosaic anastomosis of different geomorphological units at slightly different elevations (Marchetti et al., 2013). The altitude of the floodplain can vary between 4 and 2 m from the height with respect to the main channel, which generates different levels of depth and permanence of the overflow during floods (Latrubesse, 2008).

The middle reach of the Paraná receives water from the main tributaries that still maintain relatively natural flow regimes, with a wide floodplain and a hydrological regime that has been minimally affected by dams and other human impacts, unlike the Upper Paraná River in Brazil. About 40 large dams are located in the upper reach, modifying the hydrological regime as well as their attributes (intensity, duration, etc., Rodrigues et al. 2005; Agostinho et al. 2007; Pereira et al. 2018).

In the Middle Paraná River, the low-water period usually occurs in August-September and levels may stay below 2.30 m at Santa Fe gauging station. During those conditions, most of the fluvial lakes in this area have no connection with the main channel (Paira & Drago, 2007; Abrial et al., 2019). The high-water period usually occurs during December-March, and levels attain or surpass 4.50 m. The alluvial plain is completely flooded when the hydrological level reaches 5 m above the base-flow level (Bonetto et al., 1969; García & Vargas, 1998).

Specifically, this study analyzes fish assemblages in the Catarata Brook, a secondary channel of the Middle Paraná floodplain about 50 m in width and 5 m in depth, located at the south of Santa Fe city (Fig. 1). The Catarata Brook is a side

channel of the Coronda River, itself a braid of the Paraná within an area of the

alluvial plain containing a network of anastomosing channels, lakes and wetlands.

Figure 1.

Fish surveys

Two lotic and two lentic habitats were surveyed (Fig. 1) in this sector of the

floodplain during five years (2010-2016). Lotic sites are located in the Catarata

Channel, 1.5 km apart from each other, and lentic sites are fluvial lakes connected to

this channel. At each site, fish were captured during two or three surveys each year

in different hydrological phases (August and December 2010; April and August 2011;

March, August and December 2012; April, July and December 2013, 2014; April,

August and December 2015 and May, August and December 2016). Fish were

captured with gill-nets with different mesh sizes (3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm

between opposite knots), with a total net area of 180.9 m². Each gill-net was set for

24 h and checked every 8 h. Sampling effort was the same for each period and site.

Additionally, temperature (T; ⁰C), conductivity (K; µS/cm), surface dissolved oxygen

(SDO; mg/L); secchi depth (Sec; m); total dissolved solids (TDS; mg.L-1) and pH

were recorded at each sampling site and survey date. The variables that presented

the greatest coefficients of variance during the study period were K (µS.cm-1); Sec

(m) and TDS (mg.L-1) (See table 1). However, these variables were not decisive in

producing changes in the structure of the fish assemblage because the duration of

hydrological phases was never as prolonged as the influence of these variables

becomes significant (Scarabotti et al., 2011; Espínola et al., 2016) that is, during the

sampling period there was nearly permanent variations of the hydrometric levels.

Table 1

Easy-to-identify specimens were processed in the field (species

determination, standard length (Ls; cm), and body weight (Wt; gr) were recorded).
Other fish were preserved in 10% formalin and transferred to the laboratory where
they were measured and identified according to keys for fishes of the Paraná River
Basin (e.g. Ringuelet et al., 1967; López et al., 2003).

Hydrological variations.

To understand the annual changes of the hydrological regime, daily water
levels were analyzed for the period 2010-2016. These data were obtained from the
Secretaria de Puertos y Vías Navegables recorded at the Santa Fe gauging station.
A level of 4.50 m was used as the average reference level for bankfull, the level
when water begins to flow into the adjacent alluvial plain within the study area given
rise to the beginning of the flood pulse phase. A level of 2.30 m was used as the
reference level for disconnection of most fluvial lakes from the river channel (Drago,
1980; Abrial et al 2019). We followed Puckridge et al. (1998) and Tockner et al.
(2000) in using the term "flow pulse" to refer to a discrete rise and fall of the water
level that remain confined within the channel banks.

We estimated the water surface area using satellite images of the study area
at different hydrometric levels between 2012-2016 obtained from Google Earth Pro.
Polygons with land and water surfaces were delimited, providing the inundated area
of the Arroyo Catarata. In this way, all lotic and lentic environments were identified
for each available level. Images were processed by using the free software QGIS V.
2.8.1 (QGIS Development Team, 2015) which enabled to compute the total
inundated area for each level. Percentages of water surface respecting the total
studied area as hydrometric levels increase, were then computed (see Abrial et al.,
2018). The strong variation of hydrological connectivity in Fig 2, i.e. a significant
increment of water surface, is largely explained by floodplain topography. The

common topographic irregularities which govern the connection between the main channel and the floodplain prevent a clear definition of the limit when begins a sharp increment of water surface. Thus, we preferred to define a range of levels for that limit (grey strip in Fig. 2). The level 3.2 m in Figure 2 is a lowest value of the strip selected where strong increment of connectivity started in the study area. To test the relationships between hydrological phases and fish assemblage structure, canonical analysis of principal coordinates (CAP software v1.0; Anderson 2004) were used. Bray–Curtis dissimilarity index (Bray and Curtis, 1957) and 999 permutations (Manly, 1997) were the selected parameters in CAP analyses (Fig. 3). In the figure, encircle numbers correspond to the samples carried out in Aug. 2015. Only the site 53 has a fish assemblage structure similar to samplings made during Flood, whereas the other sites have a structure similar to samplings made during HFP. For this reason Aug. 2015 was characterized as HFP. Supported by these two characters (hydrological and fish assemblage characters), and considering the established floodplain isolation level (2.3 m) and overflow level (4.5 m), three hydrological phases were differentiated: low flow pulses (LFP; between 2.3 and 3.2 m); high flow pulses (HFP; between 3.2 and 4.5 m) and floods (Floods; > 4.5 m, bankfull).

Figure 2

Figure 3

Data analysis.

Diversity attributes.

To characterize fish assemblages during each hydrological phase at each sampling site, we calculated some diversity attributes (Shannon's diversity index, species evenness, species richness) and the total fish abundance by sampling period (CPUE: catch-per-unit effort; number of individuals / 1000 m^2 of gill nets in 24

hours).

Differences in fish assemblages according to the hydrological variations.

To examine the relationships between water levels and fish ß-diversity, it was applied an analysis of multivariate homogeneity of group dispersions (PERMDISP2; Anderson et al., 2006) using the function "betadisper" from the R package "vegan" (Oksanen et al., 2018). This analysis enables to test for differences in: (i) multivariate dispersions among hydrological phases categories, and (ii) multivariate dispersions among months within a given phase category. This procedure has been used as a means for assessing ß-diversity by estimating distances between individual sites and their group centroid. Here, groups were defined according to the hydrological phases. Greater average distance between sampling sites and the group centroid indicates greater variability (ß-diversity). The statistical significance of mean differences during different hydrological phases was estimated using a permutation test with 999 permutations (Manly, 1997). The SCBD values for each phase represent the uniqueness un terms of community composition and abundance.

It is known that patterns in ß-diversity can be affected by changes in the number of species or individuals (Harrison et al., 1992; Chase, 2007). Thus, ß-diversity was corrected by rarefaction applying the beta function in the R package "BAT" (see Cardoso et al., 2017). The rarefaction allows standardization and significant comparison (Gotelli & Colwell, 2001) of different phases with different numbers of species or individuals. As rarefaction used a matrix of presence and absence, it was chosen the symbol p/a_r to indicate this procedure. In order to reduce the bias given by a sample with a low number of species, the square root transformation of the CPUE ($\sqrt{CPUE}$) was used. In brief, the ß-diversity values were obtained based on p/a_r and $\sqrt{CPUE}$.

To visualize the main patterns of homogeneity of hydrological phase dispersions, data based on √CPUE and p/a_r were subjected to a principal coordinate analysis (PCoA; Legendre & Legendre, 1998).

All statistical analyses were carried out with the R software version 3.3.3 (R Development Core Team, 2017). The statistical significance level of $p < 0.05$ was used for all analyses.

Results

Interannual hydrological variations

Connectivity of fluvial lakes was revealed from the analysis of satellite images as it was described in the methodology (Fig. 2). From 2.3 to 3.2 m, connectivity varies very little (water surface increases from 7.3-9.7% in the study area). When the water level exceeded 3.2 m, the water surface increases immediately, from 1.5 to 3.25 km^2 between 3.2 and 3.6 m and nearly double the coverage (9.7 to 21%). At bankfull level (4.5 m), the water surface area was 36 km^2 representing a coverage of 84% of the total study area, and all water bodies were connected. Up to 6 m, all the floodplain is under water. According to the classification that turned out from hydrological and fish assemblage structure characterization, three hydrological phases were differentiated (see methodology : Fig. 2 and Fig. 3). Five surveys were treated as Floods, six were considered as HFP and eight as LFP (Fig. 4).

Figure 4.

Diversity attributes in fish assemblages

A total of 7,681 fish belonging to 89 species, 27 families and 8 orders was caught (Table 2). Characiformes (N = 36 species) and Siluriformes (N = 35) showed almost the same species richness. However, Characiformes largely dominated in

CPUE, accounting for 69.21% of total CPUE. *Prochilodus lineatus* was the most abundant species (CPUE = 7,557), accounting for 21.35% of the total CPUE. CPUEs of *Megaleporinus obtusidens, Hoplias* and *Schizodon plata*e varied between 2,864 and 1,830.

Table 2

The means of richness, abundance (Figure 5) and diversity alpha were higher in the LFP phase than in HFP and Floods. Nevertheless, evenness was lower in the LFP than in two other phases, which presented almost the same species distribution (Table 3).

Figure 5.

Table 3

Fish assemblage variability between phases

LFP had the lowest average dissimilarity (0.72 ± 0.10), HFP an intermediate dissimilarity (0.79 ± 0.10), and Floods the highest dissimilarity (0.85 ± 0.09). Hence, dissimilarity in fish assemblage structure gradually increases from LFP to Floods.

The water level variation strongly affected the fish assemblages structure, which differed significantly between hydrological phases. The ß-diversity increases from LFP to HFP and Floods. This pattern is indicated by a low average value of the distance to the centroid which increases during HFP and Floods. Analyzing the SCBD of the first ten species between the different phases (LFP; HFP and Floods), *Loricariichthys melanocheilus*, *Hoplias argentinensis* and *Megaleporinus obtusidens* are the most contributing species in each phase respectively (Fig. 6). The figure shows that SCBD of LFP is significantly lower than the SCBDs of HFP and Floods. Although the two last phases present different species, the SCBDs were similar.

Figure 6

Although the outcome revealed a gradual divergence in the ß-diversity of fish fauna from LFP to Floods, non significant differences were checked between HFP and Floods, neither for √CPUE or p/a$_r$ (table 4; Fig. 7).

table 4

Fish assemblage variability within phases

Fish assemblage structure varied between LFP, HFP and Floods, indicating a greater variability among the months corresponding to each hydrological phase. During the months of LFP, the variability of the fish assemblage structure was lower (low dispersion among the samples) than during the months of HFP and Floods (high dispersion among the samples in both phases). However, fish assemblage structure during the months of HFP and Floods showed a similar variability. The same pattern can be observed for both √CPUE and p/a$_r$ (Fig. 8). In this sense, ß-diversity of the fish assemblages during the LFP months was smaller than the HFP and Floods ones, which present high values of ß-diversity and therefore similar variability.

Figure 8.

Discussion

Hydrological phases and connectivity

Overall results, based on fish assemblage and hydrological analyses, highlighted three main ecohydrological patterns in the study area. They respond to the interaction between hydrological variations and floodplain topography (i.e. lateral connectivity variations), which produced changes in ß-diversity of fish assemblages. These results are in line with Tejerina-Garro and de Mérona (2010), Mims and Olden

(2013), Abrial et al. (2014), Górski et al. (2014), Rabuffetti et al. (2017), Scarabotti et al. (2017), Abrial et al. (2019), highlighting the importance of the hydrology in the structuring of fish assemblages.

Hydrological variations were discriminated into three ranges: the low flow pulses (LFP; from 2.3 to 3.2 m) which do not significantly modify connectivity patterns, the high flow pulses (HFP; from 3.2 to 4.5 m) which significantly increase floodplain connectivity and the floods (Floods; higher than 4.5 m) whose connectivity is almost total (Figs. 2 and 4). Spatial fish assemblage distribution showed a gradient of ß-diversity that increases from LFP to Floods (i.e. similarity between assemblages decreases). A combination of processes associated with the gradual increase/decrease of connections between lentic/lotic environments is likely to yield such results. They evidence the importance of available floodplain habitats in structuring patterns of aquatic organisms (Junk & Wantzen, 2004; Dudgeon et al., 2006).

Flow pulse relevance on the spatial distribution of fish assemblages

The spatial and temporal distribution patterns of aquatic organisms and the degree of environmental heterogeneity in floodplain-rivers are closely linked with long periods of droughts, extraordinary floods, timing of flood pulses, but also with minor fluctuations of water levels which modulate the connectivity between the floodplain habitats and its channels network (Puckridge et al., 1998; Junk et al.,1989; Neiff, 1990; Simões et al., 2012; Garner et al., 2015; Espínola et al., 2014, 2016). In this way, our analyses support the importance of not only the high and low peaks of the annual hydrological regime, but also the changes that occur during the gradual rising and falling waters that separate the two extremes, that is, the water

fluctuations occurring below the bankfull level considered as flow pulses by Tockner et al. (2000), and specifically the HFP in the study.

Indeed, several results showed that spatial structuring of fish assemblages presents similar trends at HFP and Floods whereas they are different during LFP. For example, richness, fish abundance and alpha diversity are lower during HFP and Floods than LFP, and the opposite occurs for species evenness (Fig. 4 and Table 3). On the other hand, dispersion of fish assemblage structure gradually rises from LFP to Floods, with intermediary values during HFP (Figs.7 and 8).

Apparently, the HFP would allow significant lateral interactions between lotic and lentic environments of the alluvial plain, but to a lesser degree than Floods would do, being that this phase presents a greater value of ß-diversity. Clearly, and on the base of our results, HFP could be considered as an intermediate phase between LFP and Floods. This gradualism in the hydrological variations of such unregulated lowland river is likely to trigger significant fish movements, being of great importance in floodplain dynamics and ecological interactions.

Dispersion processes during HFP and Floods

Fish dispersion between floodplain habitats and channel networks is modulated by the connectivity (Stoffels et al., 2016).The ultimate consequence may be an increment of the ß-diversity in floodplains during floods if they lead to the inundation of a wide area with many lakes subjected to different successional dynamics (Vitorino et al., 2016). More species are able to come from recently connected water bodies throughout the system, and so, a high ß-diversity could indicate important spatial or temporal transitions (Sepkoski, 1988; Williams, 1996).

As mentioned above, dispersion processes in the study area significantly increase during the HFP phase. In line with these results, we observed that during

significant water rises (HFP and Floods), dispersion processes are more important than the homogenization ones. Indeed, the spatial variability of fish assemblage structure was much higher during HFP and Floods than LFP (higher ß-diversity, thus higher dissimilarity between fish assemblages). This means a reduction in the similarity of fish assemblages when the availability of floodplain habitats increases.

The homogenization effect of floods (HFFP; Thomaz et al., 2007) seems to be hardly evaluable during high floodplain connectivity degrees (HFP and Floods) because of the high dispersion of fish into the floodplain and thus, the lower catch efficiency of gill nets. Fish abundance and richness are not lower during such events, but species are much more dispersed into the floodplain. An explanation of higher ß-diversity under such conditions is that the heterogeneity of aquatic habitats is greater, due to a higher availability of inundated areas, which allows fish more opportunities to segregate in space as result of species specific habitat selection.

This may explain why species with higher contribution to ß-diversity (SCBD) are mostly represented by migratory species during Floods (Fig. 6). That is, *M. obtusidens*, *P. lineatus* and *S. brasiliensis*, with the highest SCBD during Floods, are typical periodic species making long migrations. They have major probability of dispersion into the plain and consequently major probability of capture with nets. The opposite pattern was found during LFP. Many sedentary species (i.e. lower expected displacements into the floodplain) presented the highest SCBD. In HFP, the highest SCBD were found in species with diverse life histories, and they have sedentary behaviors, or make short lateral migrations into the floodplain or long upstream migrations. These characters support the transitional nature of this hydrological phase (see species reproductive traits in Abrial et al., 2018)

High fish dispersion during HFP and Floods against a higher similarity of the fish assemblage structure during LFP suggest a time-lag in the floodplain homogenization process. The lower spatial variability of fish structure during LFP could be a consequence of a previous increase of water levels which favors the dispersion of organisms all over the floodplain as suggested by Thomaz et al. (2007) and Espínola et al. (2016). In the study area, and it would be the same for the Middle Paraná River or at least for a great portion of the floodplain, the HFFP (Thomaz et al., 2007) is likely to occurs when flooding process is ended, that is during low water levels (LFP). In this case, the homogenization concept should be considered as a process covering both phases of the flood pulse, the low and high water phases.

These results are in line with the suggestions and findings of several authors (Amoros & Bornette, 2002; Henry et al., 2011; Mayora et al., 2013; Dos Santos Bertoncin et al., 2019), meaning that the homogenizing effect of the flood pulse is not a general rule and must be adjusted to the kind of situation, aquatic organism and river. For example, while zooplankton beta diversity and environmental heterogeneity decrease during flooding (Bozelli, 1992; Bozelli et al., 2015), fish dispersal is likely to increases and fish assemblage homogenization may occurs later, during low water phases.

Moreover, it should be noted that the extent and intensity of the low water phases would be as important as floods in floodplain structuring processes. High values of richness and abundance during LFP (Table 3; Fig. 4) is related to fish confinement in the reduced floodplain environments. Ward et al. (1999) referred to this period as a "biological interaction phase" because space decreases while density of individuals and species increases. Intense water recessions would conduce to significant isolation processes (Abrial et al., 2019), and thus, local

internal factors (abiotic processes and interaction between species) would lead to a differentiation of fish assemblages between fluvial lakes of the Middle Paraná River (Scarabotti et al., 2011). However, during the studied period, no significant isolations of the floodplain habitats occurred (Fig. 4). This aspect may explain why processes related to fish assemblage heterogeneity were not observed in the area of study.

Concluding remarks

This work provides further knowledge about floodplain homogenization processes. Such information would be specifically applicable to fish assemblages of large floodplains with high degrees of connectivity. It highlights that homogenization processes are not observed during flooding because of a high fish dispersion into the floodplain. They occur later, during the low water phases that follow the flooding. As significant isolation processes are not frequent in these kind of environments, they would explain why ecological processes that increase habitat heterogeneity, and thus spatial dissimilarity between fish assemblages, are not detected.

Main conclusions were based on patterns of ß-diversity that revealed distinct spatial distributions of fish assemblages during three hydrological phases: low flow pulses (LFP), high flow pulses (HFP) and overflow levels (Floods). They evidenced an increase of assemblage dissimilarity from low to high water levels, and underlined the importance of flow pulses (HFP), which played a significant role on the structuring of the fish assemblages in the large floodplain of the Middle Paraná River.

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Table 1. Range (minimum and maximum), mean, standard devision and coefficient of variation of the abiotic variables in each phase (Black circle: Floods; red circle: High flow pulses; HFP and grey circle: Low flow pulses: LFP) of the Paraná River floodplain during 2010-2016. Temperature (T; ºC), conductivity (K; µS/cm), surface dissolved oxygen (SDO; mg/L) ; secchi depth (Sec; m) ; total dissolute solid (TDS; mg.L-1) and pH.

Hydrological phases	LFP					HFP					Flood				
Abiotic variables	Range Min - Max		Mean	Sd	CV	Range Min – Max		Mean	Sd	CV	Range Min - Max		Mean	Sd	CV
Temperature (ºC)	12.7	32.8	23.07	6.2	0.2	14.9	27.5	20.7	4.0	0.2	11	29.3	19.6	6.7	0.3
K (µS.cm-1)	104	573	289.5	150.4	0.5	88.5	200	132.9	39.3	0.3	81.8	142.4	104	15.5	0.2
Sec (m)	0.1	1.0	0.3	0.2	0.7	0.19	1.4	0.5	0.31	0.6	0.2	0.9	0.5	0.2	0.4
pH	5.5	7.9	6.7	0.8	0.1	6	7.4	6.4	0.40	0.1	5.5	6.9	6.1	0.4	0.1
SDO (mg.L-1)	3.3	11.2	7.5	2.0	0.2	2.9	11.0	6.8	2.2	0.3	1.6	9.8	6.9	2.3	0.3
TDS (mg.L-1)	144.6	52.2	283	75.4	0.2	44.3	100	67.2	19.4	0.2	41	7.1	52	8.2	0.2

Table 2. Catch-per-unit effort; (number of individuals / 1000 m^2 of gill nets in 24 hours) of the whole sampling period of the 89 fish species caught in the Middle Paraná River floodplain.

Order, Family, Genus,Species, Author	CPUE
Characiformes	
Acestrorynchidae	
Acestrorhynchus pantaneiro (Menezes, 1992)	1006.08
Paradontidae	
Apareiodon affinis (Steindachner, 1879)	5.53
Anostomidae	
Megaleporinus obtusidens (Valenciennes, 1837)	2863.46
Schizodon borellii (Boulenger, 1900)	425.65
Schizodon platae (Garman, 1890)	1829.74
Characidae	
Astyanax abramis (Jenyns, 1842)	1022.66
Astyanax correntinus (Holmberg, 1891)	5.53
Astyanax erythropterus (Holmberg, 1891)	38.7
Astyanax asuncionensis (Géry, 1972)	486.46
Astyanax rutilus (Jenyns, 1842)	751.8
Charax stenopterus (Cope, 1894)	16.58
Roeboides microlepis (Reinhardt, 1851)	55.28
Roeboides affinis (Günther, 1868)	22.11
Roeboides descalvadensis Fowler, 1932	11.06
Salminus brasiliensis (Cuvier, 1816)	995.02
Cynopotamus argenteus (Valenciennes, 1836)	541.74
Cynopotamus kincaidi (Schultz, 1950)	5.53
Galeocharax humeralis (Valenciennes, 1834)	132.67
Oligosarcus jenynsii (Günther, 1864)	60.81
Triportheidae	
Triportheus nematurus (Kner, 1858)	93.97
Bryconidae	
Brycon orbignyanus (Valenciennes, 1850)	66.33

Curimatidae

Cyphocharax platanus (Günther, 1880) — 1304.59

Cyphocharax spilotus (Vari, 1987) — 33.17

Cyphocharax voga (Hensel, 1870) — 685.46

Potamorhina squamoralevis (Braga & Azpelicueta, 1983) — 66.33

Steindachnerina brevipinna (Eigenmann & Eigenmann 1889) — 44.22

Steindachnerina conspersa (Holmberg, 1891) — 33.17

Steindachnerina biornata (Braga & Azpelicueta, 1987) — 5.53

Psectrogaster curviventris Eigenmann & Kennedy, 1903 — 22.11

Cynodontidae

Rhaphiodon vulpinus (Spix&Agassiz 1829) — 392.48

Erythrinidae

Hoplias malabaricus (Bloch, 1794) — 1984.52

Prochilodontidae

Prochilodus lineatus (Valenciennes,1837) — 7556.66

Serrasalmidae

Mylossoma duriventre (Cuvier, 1818) — 22.11

Pygocentrus nattereri (Kner, 1858) — 685.46

Serrasalmus maculatus (Kner, 1858) — 851.3

Serrasalmus marginatus (Valenciennes, 1837) — 375.9

Siluriformes

Heptapteridae

Pimelodella gracilis (Valenciennes, 1835) — 16.58

Pimelodidae

Luciopimelodus pati (Valenciennes, 1835) — 16.58

Surubim lima(Bloch & Schneider, 1801) — 44.22

Rhamdia quelen (Quoy & Gaimard, 1824) — 5.53

Parapimelodus valenciennis (Lüken, 1874) — 1055.83

Pimelodus albicans (Valenciennes, 1840) — 33.17

Pimelodus argenteus Perugia, 1891 — 11.06

Iheringichthys labrosus (Lütken, 1874) — 176.89

Pimelodus maculatus (Lacepède, 1803) — 823.66

Pseudoplatystoma corruscans (Spix & Agassiz 1829) — 88.45

Pseudoplatystoma reticulatum Eigenmann & Eigenmann, 1889	11.06
Auchenipteridae	
*Ageneiosus inermis (*Linnaeus, 1766)	154.78
Ageneiosus militaris (Valenciennes, 1835)	364.84
Auchenipterus nigripinnis (Boulenger, 1895)	148.25
Auchenipterus osteomystax (Miranda-Ribeiro, 1918)	88.45
Trachelyopterus galeatus (Pezzi da Silva & Pereira 1995)	569.38
Trachelyopterus striatulus (Steindachner, 1877)	1188.5
Loricariidae	
Sturisoma robustum (Regan, 1904)	49.75
Hypostomus commersoni (Valenciennes, 1836)	420.12
Hypostomus luteomaculatus(Devincenzi, 1942)	11.05
Loricaria apeltogaster Boulenger, 1895	66.33
Brochiloricaria chauliodon Isbrücker, 1979	16.58
Loricaria simillima (Regan, 1904)	281.92
Loricariichthys anus (Valenciennes, 1835)	116.09
Loricariichthys melanocheilus (Reis & Pereira, 2000)	1376.45
Loricariichthys platymetopon (Isbrücker & Nijssen, 1979)	1525.7
Paraloricariavetula (Valenciennes, 1835)	199
Pterygoplichthys anisitsi (Eigenmann& Kennedy, 1903)	127.14
Pterygoplichthys ambrosettii (Holmberg, 1893)	33.17
Ricola macrops (Regan, 1904)	199
*Pseudohemiodon laticeps (*Regan, 1904)	11.06
Doradidae	
Rhinodoras dorbignyi (Kner, 1855)	5.53
Oxydoras kneri (Bleeker, 1862)	22.11
Pterodoras granulosus (Valenciennes, 1821)	403.54
Callichthyidae	
Hoplosternum littorale (Hancock, 1828)	210.06
Perciformes	
Sciaenidae	
Pachyurus bonariensis (Steindachner, 1879)	182.42
Plagioscion squamosissimus (Heckel, 1840)	11.05
Cichlidae	

Crenicichla lepidota (Heckel, 1840)	160.31
Crenicichla vittata (Heckel, 1840)	66.33
Astraloheros facetus (Jenyns, 1842)	44.22
Astraloheros scitulus (Rícan & Kullander, 2003)	16.58
Cichlasoma dimerus (Heckel, 1840)	55.28
Gymnogeophagus australis (Eigenmann, 1907)	5.53
Gymnogeophagus meridionalis Reis & Malabarba, 1988	16.58

Atheriniformes

Atherinopsidae

Odontesthes bonariensis (Valenciennes, 1835)	33.17
Odontesthes perugiae Evermann & Kendall, 1906	5.53

Clupeiformes

Pristigasteridae

Pellona flavipinis (Valenciennes, 1836)	187.95

Engraulidae

Lycengraulis grossidens (Agassiz, 1829)	127.14

Pleuronectiformes

Achiridae

Catathyridium jenynsii (Günther, 1862)	11.06

Myliobatiformes

Potamotrygonidae

Potamotrygon motoro (Müller & Henle, 1841)	5.53

Gymnotiformes

Rhamphichthyidae

Rhamphichthys hahni (Meinken, 1937)	5.53

Gymnotidae

Gymnotus inaequilabiatus (Valenciennes, 1839)	11.06

Sternopygidae

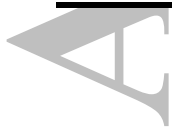|	
Eigenmannia trilineata López& Castello, 1966	77.39

Table 3. Mean and Standard Deviations of the diversity attributes in the floodplain of the Middle Paraná River during the period 2010–2016. (Flood Pulses : Floods; High Flow Pulses: HFP and Low Flow Pulses: LFP).

Hydrological phases	Alpha diversity Mean—SD	Species evenness Mean—SD	Species richness Mean—SD	Abundance (CPUE) Mean—SD
Floods	2.06 ± 0.46	0.75 ± 0.15	11.94 ± 5.79	197.84 ± 147.42
HFP	2.04 ± 0.57	0.64 ± 0.21	14.21 ± 5.80	340.80 ± 269.65
LFP	2.28 ± 0.34	0.58 ± 0.16	18.62 ± 6.69	963.41 ± 950.54

Table 4. Average distance to centroid in each hydrological phase in the floodplain of the Middle Paraná River during the period 2010–2016. (Flood Pulse : Floods; High Flow Pulses: HFP and Low Flow Pulses: LFP). In both methods: transformed ($\sqrt{}$CPUE) and presence/absence corrected by rarefaction (p/a$_r$), different letters express significant differences ($P < 0.05$) between centroid means in each hydrological phase, while similar letters represent non-significant differences ($P > 0.05$).

Fish matrix	LFP	HFP	Floods
$\sqrt{}$CPUE	0.47^a	0.52^{ab}	**0.55^b**
p/a$_r$	0.50^a	**0.55^b**	**0.60^b**
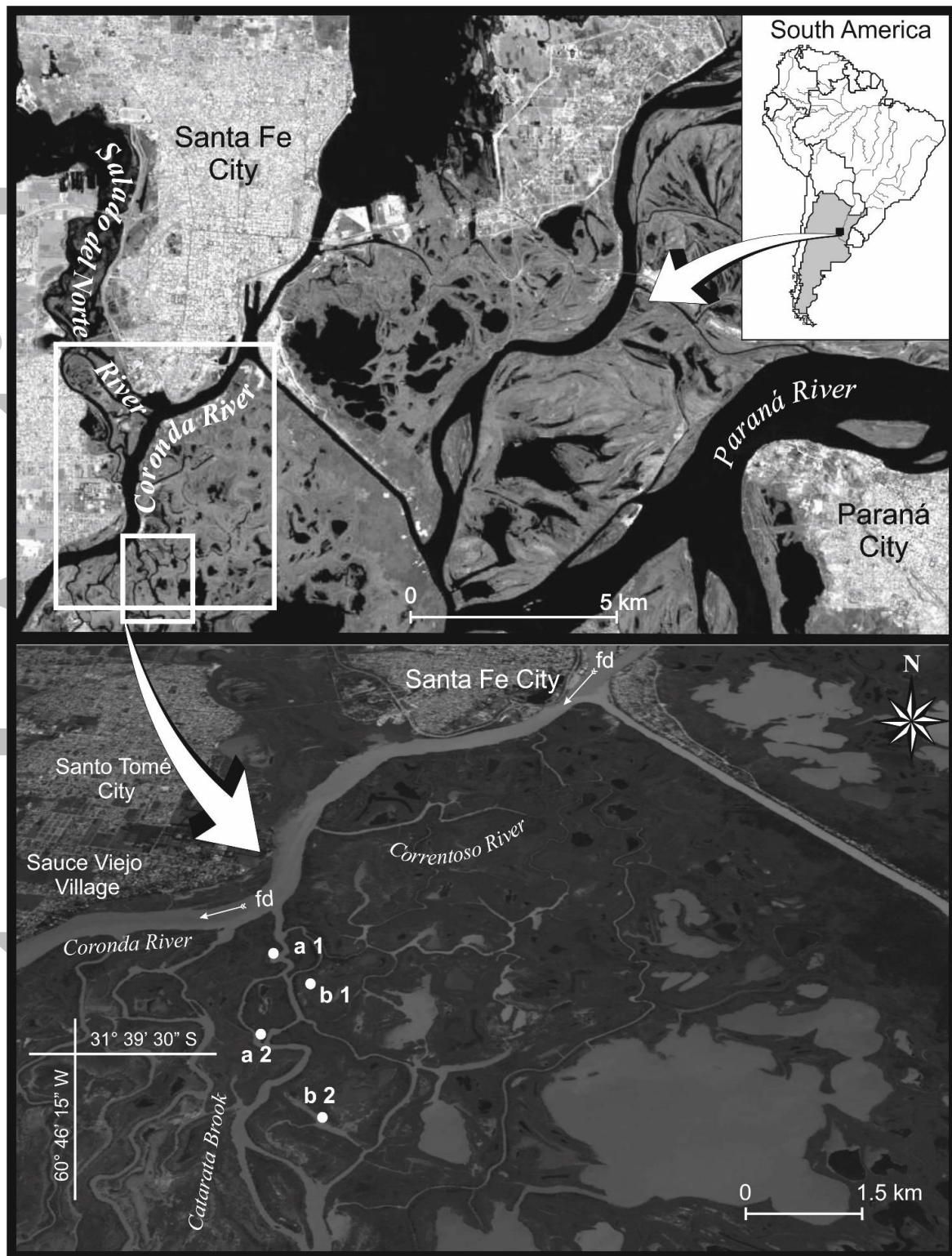
Figure 1. Study area in the floodplain of the Middle Paraná River. Numbers show the sampling sites and type of environment: a 1 and a 2, lotic environments; b 1 and b 2, fluvial lakes. fd: flow direction (modified from Espínola et al., 2016).
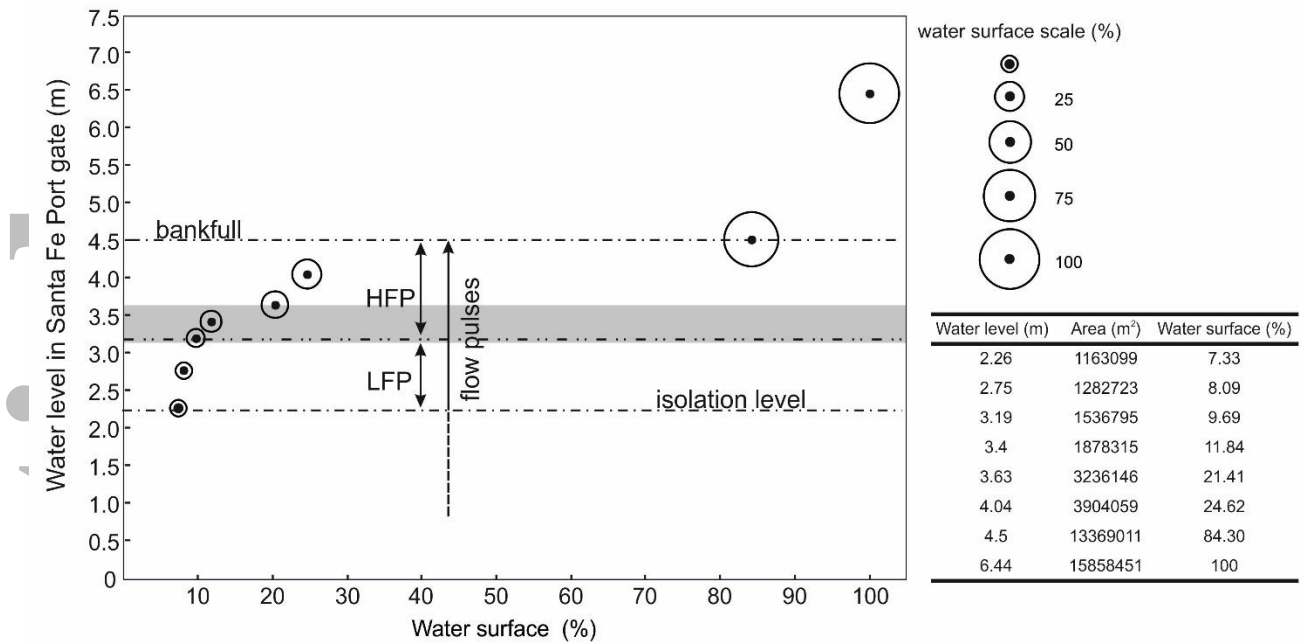
Water level in Santa Fe Port gate (m)

7.5
7.0
6.5
6.0
5.5
5.0
4.5 — bankfull
4.0
3.5 — HFP
3.0
2.5 — LFP — isolation level
2.0
1.5
1.0
0.5
0

flow pulses

Water surface (%)
10 20 30 40 50 60 70 80 90 100

water surface scale (%)

25
50
75
100

Water level (m)	Area (m²)	Water surface (%)
2.26	1163099	7.33
2.75	1282723	8.09
3.19	1536795	9.69
3.4	1878315	11.84
3.63	3236146	21.41
4.04	3904059	24.62
4.5	13369011	84.30
6.44	15858451	100

Figure. 2. Water levels in the Middle Paraná River floodplain as a function of surface of inundated areas. The size of the circle indicates the surface of flooded area. The grey band indicates the range of variation of the hydrological connectivity from which the increase of surface becomes topographically significant. The 3.2 water level (doubly dotted line) indicates the lower and upper limit average of Low Flow Pulses (LFP) and High Flow Pulse (HFP).Threshold for over-banking flows or flood pulses is above 4.5 m; high flow pulses: between 3.2-4.5 m; low flow pulses: between 2.3-3.2 m. Below 2.3 m is the isolation of floodplain lakes. The range between the bankfull and the isolation levels (full line) define the flow pulses considered in this study.
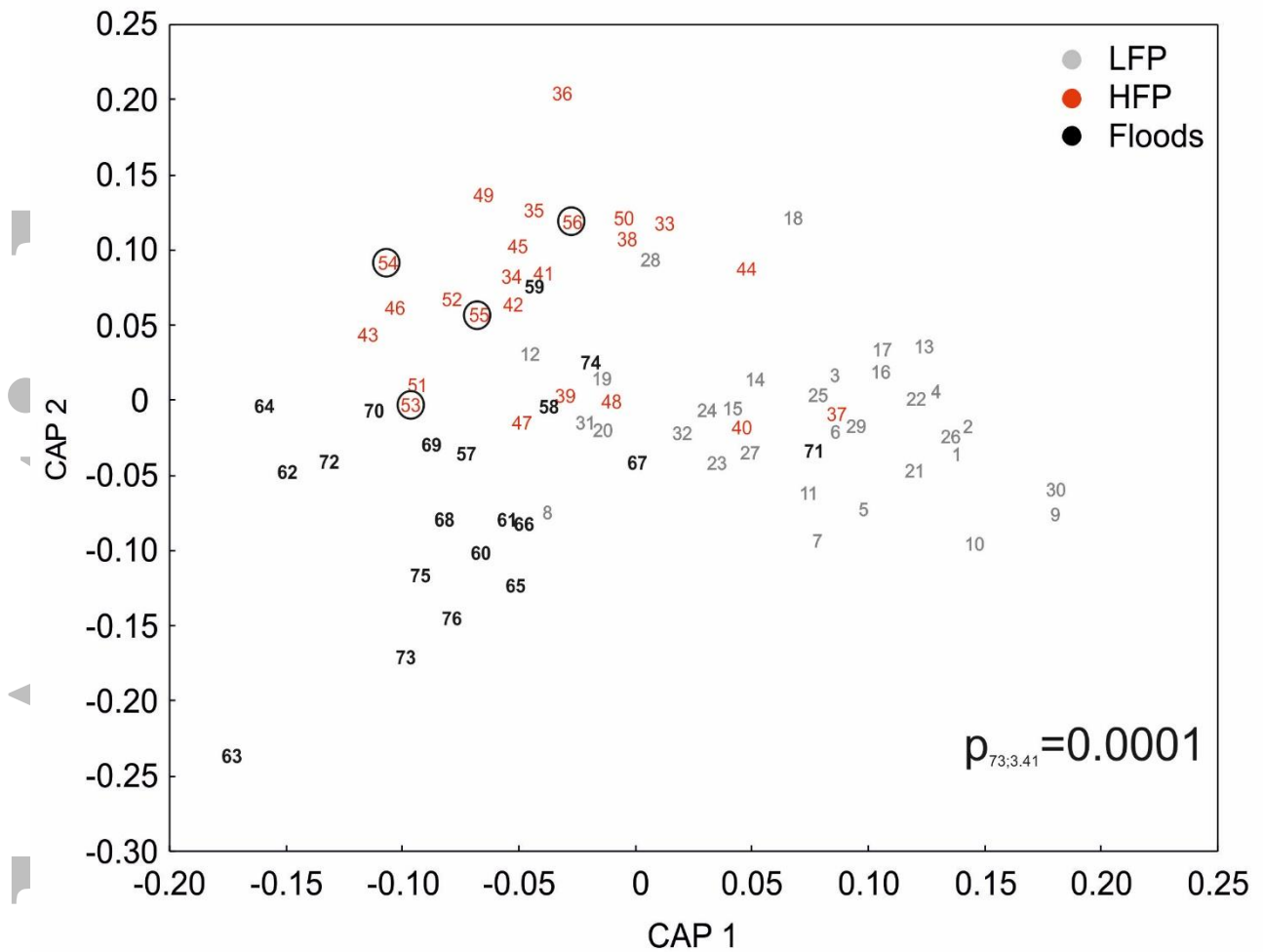
Figure 3.Variation of fish assemblages structure in lotic and lentic environments of the Middle Paraná River floodplain during the studied 2010–2016 according to the hydrological phases. Encircled numbers show the samples carried out in Aug. 2015. Only the site 53 has a fish assemblage structure similar to the samplings made during Floods. For this reason, Aug. 2015 was characterized as HFP.
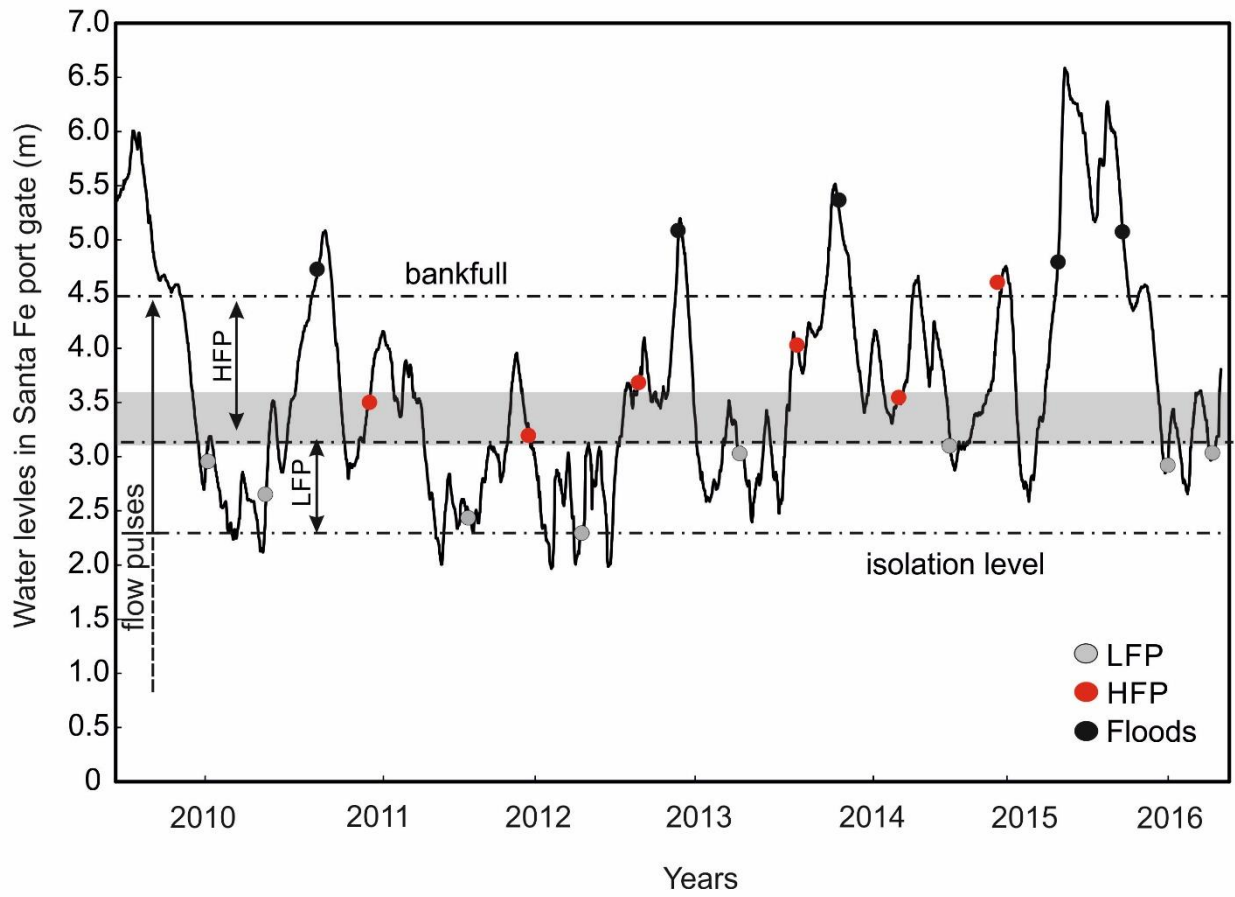
Figure 4. Daily variations of the water level in the Middle Paraná River between January 2010 and December 2016. Fish surveys were conducted during three hydrologic phases: black circles: Overflows (Floods); red circles: High flow pulses (HFP); and: white circles: Low flow pulses (LFP). The range between the bankfull and the isolation levels define the flow pulses (full line) considered in this study.
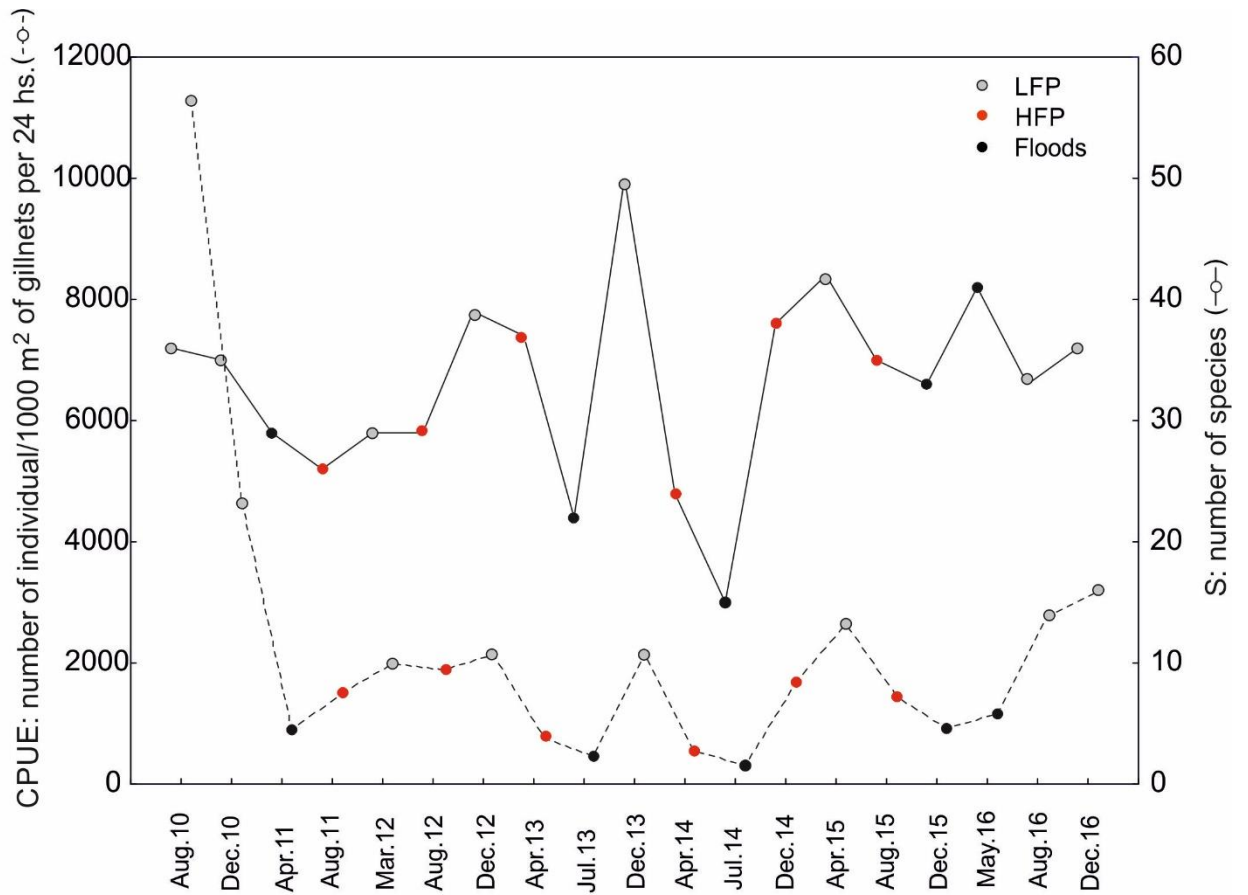
Figure 5. Fish abundance (CPUE, dotted line) and species richness (solid line) at survey locations in the Middle Paraná River floodplain during 2010-2016: black circles: Overflows (Floods); red circles: High flow pulses (HFP); and white circles: Low flow pulses (LFP)
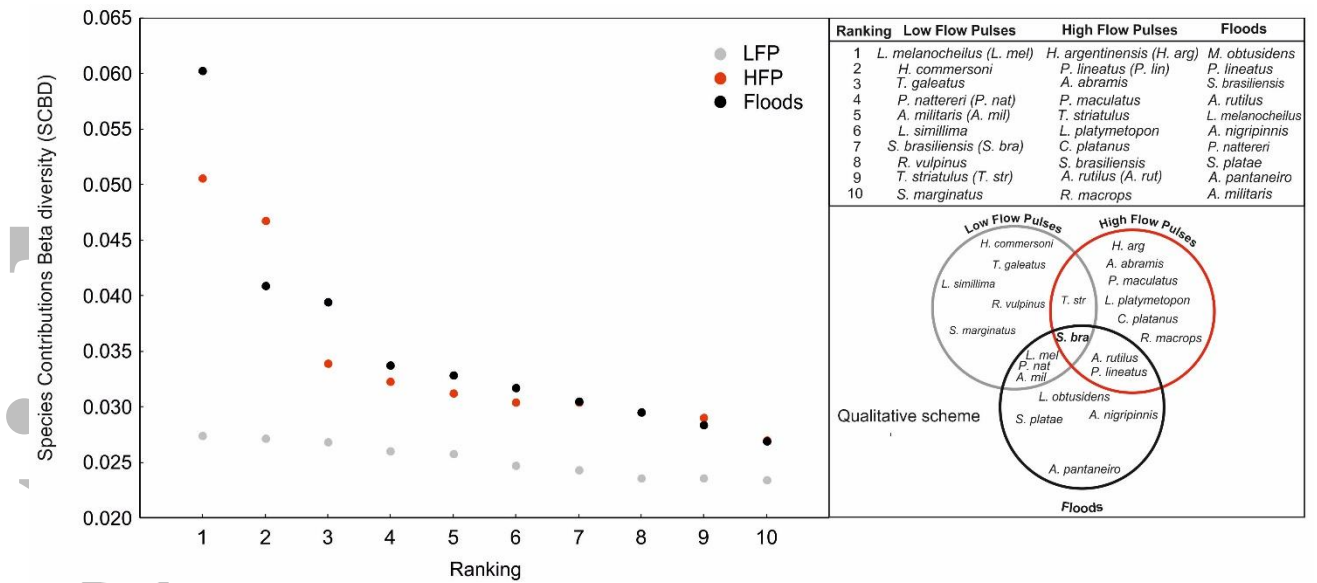
Figure 6.Species contribution of ß diversity in each hydrological phase in the Middle Paraná River between January 2010 and December 2016. Black circle (Floods); red circle: High flow pulses (HFP); and grey circle: Low flow pulses (LFP)
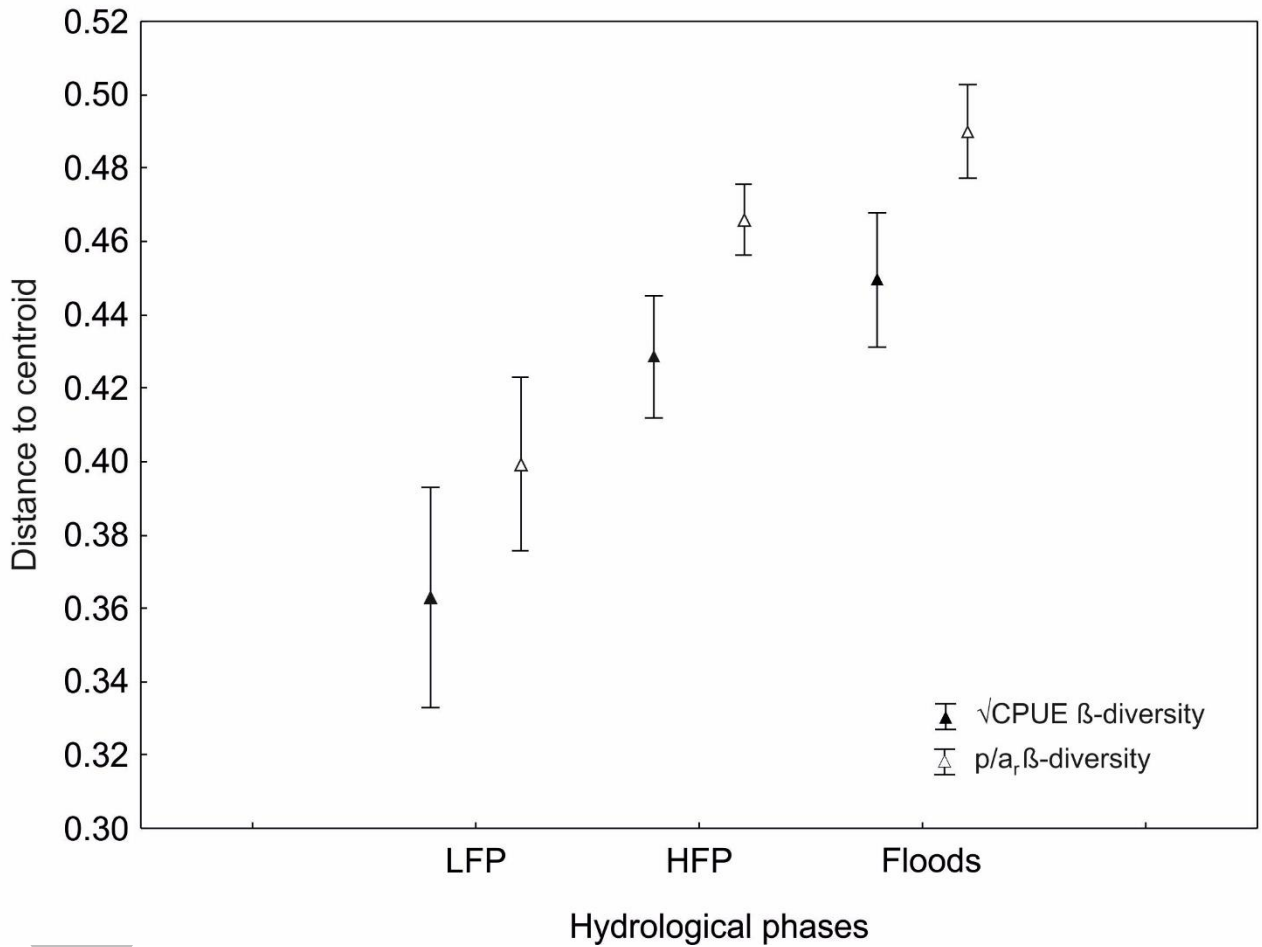
Figure 7. Mean values (triangles) and ± standard error (lines) of distance to centroid of the structure on the fish assemblages in each hydrologic phase (LFP: Low Flow Pulses; HFP: High Flow Pulses; Floods: overflows) in the Middle Paraná River. Black and white triangles represent the ß-diversity based on CPUE square root-transformed data ($\sqrt{CPUE}$) and presence and absence corrected by rarefaction (p/a_r)

√CPUE   p/a_r

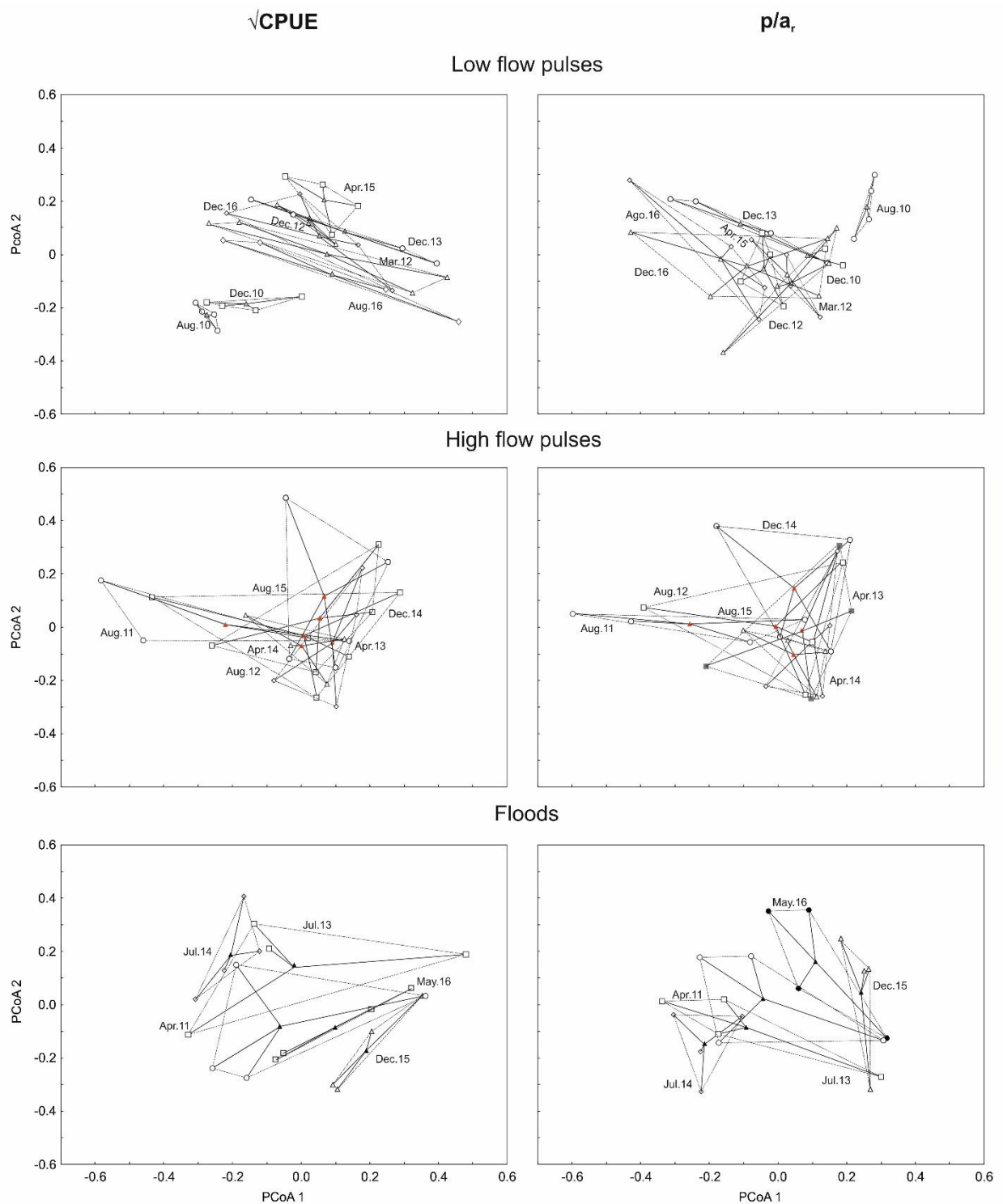Low flow pulses

High flow pulses

Floods

Figure 8. Two-dimensional representation of PCoA variation of the structure on the fish assemblages in each hydrologic phase in the Middle Paraná River floodplain. Lines represent the distances between the survey sites in each month (points) and the centroid (triangles) as defined by the sampling months. Figures of the left are based on CPUE Square root-transformed data: (√CPUE). Figures of the right are base on presence and absence corrected by rarefaction (p/a_r).