PRIMARY RESEARCH PAPER

Spatio-temporal organization patterns in the fish assemblages of a Neotropical floodplain

Jean C. G. Ortega · Rosa M. Dias · Ana C. Petry · Edson F. Oliveira · Angelo A. Agostinho

Abstract Communities can be structured over time by deterministic, stochastic, or both mechanisms. This study evaluated whether the fish assemblages of the Upper Paraná River floodplain were spatio-temporally structured and examined the mechanisms driving these organizational patterns. The floodplain ichthyofauna was sampled quarterly with seines and gillnets. The structure of the assemblage was assessed using the C-Score co-occurrence index and null models. The influence of both the environment (physical and chemical variables and hydrometric levels) and time on the species' organization patterns was assessed via principal component analysis, multiple and simple regressions, and analyses of variance. Assemblages with larger species showed patterns of species segregation at both spatial and temporal scales, while those composed of smaller species often exhibited random patterns. The physical and chemical variables did not predict co-occurrence among species. For assemblages of large species, the patterns of co-occurrence tended to be random when the river level increased but only during high-water months. Therefore, the life history traits of the species, such as body size, may predict the structure of the assemblages in floodplains, but this effect depends on variations in the hydrometric level.

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Introduction

A community can be structured over time by deterministic (Gotelli & McCabe, 2002) and stochastic

processes (Ulrich, 2004) or both (Ruhí et al., 2014), resulting in different co-occurrence patterns. Although communities structured by deterministic processes can present patterns of species segregation (e.g., Gotelli & McCabe, 2002; Heino & Grönroos, 2013) or aggregation (e.g., Boschilia et al., 2008; Presley, 2011) in space and time, stochastic mechanisms tend to reveal random co-occurrence patterns in structured communities wherein one species is independent of the others.

When segregated, species do not tend to co-occur in the same site or time. This segregation among species can be due to competition (Diamond, 1975; Gotelli & McCabe, 2002), predation (Englund et al., 2009; Fernandes et al., 2009), or even environmental filtering (Mouchet et al., 2013; Ruhí et al., 2014). Aggregated co-occurrence indicates that species tend to occur together. Such patterns can arise because of similar ecological requirements (Presley, 2011; McCreadie & Bedwell, 2013) and facilitative interactions between species pairs or between host and parasite (Krasnov et al., 2014). However, neutral processes (e.g., the dispersal ability or demographic stochasticity; Ulrich, 2004) or interactions among deterministic process (Boschilia et al., 2008; Caruso et al., 2011) can generate random co-occurrence patterns.

There is evidence that segregated patterns are widespread in many taxa, such as aquatic macrophytes (Boschilia et al., 2008), amphibians (Both et al., 2011), and fish (Oliveira et al., 2005), and functional groups, such as trophic and reproductive groups in freshwater fish (Hoeinghaus et al., 2007). However, controversy remains over how well co-occurrence patterns can be generalized (Gotelli & McCabe, 2002; Oliveira et al., 2005; Boschilia et al., 2008; Ruhí et al., 2014). Part of this theoretical controversy is the result of analyses that do not explicitly consider the presence of guilds or functional groups and therefore omit the effect of competition on segregation among species (Gilpin & Diamond, 1982; Both et al., 2011). Failing to analyze co-occurrences through time may also contribute to the difficulties in generalizing these patterns. One of the hypotheses of community assembly through time predicts that after perturbations, a community is initially disorganized and progressively increases its organization (i.e., first showing a random co-occurrence pattern, then segregating or aggregating over time with the recovery of system stability; Sanders et al., 2003; Arrington et al., 2005; Fernandes et al.,

2009; Boschilia et al., 2012). In the face of such variability on a temporal scale, studies conducted only at spatial scales can lead to incomplete conclusions about community assembly.

Temporal analyses permit stronger inferences about the mechanisms underlying organization patterns in communities (Sanders et al., 2003; Mouchet et al., 2013). Because each community has a particular spatio-temporal context, assessing how a community organizes itself through time can help to distinguish the action of distinct evolutionary mechanisms on community organization (e.g., Mouchet et al., 2013). In addition, it may allow observers to perceive natural (e.g., Arrington et al., 2005; Boschilia et al., 2012) or anthropogenic disturbances (e.g., Sanders et al., 2003).

For fish communities, there is currently an intense debate about co-occurrence patterns. Some authors have provided evidence that fish assemblage can exhibit random patterns (Gotelli & McCabe, 2002; Fernandes et al., 2009), while others have shown that they segregate (Oliveira et al., 2005; Bhat & Magurran, 2007). These contrasting co-occurrence patterns may not result from the same structuring mechanisms because fish are a group that is diverse in life history strategies and exploits a great diversity of environments (Matthews, 1998).

In tropical ecosystems that are subjected to seasonal regimes of drought and flood, fish assemblages can display a progressive increase in organization following hydrometric variations (Arrington et al., 2005; Fernandes et al., 2009). As water levels increase during floods, the aquatic physical, chemical, and biological conditions tend to become homogenized (Thomaz et al., 2007). For fishes in particular, the increase in the water level provides an increase in the area available for dispersal, resetting the organizational process for assemblages (i.e., assemblages tend to show random patterns; Arrington et al., 2005; Fernandes et al., 2009). As water levels decrease, some places become isolated and the effect of biological interactions on assemblage organization can prevail, resulting in segregation patterns, possibly due to the exclusion of some species (Fernandes et al., 2009).

This study assessed whether the assemblage of Neotropical floodplain fish shows a spatio-temporal structure and determined the mechanisms that are primarily responsible for any observed patterns. The first hypothesis was that (I) the fish assemblage is

spatially structured at different spatial scales based on the entire floodplain or sub-basin and environments that make up the floodplain (river channels and lagoons). It was expected that the floodplain fish assemblage would show more species segregation than would be expected at random. The second hypothesis was that (II) these assemblage structures would temporally follow the seasonal drought and flood pulses and inter-annual variation. Thus, it was expected that (i) in isolation periods (droughts), the assemblage would be structured (i.e., show segregation patterns), while in periods of hydrological connection (floods), the assemblage would disassemble (i.e., show random co-occurrence), and that (ii) assemblage organization would increase with time (show inter-annual variation). Finally, the contributions of physical and chemical variables as mechanisms structuring co-occurrence in this assemblage were assessed. These hypotheses were evaluated through long-term fish assemblage monitoring in the Upper Paraná River floodplain. Considering that the floodplain is a heterogeneous and diverse environment that is colonized by small- and large-sized fish (Agostinho et al., 2007) that can explore different environments, these hypotheses were tested separately in fish assemblages that differed according to body size.

Materials and methods

Study area

Sampling was carried out in the Upper Paraná River floodplain, situated between 22°40′ and 23°40′S and 53°10′ and 53°40′W (Fig. 1). The floodplain consists of a lotic stretch of 230 km, and it is the last undammed reach in the Upper Paraná River basin. It is bordered upstream by the Porto Primavera dam and downstream by the backwater of the Itaipu dam. The studied floodplain area consists of three sub-basins: the Ivinhema River sub-basin, which is undammed and flows in a north–south direction in the floodplain, the Baia River sub-basin, which flows in the floodplain parallel to the Paraná River, and the Paraná River, which flows northeast–southwest and exhibits dams arranged in a series upstream of the floodplain (Agostinho et al., 2007; Boschilia et al., 2008).

The upstream dams affect the floodplain hydrological cycle, causing daily fluctuations in the river level

(Agostinho et al., 2004b) and making the annual flood regime discontinuous. In some years, low water levels of the Paraná River prevent any hydrological connection between isolated environments and the main river channels (Fig. 2). However, the flood pulse is still the main force that determines the function, structure, and composition of the biotic community of the floodplain (Agostinho et al., 2004b; Thomaz et al., 2007; Suzuki et al., 2009). Therefore, the floodplain hydrological cycle is composed of a high-water (November to March) and a low-water period (April to October; Agostinho et al., 2004a), showing inter-annual variations associated with the precipitation intensity in the upper stretch of the basin.

More than 150 species constitute the ichthyofauna of this region, which exhibit high spatial and temporal species turnover rates (Agostinho et al., 2004a). These species occur in different environments in the floodplain, such as the main river channels, lagoons that are permanently connected to the river channel and lagoons that only connect to the river during high-water periods (hereafter referred to as connected and disconnected lagoons, respectively). Each sub-basin (Baía, Ivinhema and Paraná) presents conspicuous limnological differences (see details in Online Resource 1). Although the floodplain is mostly affected by the water level of the Paraná River, local differences occur in response to the hydrology of each river. The Baía River is richer in total phosphorous, total nitrogen, and chlorophyll-a (mean $\pm$ standard deviation: 66.67 ± 49.15 µg/l^{-1}; 882.66 ± 545.53 µg/l^{-1}; $11.28 \pm 14.34\chi$, respectively) and has the lowest conductivity (31.11 ± 8.89 µS/cm). The Ivinhema River has intermediate total phosphorous, total nitrogen, and chlorophyll-a concentrations (53.94 ± 27.65 µg/l^{-1}; $763.~64 \pm 465.45$ µg/l^{-1}; $7.37 \pm 10.24\chi$, respectively) as well as the lowest transparency (55.04 ± 33.29 cm). The Paraná River has the highest conductivity and transparency (57.67 ± 5.44 µS/cm; 183.96 ± 103.78 cm, respectively) and lowest total phosphorous, total nitrogen, and chlorophyll-a (21.85 ± 26.94 µg/l^{-1}; 476.09 ± 246.78 µg/l^{-1}; $5.03 \pm 6.42\chi$, respectively).

Sampling

Sampling was conducted quarterly between March of 2000 and December 2012 (i.e., one sampling in each season) as part of the Long-Term Ecological Research
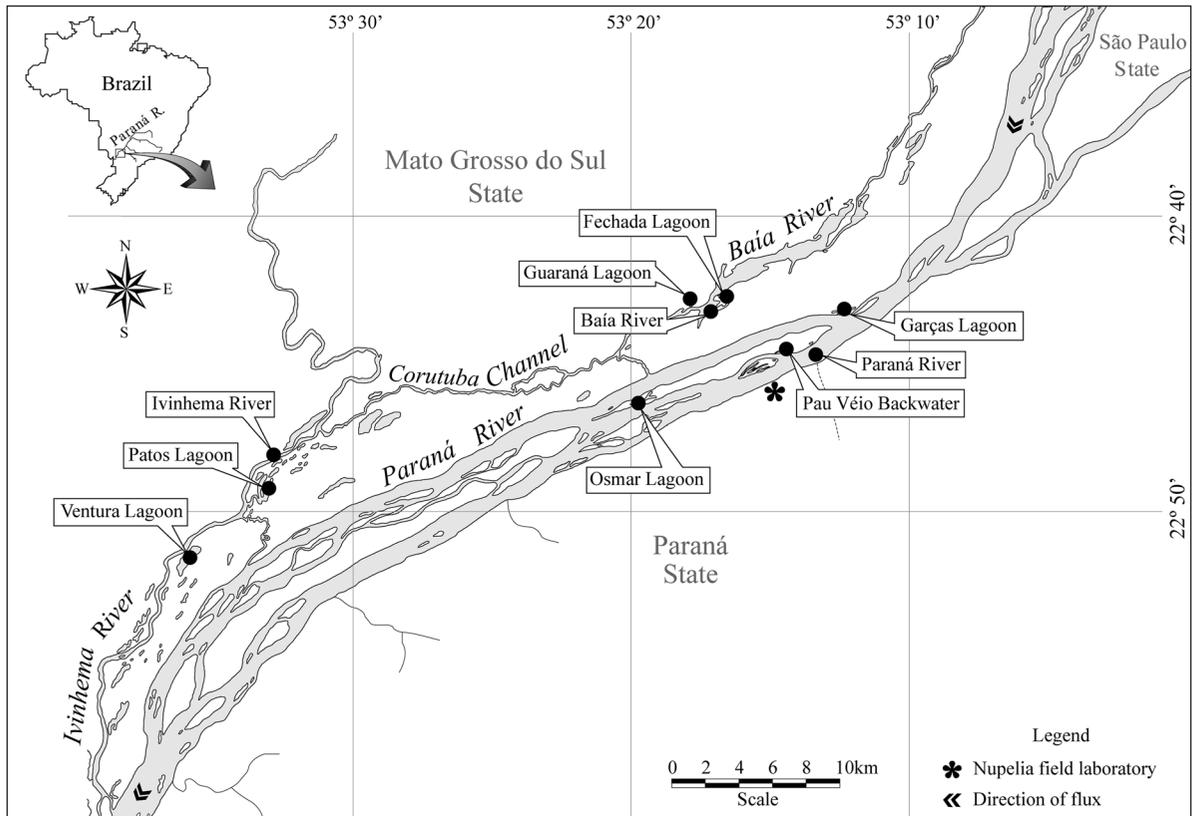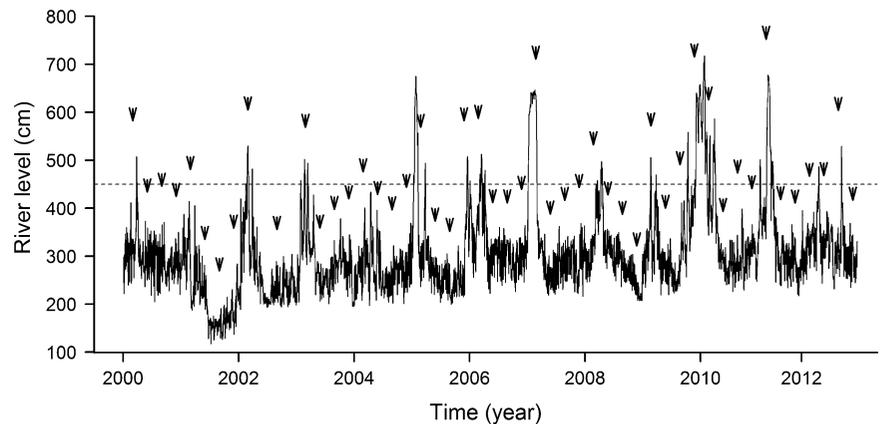
Fig. 1 Map of the Upper Paraná River floodplain

Fig. 2 The level of the Paraná River throughout the study period. The *dashed line* indicates the level at which the lagoons begin to connect hydrologically to the main river (460 cm; following Souza Filho, 2009). *Arrows* sampling months

Program (PELD/CNPq) conducted by the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura - Universidade Estadual de Maringá (Nupélia/UEM). Fishes were sampled in the channel of the main rivers and in four open and three closed lagoons (Fig. 1; Online Resource 1) using a set of 11 gillnets in each

sampling and site with mesh sizes of 2.4, 3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between knots. The gillnets were installed perpendicular to the shore. The nets remained exposed for 24 h and were inspected every 8 h. Thus, both the littoral and pelagic regions of each environment were sampled with the gillnets. Fishes

were also sampled in the littoral regions of each lagoon using a seine with mesh size of 0.5 cm. After sampling, the specimens were anesthetized (Eugenol), sacrificed, and identified by specialists. Voucher specimens were deposited in the Ichthyological Collection of Nupélia (NUP).

At each sampling site, the water temperature, transparency of the water column (Secchi disk), pH, electrical conductivity, and concentrations of dissolved oxygen, chlorophyll-*a*, and total nitrogen and phosphorus were measured. The river level was obtained from the fluviometric station of Porto São José—PR (National Water Agency—Station 2253016; Agência Nacional de Águas—Estação 2253016).

Data analysis

Occurrence matrices were set up so that the lines represented the sampled species and each column contained the sampled sites or periods. A general matrix (whole floodplain) was set up, in which each column corresponded to a site and sampling month. The remaining matrices were set up separating spatial and temporal scales, considering three spatial (sub-basin, type of environment, and site sampled) or temporal scales (year, season, and month sampled). It is important to note that in the co-occurrence analysis, the effects of each type of scale (spatial or temporal) are not independent of each other; i.e., in each co-occurrence analysis at any spatial scale, there is still noise due to the temporal scale and vice versa.

The occurrence matrices were set up separately for the fish sampled by gillnets and seines. The fishes were separated based on the sampling gear used because the gear type selects for species and sizes (Olin & Malinen, 2003; Online Resource 2), and seine sampling was only conducted in the littoral regions of the lagoons.

Spatio-temporal organization patterns were estimated based on the co-occurrence index *C*-Score (Stone & Roberts, 1990). This index calculates the average co-occurrence of species pairs as a checkerboard model in each assemblage (Stone & Roberts, 1990; Gotelli & McCabe, 2002):

$$C\text{-Score} = \sum_{i} \sum_{<j} \frac{C_{ij}}{\left(\frac{M(M-1)}{2}\right)},$$

$$C_{ij} = (r_i - S_{ij})(r_j - S_{ij}),$$

where C_{ij} is the checkerboard units of the species pair ij; r_i is the total occurrence of species i in the incidence matrix (sum of line i); r_j is the total occurrence of species j in the incidence matrix (sum of line j); S_{ij} is the number of co-occurrences of species i and j (sites or times shared by both species); and M is the number of species in the matrix. The higher the *C*-Score value, the lower the species co-occurrence in an assemblage.

A null model was used to assess whether the organization differed from random patterns (Gotelli & McCabe, 2002). The null model is a pattern-generating model that is based on randomized ecological data (Gotelli & McGill, 2006). Thus, it is possible to make inferences about a certain pattern or process observed compared to what would be expected by chance (the pattern or process generated by the null model). To create the null model, occurrence in the matrices was sequentially randomized using an algorithm that kept the total of occurrence by species (lines) and by sampling sites or periods (columns) fixed (Gotelli, 2000). *C*-Score was calculated for each simulated matrix, and the observed *C*-Score was compared to the mean of the simulated *C*-Scores. For each matrix, 30,000 simulations were performed (Lehsten & Harmand, 2006). *C*-Score values higher than those generated by chance indicated that the assemblage showed a segregation pattern, while values lower than those generated by chance indicated an aggregated occurrence pattern among species (Gotelli, 2000; Gotelli & McCabe, 2002; Presley, 2011; Krasnov et al., 2014). *C*-Score values that were not significantly different from those expected by chance indicated a random co-occurrence pattern (Gotelli, 2000; Gotelli & McCabe, 2002).

To compare the degree of organization for each assemblage between the matrices, *C*-Score standard effect sizes (SES; Gotelli & McCabe, 2002; Horner-Devine et al., 2007) were calculated. This index estimates the deviation of the observed co-occurrence from the mean simulated co-occurrence in units of standard deviation (Horner-Devine et al., 2007; Heino & Grönroos, 2013):

$$\text{SES} = \frac{C\text{-Score}_{\text{obs}} - C\text{-Score}_{\text{sim}}}{s_{\text{sim}}},$$

where *C*-Score$_{\text{obs}}$ is the observed *C*-Score; *C*-Score$_{\text{sim}}$ is the mean of the simulated *C*-Scores; and s_{sim} is the standard deviation of the simulated *C*-Scores.

A principal component analysis (PCA) was subsequently conducted using a correlation matrix to summarize the floodplain's physical and chemical characteristics throughout the studied period. All axes with eigenvalues greater than 1 (Kaiser–Guttman criterion; Jackson, 1993) were considered. To assess whether there was a relationship between environmental heterogeneity and the obtained co-occurrence patterns, multiple linear regressions were performed between the SES values for the temporal scale (response variable) and the scores of the retained PCA axes (predictor variables).

Because increasing water levels can disorganize aquatic assemblages by connecting isolated environments and allowing for the dispersion of organisms (Fernandes et al., 2009), the influence of the river level on the observed co-occurrence patterns was assessed through time. Simple linear regressions were performed between the SES values (response) and the river level (predictor) in both high- and low-water periods of the hydrological cycle. Prior to this analysis, the sampling months were categorized as high-water months when the Paraná River level reached 460 cm (the minimum flood level; Souza Filho, 2009) and as low-water months when the river level was below 460 cm. All regressions met the assumptions.

Finally, to assess whether the SES varied among years, a one-way analysis of variance (ANOVA) was conducted using the year as a predictor variable. For the gillnet data, the assumption of homogeneity of variances was met. However, for the seine data, this assumption was not met (Bartlett's test: $K^2 = 24.623$, $P < 0.01$). Thus, for the seine data, an ANOVA assuming heterogeneous variances was applied.

All analyses were performed in R 3.0.1 (R Core Team, 2013; Online Resource 3) using the package 'vegan' (Oksanen et al., 2013) to calculate the C-Score and null models. A significance level of 5% was adopted.

Results

Throughout the sampling period and considering both sampling gears, a total of 136 species were captured (Online Resource 4). Of these species, 71 were exclusively captured in gillnets and 18 in seines. Forty-seven species were caught with both types of sampling gear.

Table 1 The absolute (N) and relative (%) frequencies of C-Scores that were significantly higher than the mean of the simulated values[a]. The total numbers of matrices assessed at each level of analysis are shown in parentheses

Models	Gillnet		Seine	
	N	%	N	%
Whole floodplain	1(1)	100	0(1)	0
Spatial scale				
Sub-basin	3(3)	100	1(3)	33.33
Type of environment	3(3)	100	0(2)	0
Sampling site	8(9)	88.89	2(7)	28.57
Temporal scale				
Season	4(4)	100	0(4)	0
Year	13(13)	100	0(11)	0
Month[b]	24(50)	48	1(44)	2.27
March	7(13)	53.85	0(11)	0
June	4(12)	33.33	1(11)	9.09
September	9(13)	69.23	0(11)	0
December	4(12)	33.33	0(11)	0

[a] No model presented a C-Score higher than the mean of the simulated C-Scores

[b] The total number of matrices for all months

In the gillnet matrices, the general pattern of co-occurrence was significantly higher than would be expected at chance (Table 1; Online Resource 5). At smaller spatial scales (sampling sites), only the Pau Véio backwater showed random patterns, while at larger scales (types of environments and sub-basins), all of the matrices were non-random. At the shorter temporal scale assessed (sampling months), 52% (26) of the matrices presented co-occurrence values that were similar to those generated by chance. However, at longer temporal scales (seasons and years), all of the matrices showed co-occurrences that were higher than would be expected by chance (Table 1).

In the seine matrices, the general co-occurrence pattern was random (Table 1; Online Resource 6). Of the twelve matrices assessed at spatial scales, only three presented co-occurrences that were higher than would be expected by chance: two at sampling site scale and one at the sub-basin level (Ivinhema River). At the scale of environment type, all of the seine matrices presented random patterns of species distribution. At smaller and greater temporal scales, the distribution of species pairs was also random except for that in June 2005 (Table 1).

Table 2 A summary of the principal component analysis (PCA) performed on the physical and chemical variables measured quarterly from 2000 to 2012. The eigenvectors of each variable, eigenvalues, and percent of variability explained by each axis are presented. Only the PCA axes with eigenvalues greater than 1 were retained for interpretation

Variables	PCA 1	PCA 2	PCA 3
Water temperature	−0.137	−0.673	−0.570
Transparency	0.803	−0.243	0.155
pH	0.589	0.372	−0.634
Conductivity	0.677	−0.388	−0.306
Dissolved oxygen	0.407	0.811	−0.190
Chlorophyll-a	−0.562	0.133	−0.398
Total nitrogen	−0.587	0.101	−0.112
Total phosphorous	−0.867	0.056	−0.192
Eigenvalue	3.048	1.489	1.090
Percent of variability explained	38.10	18.62	13.62

Fig. 3 The relationship between the *C*-Score standard effect size (SES) and the river level in low (**a**, **c**) and high-water periods (**b**, **d**). *Closed circles* gillnets; *open circles* seines; sample sizes (n) = 41 (**a**), 9 (**b**, **d**) and 33 (**c**)

The first three PCA axes exhibited eigenvalues >1. Together, these axes explained approximately 70.34% of the physical and chemical variation at the sites (Table 2). The first axis was positively correlated with transparency and negatively correlated with total phosphorus. The second axis showed the greatest positive correlation with dissolved oxygen and the greatest negative correlation with water temperature. The third axis was negatively correlated with pH. The *C*-Score standardized effect size (SES) was not related to either the PCA axes for the gillnet (linear regression, $F_{3,44} = 1.787$, $r^2_{adjusted} = 0.048$, $P = 0.164$) or the seine matrices (linear regression, $F_{3,38} = 0.437$, $r^2_{adjusted} = -0.043$, $P = 0.836$).

The variation of the SES was not related to the river level in low-water periods (gillnet: $F_{1,39} = 3.67$, $r^2 = 0.09$, $P = 0.063$, Fig. 3a; seine: $F_{1,31} = 0.25$, $r^2 = 0.01$, $P = 0.618$, Fig. 3c). However, in high-water periods, months with higher river levels presented significantly lower SES values for species captured with gillnets (i.e., showing a tendency toward random co-occurrence; $F_{1,7} = 5.75$, $r^2 = 0.45$, $P = 0.048$; Fig. 3b), whereas for seines, a significant relationship between the SES and hydrometric level was not detected ($F_{1,7} = 0.36$, $r^2 = 0.05$, $P = 0.570$; Fig. 3d).

For species sampled with gillnets, the variation of the SES did not differ among years ($F_{12,37} = 0.79$, $P = 0.659$; Fig. 4), whereas for those sampled with seines, the differences were detected in the values of the SES among years ($F_{10,12.38} = 4.85$, $P < 0.01$; Fig. 4).
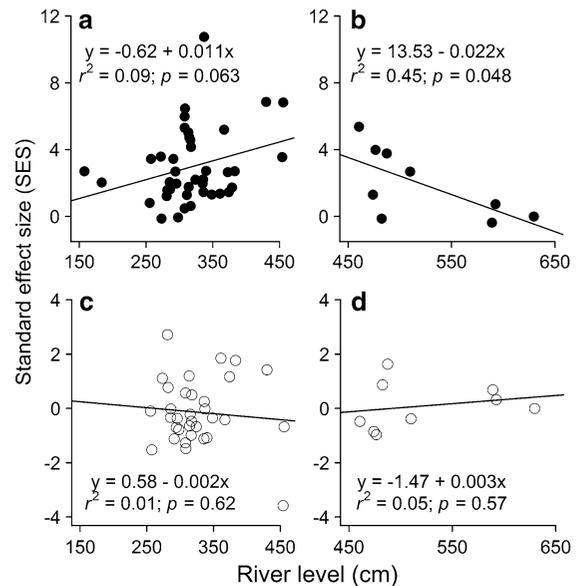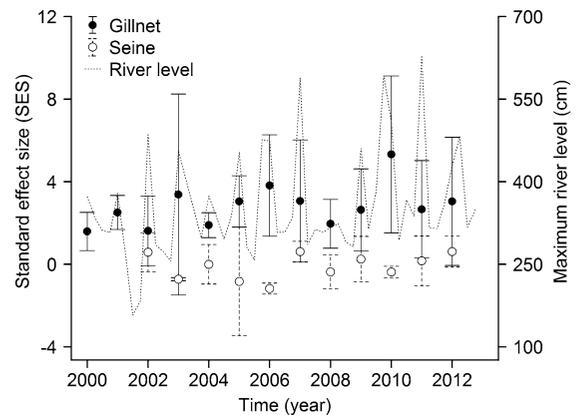

Fig. 4 Variation in the *C*-Score standard effect size (SES) over the time. *Closed* and *open circles* indicate the mean SES of each year and the *error bars* indicate standard deviation. The presented river levels are the maximum in each month. In 2000 and 2001, there was no sampling using seines; $n = 4$ in each year (except in 2003 which had 2 samples)

Discussion

Considering fishing gear as a proxy for assemblage size structure, this study indicates that the fish assemblages of the Upper Paraná River floodplain

are structured by the segregation of large species on both spatial and temporal scales. In contrast, the organization of small species is random, presenting little spatial segregation. These results suggest that the assemblages may exhibit different structuring mechanisms.

Segregated patterns can be generated by several mechanisms in communities. Interactions such as competition (Diamond, 1975; Gilpin & Diamond, 1982; Gotelli & McCabe, 2002) or predation (Englund et al., 2009), and the distributions of species according to their abiotic requirements (Gilpin & Diamond, 1982; McCreadie & Bedwell, 2013) are often considered the main mechanisms driving community structure. The coexistence of competitively similar species is theoretically possible only if there is some difference in their resource use (MacArthur & Levins, 1967). Thus, throughout the evolutionary scale, competitive interactions may have caused niche differentiation between species (Douglas et al., 1994), resulting in a change in distribution in space or time. Predation can also result in segregated patterns (Oliveira et al., 2005; Englund et al., 2009; Fernandes et al., 2009) because the predation regime regulates prey abundance (Piana et al., 2006) and may drive prey populations to local extinction in extreme cases (Englund et al., 2009).

Because the persistence of a given species at a site depends on suitable conditions and resources for its growth and reproduction, the requirements for a specific resource (e.g., prey or oxygen availability) or condition (e.g., ideal temperature or pH range) could have produced the observed segregation patterns (Gilpin & Diamond, 1982). Such patterns would occur for two species exhibiting different specific requirements because they will likely occur in distinct environments (i.e., showing a habitat checkerboard; McCreadie & Bedwell, 2013).

Agostinho et al. (2004b) described two primary reproductive strategies that are adopted by fish species with medium and large body sizes in the Upper Paraná River floodplain: long distance migrants (such as *Prochilodus lineatus* and *Salminus brasiliensis*) that depend directly on migration to complete the development of their gonads as well as the spawning process; and short distance or non-migratory species. Within this latter group, there are species that present external fecundation with parental care (such as *Serrasalmus* spp. and *Cichla*

spp.) that are more independent of the flood cycle and those without parental care (such as *Pimelodus* spp.) that depend on migration and the flood regime to complete their life cycles. These different reproductive strategies lead to particular requirements that produce a tendency to explore different habitats along the cycles of flood and drought on a floodplain. These different requirements may form a pattern of spatio-temporal segregation of the floodplain species.

Random patterns were frequent for the small-sized fish (captured by seine). This pattern may arise due to the high dispersal ability of these species and demographic stochasticity (Ulrich, 2004; Gotelli & McGill, 2006), which determine the occupation and persistence of species at a given site or time (Ulrich, 2004; Gotelli & McGill, 2006). Random patterns can also be generated by resources or environmental fluctuations (Grossman et al., 1998; Arrington et al., 2005; Boschilia et al., 2012), which have been particularly frequent in the Upper Paraná River floodplain, given that upstream dams cause daily fluctuations in the river level (Agostinho et al., 2004a). Such impacts can lead to the disorganization of an assemblage (Bhat & Magurran, 2007; Boschilia et al., 2012), as the daily oscillation in the habitat size (e.g., retraction and expansion of the littoral region) selects species that can adapt to this dynamic.

Oliveira et al. (2001) analyzed the fish community structure of littoral areas of the Upper Paraná River floodplain that are dominated by fish species with small body size. According to these authors, the littoral zones of rivers and lagoons had high richness but low diversity because of the reduced uniformity in species distribution. The low species uniformity may be related to broad variations in the abiotic parameters (especially temperature and dissolved oxygen) that cause the establishment of stressful conditions for the resident fish assemblages. These restrictive environmental conditions might be related to the observed random patterns in the spatio-temporal organization of species.

Neither physical nor chemical variables explained the co-occurrence observed in large species. Furthermore, there was a negative relationship between the co-occurrence pattern and hydrometric level of large fish in the high-water period. These results suggest that the flood pulse alone, rather than any other physical or chemical predictor assessed, could have driven the

organization of the assemblages of larger fish. In floodplains, flood pulses determine both the distribution of organisms and abiotic conditions (Thomaz et al., 2007), and reflect the community organization (Arrington et al., 2005; Fernandes et al., 2009) because flood pulses can directly influence the dynamics of biotic interactions and local patterns of abundance and diversity.

In low-water periods, biotic interactions or abiotic gradients in isolated habitats can determine the species that persist (Piana et al., 2006). As the river level rises, aquatic environments are expanded through the connections between isolated sites and the main channels of rivers. Fish may thereby disperse to different floodplain environments for a variety of reasons, such as migrating for reproduction or searching for food, because the flood increases the availability of accessible habitats (Fernandes et al., 2009). Within this gradient of hydrometric connections, it is feasible that communities could shift from showing structured patterns in low-water periods to random patterns in high-water periods (Arrington et al., 2005; Fernandes et al., 2009). This study partially corroborates this hypothesis. In high-water periods, the assemblages composed of large-sized species became less organized (as seen in Fig. 3b), whereas in low-water periods, wide variation in co-occurrence patterns was observed, which could explain the absence of a relationship with the river level. The pattern observed in low-water periods may result from variations in the relative importance of structuring mechanisms (i.e., interactions, species-specific environmental requirements, or abiotic restrictions after a flood; Fernandes et al., 2009).

In the Upper Paraná River floodplain, reproductive migration of large-sized fish species is well known, whereas smaller species do not exhibit this strategy (Suzuki et al., 2004, 2009). The timing of reproductive migration is highly influenced by the timing and duration of flooding (Suzuki et al., 2009). Considering the striking contrast observed in the co-occurrence patterns between large and small species and differing importance of the hydrometric level, we can infer that life history traits such as body size might influence the spatio-temporal organization patterns. This hypothesis can be further explored at a temporal scale based on species co-occurrence patterns in functional groups (e.g., Hoeinghaus et al., 2007).

Conclusion

Overall, this paper presented evidence that the fish assemblages of the Upper Paraná River floodplain exhibited co-occurrence patterns that vary according to the body size of the species, which suggests an influence of species life history traits on co-occurrence patterns. Furthermore, the flood pulse acts as a mechanism driving community structure. Although the flood pulse in this floodplain is regulated by upstream damming (Agostinho et al., 2004a) and influences the limnological dynamics of this environment (Thomaz et al., 2007), it still plays a major role in driving the co-occurrence and spatio-temporal organization patterns of these assemblages.

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