Climatic seasonality, hydrological variability, and geomorphology shape fish assemblage structure in a subtropical floodplain

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Abstract: We applied a multiscale approach to understand the patterns of longitudinal, lateral, and temporal variability in fish assemblage structure of a large floodplain river and explored their relationships with climatic seasonality, hydrological variability, and floodplain geomorphology. We studied the fish assemblage structure of 35 connected lakes along a 600-km section of the Paraná River over 5 y. Longitudinal changes in fish assemblage structure were associated with a latitudinal climatic gradient, whereas temporal changes were associated with climatic seasonality and hydrological variability. Longitudinal and seasonal changes in assemblage structure were probably based on different thermal preferences of species that migrate seasonally along the main river axis. Extraordinary floods in summer promoted downstream dispersal of several species, which increased similarity between downstream and upstream regions. Thermal seasonality of this subtropical system was a strong factor driving temporal changes in assemblage structure, and the effects of the hydrological regime largely depended on flood pulses coincident with periods of warmer temperatures. Fish assemblages varied secondarily along a lateral gradient represented by types of geomorphic units distributed in the floodplain. The geomorphic units generated patchy environmental heterogeneity at the landscape scale that resulted in discontinuous patterns of fish assemblage structure. Assemblage composition was more similar among lakes belonging to similar geomorphic units but situated at geographically distant regions than among lakes belonging to different geomorphic units situated in the same region. Therefore, patterns in fish assemblage variation at regional and landscape scales appear to be determined largely by the dispersal and selection of suitable habitats by fish across the hierarchy of spatial and temporal scales.

Key words: flood pulse, temperature, dispersal, neotropical fish, community ecology

A main goal of community ecology is to identify the processes that influence the patterns of community structure along spatial and temporal scales. Patterns observed in communities at a particular scale are often the consequence of complex interactions among several processes occurring at multiple scales (Dray et al. 2012). Therefore, multiscale approaches are strongly recommended to analyze the patterns of community structure (Dray et al. 2012, McGarigal et al. 2016). Many authors encourage broadening spatial and temporal scales of studies to recognize the hierarchical organization of the ecological systems and effects of environmental heterogeneity or patchiness at each scale (Wu and Loucks 1995, Leibold et al. 2004, Vellend 2010).

Floodplain rivers are complex ecosystems with patchy environmental heterogeneity at multiple spatial and temporal scales (Amoros and Bornette 2002, Poole 2002, Ward et al. 2002, Winemiller et al. 2010). Several authors have proposed theoretical frameworks to integrate longitudinal (upstream–downstream), lateral (main channel–floodplain), and temporal (seasonal) dimensions of river ecosystems, incorporating geomorphological, hydrological, and ecological characteristics (e.g., Poole 2002, Thorp et al. 2008,

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Humphries et al. 2014). Changes in community structure along the longitudinal dimension have been attributed to environmental gradients generated as stream order increases along the altitudinal gradient (Vannote et al. 1980), or by geomorphic patches at the landscape scale (Montgomery 1999). Changes along the lateral dimension generally have been associated with channel–floodplain connectivity (Ward et al. 2002, Junk and Wantzen 2004, Pouilly and Rodríguez 2004). Variability in community structure along the temporal dimension generally is related to the seasonal variation in temperature and interannual pattern of river flow regimes (Poff et al. 1997, Junk and Wantzen 2004, Winemiller 2004). However, few investigators have analyzed simultaneously the processes influencing community structure at multiple scales in large rivers. We evaluated the factors driving changes in fish community structure along longitudinal, lateral, and temporal dimensions in lakes of a large South American river with an intact floodplain.

The dynamics of fish assemblage structure in rivers have been explored at a diversity of temporal and spatial scales and have been associated with multiple factors (reviewed by Matthews 1998, Jackson et al. 2001, Helfman et al. 2009). Fish assemblages show gradual changes in species richness and composition along the longitudinal dimension as stream order and habitat complexity increase, giving rise to nested patterns of species composition (Matthews 1998, Jackson et al. 2001). In river systems with large longitudinal variation in climate, geology, and relief, assemblage composition generally shows strong discontinuities with high species turnover between adjacent sites (Balon and Stewart 1983, Ibarra and Stewart 1989, Montgomery 1999, Walters et al. 2003, Boys and Thoms 2006). The longitudinal distribution of fish species also can vary seasonally by migratory movements in response to the flow regime and thermal seasonality of rivers, producing temporal changes in assemblage composition (Jackson et al. 2001, Hoeinghaus et al. 2003, Grossman et al. 2010). Differences in temperature along the longitudinal dimension have been associated with the altitudinal gradient, but large lowland rivers with a large latitudinal extent can develop considerable climatic gradients that, in turn, affect the structure of fish assemblages. In temperate regions of southern South America, fish species can differ substantially in their thermal preferences (Cussac et al. 2009). In this context, we expect that migratory species will use different river sections on the basis of their thermal preferences, producing longitudinal changes in fish assemblage structure.

Changes in fish assemblage structure on the lateral dimension of rivers (from the main river to the floodplain) are related to the channel–floodplain connectivity (Persat et al. 1994, Rodríguez and Lewis 1997, Pouilly and Rodríguez 2004, Pouilly et al. 2004, Zeug et al. 2005, Zeug and Winemiller 2008, Lasne et al. 2007, Górski et al. 2013). The dynamics of the lateral connectivity in these environments are largely determined by the interaction between the flood pulse and floodplain geomorphology (Górski et al. 2013). The relationship between geomorphic units and fish distribution has been tested in small and medium streams (Walters et al. 2003, Boys and Thoms 2006), where geomorphic heterogeneity occurs largely through the longitudinal dimension, but evidence is limited for large rivers (Rodríguez and Lewis 1997, Pouilly and Rodríguez 2004, Górski et al. 2013), where geomorphic heterogeneity is high in both longitudinal and lateral dimensions (Gupta 2006). Large lowland rivers develop wide floodplains with many types of geomorphic units, identified as landscape patches supporting several types of lakes and water courses that differ in size, shape, and connectivity, and in the characteristics and dynamics of the surrounding terrestrial areas (Gupta 2006, Marchetti et al. 2013). The variation in lake morphometry and connectivity across the floodplain can determine different fish assemblages through their effect on lake transparency (Rodríguez and Lewis 1997, Pouilly and Rodríguez 2004, Scarabotti et al. 2011, Górski et al. 2013) and can select species on the basis of their trophic specializations (Pouilly et al. 2004). Consideration of geomorphic units as environmental patches at the landscape scale can contribute to understanding the discontinuous patterns of fish assemblage on the lateral and longitudinal dimension (Boys and Toms 2006, Thorp et al. 2008).

The pattern of seasonal variation in water level has been proposed as the main factor driving the temporal changes in tropical large river ecosystems (Junk and Wantzen 2004, Humphries et al. 2014). In these environments, high seasonal predictability of flood pulses has promoted the evolution of life-history strategies closely associated with the flow regime (Junk et al. 1997, Winemiller 2005). In subtropical and temperate rivers, the flood regime can vary widely among years, whereas temperature exhibits strong and predictable seasonal variation (Tockner et al. 2000, Winemiller 2005). In these rivers, system productivity depends largely on the occurrence of flood pulses in phase with periods of warm temperatures, which can generate windows of opportunity for riverine fish to exploit the floodplain (Winemiller 2004, Humphries et al. 2014). In this way, the seasonal variation of temperature in the subtropical rivers could be a stronger predictor than hydrometrical level of the changes in fish community structure. Periods with flood pulses in phase with warmer temperatures show higher species richness and biomass in association with favorable environmental conditions and higher resource availability (Winemiller 2004, Scarabotti et al. 2011).

We present an analysis of data from fish surveys carried out by the Argentinean Bureau of Continental Fisheries along a 600-km section of the Paraná River floodplain between 2008 and 2013. This work was part of a collaborative project investigating the population dynamics of fish species exploited by commercial fisheries and patterns of abundance and biomass of noncommercial species. The large spatial and temporal extent of our study provided a unique opportunity to evaluate the relationship between environmental heterogeneity at multiple scales and the longitudinal, lateral, and temporal patterns of fish assemblages of a relatively undisturbed large river floodplain.

The objective of our study was to apply a multiscale approach to identify the main factors leading the temporal and spatial changes in the structure of fish assemblages of floodplain lakes of the middle and lower Paraná River in Argentina. We aimed to learn whether: 1) the longitudinal pattern of fish assemblage structure could be drawn in relation to longitudinal climate gradients and thermal seasonality, 2) the lateral pattern could be associated with the type of geomorphic units of the floodplain, and 3) the relative importance of climatic seasonality and hydrologic variability could explain the temporal patterns of fish assemblage structure.

METHODS

Study area

The Paraná River is one of the largest freshwater systems of South America, with a basin area of 2.6×10^6 km^2, and an historical mean annual flow of ~17,000 m^3/s at the gage station in Paraná City (Giacosa et al. 2000, Iriondo and Paira 2007). In its lower reaches, the Paraná River undergoes regular annual flood pulses corresponding to water elevations of ~2 to 3 m above mean annual level. Flood pulses have relatively low seasonal predictability and high interannual variability in their magnitude and duration (Neiff 1990). Extraordinary flow peaks occur every 2 to 7 y mainly in association with El Niño southern oscillation events (Robertson and Mechoso 1998, Depetris and Pasquini 2007). The Paraná River floodplain is a complex mosaic of geomorphic units that vary in their connectivity with the main channel, topographic level, slope, floodwater permanence, and type of vegetation (Iriondo 2004, Marchetti et al. 2013).

The sampling design of the survey was partially unstructured with regard to temporal and spatial scales. These kinds of design are useful when little is known a priori about the ecosystem being studied. In this design, the sets of explanatory variables (spatial, temporal, hydrological, and geomorphological) were inextricably confounded with one another in such a way that made attribution of the causes of patterns in the species data impossible. Therefore, the nature of our hypotheses was correlative rather than causative. In these cases, partial constrained ordination techniques (pCCA, pRDA) can be used to test hypotheses about relationships among the sets of explanatory variables and assemblage structure (Anderson and Gribble 1998, Økland 2003).

We studied 35 permanent lakes, continuously connected to the river network, in 4 regions along a latitudinal gradient of 600 km of the middle and lower reaches of the Paraná River (Fig. 1). The 4 regions surveyed were situated along a latitudinal gradient (region 1: 33°S, region 2: 32°S, region 3: 31°S, region 4: 29°S) with colder temperatures in the south (mean annual temperature = 17°C) and warmer temperatures in the north (mean annual temperature = 20°C) (Bianchi and Cravero 2010). We sampled regions 1 and 3 (15 lakes in each region), near the cities of Victoria and Cayastá, respectively, more extensively than regions 2 (3 lakes) and 4 (2 lakes).

We conducted 11 sampling surveys between March 2009 and April 2013. Surveys occurred in 2 main groups: 1) surveys 2, 5, 8, 10, and 11 were done in lakes of all 4 regions with the aim of studying the changes in assemblage structure along the longitudinal dimension (Table 1); 2) surveys 1, 3, 4, 6, 7, and 9 were done in lakes situated at different distances from main channel in regions 1 and 3 to study the changes in assemblage structure along the lateral dimension of the floodplain (Table 1).

Sampling surveys were carried out at different hydrologic periods (high and low waters) and seasons (cold and warm seasons). A survey was classified as high water if the water level was >3.42 m measured at the Paraná City gage (data provided by Prefectura Naval Argentina). At this level, water begins to overflow the natural levees that separate the floodplain from the river. Cold-season surveys were those done during winter and spring (June–November), whereas warm-season surveys were those done during summer and autumn (December–May). The occurrence of flood pulses during both seasons enabled us to have samples from all combinations of hydrologic periods and climatic seasons: cold season, low water (3 surveys); warm season, low water (4); cold season, high water (2); and warm season, high water (2).

Within each region, we sampled 1 to 3 lake types situated in different geomorphic units of the floodplain (Table 1, Fig. 1). Lake types were characterized as follows: 1) Main channel lakes (MCL) are elongated or drop-shaped lakes close to and connected directly or via a short channel with the main channel or secondary branches. These lakes are generally deep and have large macrophyte stands in their margins. They are strongly influenced by the hydrological disturbances and show high variability in water level and turbidity. 2) Scroll lakes of minor channels (SL) are small, semilunar lakes connected directly to minor floodplain channels. These channels generally run parallel to and apart from the main channel and originate during the lateral movements of minor floodplain channels. These lakes are relatively deep and develop large macrophyte stands in their margins. 3) Anastomosed floodplain lakes (AFL) are large, shallow subcircular lakes interconnected by a dense network of narrow, sinuous channels that originate from deltaic splays in sections of poor drainage of the floodplain. These lakes have a large open pelagic area relative to a small vegetated littoral

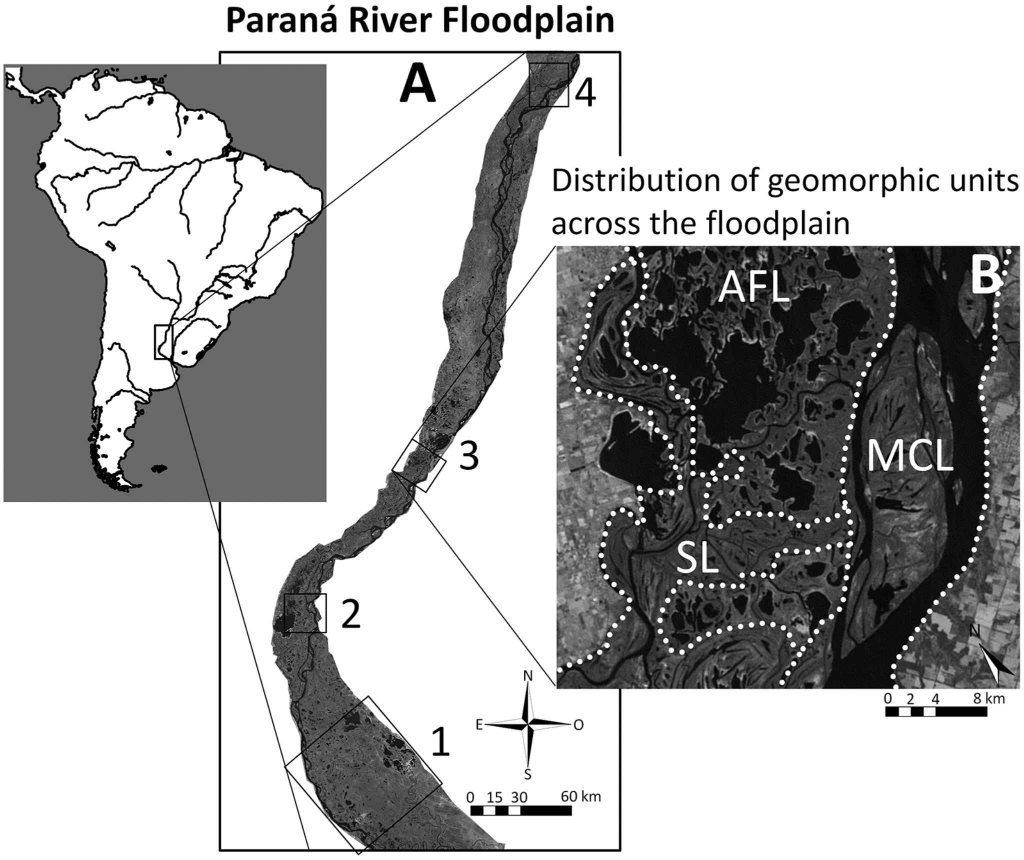

Figure 1. A.—Distribution of the 4 sampling regions (black squares) along the floodplain of the middle and lower reach of Paraná River and its location in South America. B.—Detail of the distribution of the lakes in 3 geomorphic units as defined by Marchetti et al. (2013) in region 3, near the city of Cayastá. MCL = main channel lakes, SL = scroll lakes of minor channels, AFL = anastomosed floodplain lakes.

zone and experience strong wave action that continuously resuspends fine sediments and causes high turbidity. Given the large lateral development of the floodplain and the occurrence of long natural levees bordering the main channel, these lakes can be separated from the main channel by water distances of 2 to 100 km. Therefore, we differentiated AFL close to the main channel (<10 km apart, AFL_c) from AFL far from the main channel (>10 km apart, AFL_f). All lakes,

Table 1. Number of lakes sampled during each survey for each lake type in 4 geographic regions of the Paraná River floodplain. The ranges and medians (in parentheses) for distance to main channel (DMCH), distance to secondary branches (DSB), and lake surface area are shown for each lake type. See Fig. 2 for lake type abbreviations.

			Sampling survey													
Region	Lake type	Lakes sampled	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	DMCH (km)	DSB (km)	Area (ha)
1	AFL_f	9	1	5	1	2	4	1	2	4	2	4	4	37–83 (63)	37–83 (63)	6–12399 (1571)
3	AFL_c	9	6	2	8	6	3	8	9	2	9	2	4	6–12 (7)	2–8 (4)	15–870 (98)
3	AFL_f	3		3				1		3		3	2	18–22 (20)	10–18 (14)	0.9–4191 (2096)
1	SL	2	2		2	2		2	2		2			32–49 (36)	32–40 (36)	6–68 (37)
3	SL	3			2	1		1	2					9–17 (15)	6–14 (11)	7–55 (19)
1	MCL	4	2		3	2		2	1		1			2–5 (4)	0.2–2 (2)	53–280 (203)
2	MCL	3		2			2			3		3	3	9–10 (9.5)	1.5–2 (1.7)	26–27 (26)
4	MCL	2		2			2			2		2	2	3–4 (4)	0.1–0.1 (0.1)	14–85 (50)
	Total	35														

regardless of type, were connected and permanent. Thus, differences in surface area or depth were not associated with the risk of drying.

Fish sampling

We collected fish with 2 sets of 12 multifilament nylon gill nets (25 × 2 m) of different mesh sizes (15, 20, 25, 30, 35, 40, 45, 52.5, 60, 70, 80, 90 mm) placed in different locations on each lake. To standardize sampling effort, we deployed gill nets for 12 h (dusk–dawn) on each sampling date. Nets were situated perpendicular to the shore and tied to one another in order, with smaller nets near the shore and large nets near the center in a similar way in all lakes. The gill nets enabled us to catch fish between 6 and 101 cm (Table S1). The selectivity of this method limited our analysis of fish assemblages to the medium- and large-bodied fish species inhabiting floodplain lakes of Paraná River.

We identified fish to species level (Almirón et al. 2015, Mirande and Koerber 2015), measured (standard length in mm), and weighed (total mass in g) them directly after capture. Fish collection was authorized by the Bureau of Continental Fisheries of Argentina (Ministry of Agriculture, Livestock and Fisheries). When possible, live individuals were returned to the water after identification and measurement. When necessary, the other individuals were sacrificed rapidly after the capture by percussive stunning or left in high doses of anesthetic to minimize suffering. Voucher specimens are archived in the Museo Provincial de Ciencias Naturales, Santa Fe, Argentina, and the Instituto Nacional de Limnología (UNL-CONICET), Santa Fe, Argentina. Local fish assemblages do not contain endangered or protected species.

Spatial and temporal ordination of samples

We calculated fish density and biomass from fish counts and masses, respectively, and referenced each sample to the same unit of effort corresponding to 2 sets of gill nets deployed for 12 h. For each sample, we calculated the number of species present in a standardized sample of 50 individuals by rarefaction (Heck et al. 1975). To reduce distortion caused by rare species in ordination analysis, we removed taxa occurring in <3 samples and with a total abundance of <5 individuals (29 of 112 species) from the multivariate analysis data set (ter Braak and Šmilauer 2012) and obtained a matrix of 89 species distributed among 154 samples. We $\ln(x)$-transformed abundance data. We conducted a correspondence analysis (CA) to obtain an ordination of samples (lake × date) based on variation in species abundance. To control for the disproportional effect of less abundant species in this method, we used the empirical method of down-weighting rare species (CANOCO, version 5; ter Braak and Šmilauer 2012). We selected Hill's scaling to express species turnover in standard deviation (SD) units. We conducted a similar CA based on fish biomass. This analysis produced nearly identical results, so we present only the results of the CA performed on abundance data.

Validation of ordination results by analysis of subsets

The sampling design was incomplete between longitudinal and lateral dimensions, so we assessed whether the ordination patterns observed in the full data set were consistent with those observed in 3 subsets of data (see Ejrnæs and Bruun 2000 for a similar method): 1) samples from surveys 2, 5, 8, 10, and 11, which covered 4 regions and included 68 samples and 85 species, corresponding to longitudinal dimension; 2) samples from surveys 1, 3, 4, 6, 7, and 9, which covered 2 or 3 lake types sampled in regions 1 and 3 and included 85 samples and 88 species, corresponding to the lateral dimension; 3) all samples from regions 1 and 3, which were sampled during 11 surveys and included 130 samples and 88 species, corresponding to the temporal dimension. We tested the correlations between the sample and species scores from ordinations of subsets of data with scores on the same axes from ordinations of the full data set by mean of Pearson correlations.

Relationships between assemblage structure and different sets of explanatory variables

We accounted for the intrinsic confounding of environmental, temporal, and spatial variables present in our database by means of variation partitioning. This procedure allows calculation of pure and shared components of variation resulting from different sets of explanatory variables (Anderson and Gribble 1998, Økland 2003). We considered 4 sets of variables. 1) Five *hydrological variables* described the flood-pulse properties during and before the sampling date. These variables were water level on the sampling date (H1); duration of the previous high water (H2) and of previous low water (H3), corresponding to the number of days with water level above or below overbank level (3.42 m at the Paraná City gage), respectively, during the preceding 365 d; and intensity of the high- (H4) and of the low-water phase (H5), as the total area of the hydrograph above and below the bankfull level during the previous year, respectively. 2) Six *temporal variables* were included as descriptors of temporal distance and seasonal change between sampling dates. These variables were Julian dates of samples (T1); climatic season (winter, spring, autumn, summer) included as 4 dichotomous binary variables (T2–T5); and lunar cycle (T6), which was included to consider the potential effect of moonlight on the effectiveness of nocturnal gill net sampling and was based on a sinusoidal function with a period 29.53 d (values ranged from 1 to −1, corresponding to full and new moon, respectively). 3) Seven *geomorphological variables* were related to the physical habitat and size of the lake. These variables were lake type (included as 3 dichotomous dummy variables [G1–G3]) and 4 lake morphometric variables that can affect processes occurring at the habitat level (Rodríguez and Lewis 1997), including lake surface area (G4), lake perimeter at average water level (G5), shoreline index (G6; ratio of perimeter to lake area), and shoreline development (G7; ratio of lake perimeter to the circumference of a circle of equal area). 4) Eleven *spatial variables* represented the position of the lake in the floodplain and the connectivity modality. These variables were spatial position (S1–S8) obtained from the residuals of longitude and latitude data (x, y) calculating the terms of a cubic polynomial function (x, y, x^2, y^2, xy^2, yx^2, x^3, y^3) by the method of trend-surface analysis (Legendre and Legendre 2012), which is useful for predicting coarse nonlinear patterns in the species matrix (Fortin and Dale 2005); minimum watercourse distance from the lake border to the main channel (S9); minimum watercourse distance to the nearest secondary branch (S10); and minimum overland distance (i.e., Euclidean distance) to the main channel (S11). These variables were measured on georeferenced satellite images in Google Earth Pro (Google, Menlo Park, California).

A series of CCAs and pCCAs (Økland 2003) was carried out to assess relationships between assemblage structure and the different sets of explanatory variables (Borcard et al. 1992, Peres-Neto et al. 2006). First, CCA was run separately on each set of explanatory variables (hydrological, geomorphological, temporal, or spatial). We used the forward-selection procedure to reduce multicollinearity within each set. Next, we used selected variables in a pCCA to partition the variation in fish abundance explained by each set of variables. We reported the variation explained by each component as % total variation explained (TVE), calculated as the ratio of the sum of all canonical eigenvalues and total inertia, as recommended by Økland (1999). Statistical tests were run in CANOCO (version 5; ter Braak and Šmilauer 2012).

RESULTS

We collected a total of 47,663 individuals belonging to 112 species (Table S1). The detritivorous characid *Prochilodus lineatus* was the dominant species (21.8% of the total biomass), followed by the omnivorous *Megaleporinus obtusidens* (8.2%), and the piscivorous *Hoplias malabaricus* (7.9%) and *Salminus brasiliensis* (6.2%). These species are among the larger-bodied species of the assemblage, are highly valued for regional commercial or sport fisheries, and, except *H. malabaricus*, are migratory. The most numerically abundant species was *P. lineatus* (10.8%), followed by the catfish *Parapimelodus valenciennis* (10.7%), the curimatid *Cyphocharax platanus* (6.4%), and the armored catfish *Loricariichthys melanocheilus* (6.3%).

Temporal variation of fish abundance and biomass was influenced predominantly by the extraordinary flood in 2010 and had the highest values after this flood (Fig. 2A). Species richness also increased after the 2010 flood and decreased gradually in the following surveys (Fig. 2C). This flood was the largest since 1997, with a duration of 240 d and a water level of 6.60 m at the gage in Paraná City. Spatial variation of fish abundance and biomass was influenced primarily by connectivity (Fig. 2B). Abundance and biomass generally were higher in the more connected MCLs than in the less connected and distant AFLs, whereas species richness was similar among the different lake types (Fig. 2D).

Sample and species scores on the first 2 axes of CA ordination of the full data set were highly correlated with the scores of CA ordinations of each subset (Table S2). Therefore, for simplicity we show only the results corresponding to the analysis of the full data set. CA of the full data set showed temporal (climatic seasons and hydrological periods; Fig. 3A) and spatial (regions and lake types; Fig. 3B) differences in assemblage structure. The first 2 CA axes explained 14.5 and 8.0% of total variation in the species matrix, respectively. On the temporal dimension, the 1st axis separated mean sample scores of cold-season surveys, from mean sample scores of warm-season surveys (Fig. 3A). Within cold- and warm-season groups of scores, mean sample scores of high-water surveys were displaced to the bottom right with respect to mean sample scores of low-water surveys. On the spatial dimension, mean scores of samples were separated primarily by lake type and secondarily by region (Fig. 3B).

Species scores from the same CA showed a differential distribution along CA axes (Fig. S1). The Silverside *Odontesthes bonariensis*, River Anchovy *Lycengraulis grossidens*, characids *Oligosarcus oligolepis*, *Oligosarcus jenynsii*, and *Charax stenopterus*, and the cichlid *Crenicichla lepidota* had negative scores on CA axis 1, indicating higher abundance in lakes from southern regions and during the cold season. The piscivorous catfishes *Pseudoplatystoma reticulatum* and *Sorubim lima* and the characiforms *Brycon orbygnianus*, *Mylossoma duriventre*, and *Cynopotamus kincaidi* showed the largest positive scores on CA axis 1, indicating higher abundance in samples from northern regions and during the warm season. Species that were more common during the cold season generally showed higher abundance in southern regions, whereas species common in the warm season generally showed higher abundance in the northern regions (Fig. 4).

Species with positive values on the CA axis 2, such as the loricariids *Brochiloricaria chauliodon*, *Ricola macrops*, *Loricariichthys anus*, and *Paraloricaria vetula*, the exotic European carp *Cyprinus carpio*, and the stingray *Potamotrygon brachyura*, had higher relative abundance in the less connected AFL lakes. In turn, species with negative values on CA axis 2 like small- and medium-sized characids (genera *Astyanax*, *Charax*, *Roeboides*, and *Mylossoma*) and some curimatids (genus *Psectrogaster* and *Cyphocharax*) had higher

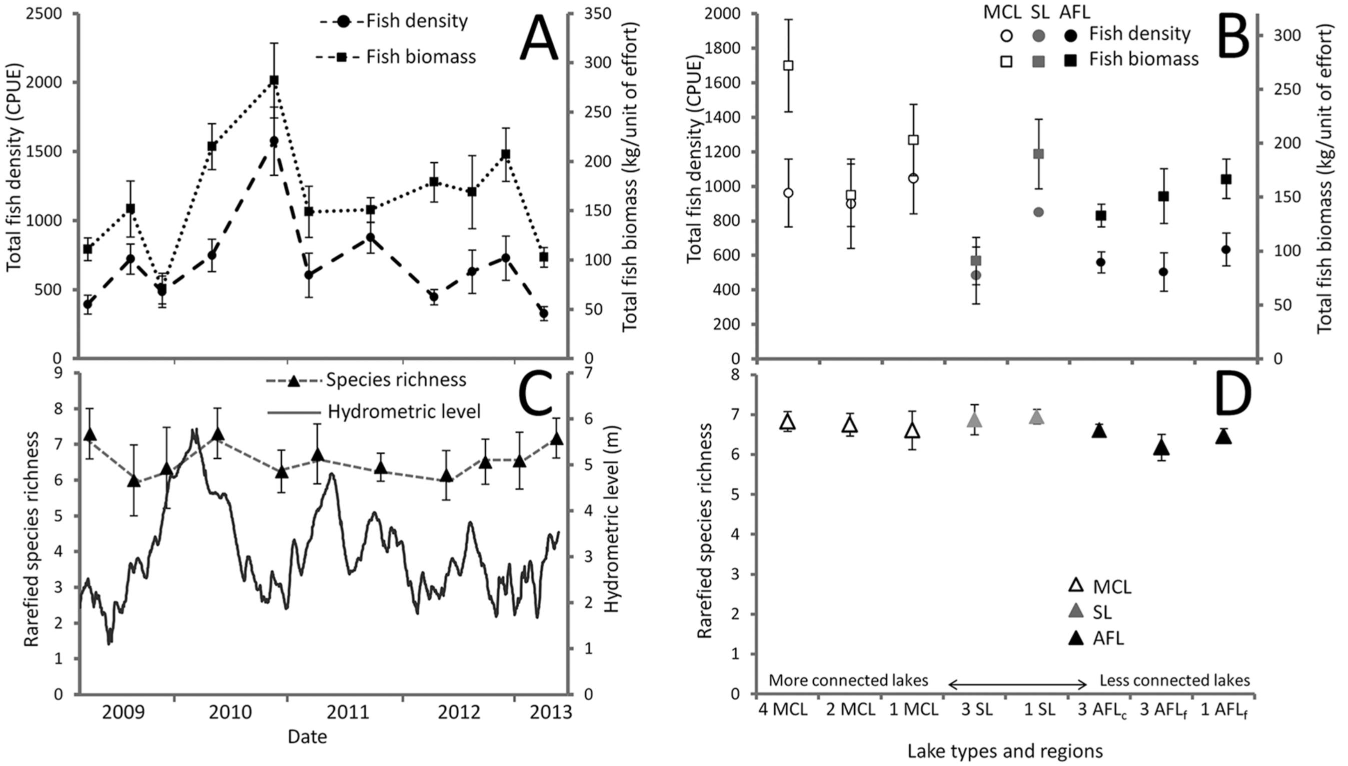

Figure 2. Mean (±SE) abundance (as density = catch per unit effort [CPUE] and biomass) (A, B) and species richness (C, D) over time (A, C), and in space (B, D) of whole fish assemblages of 35 lakes from the middle and lower reaches of the Paraná River. In panels A and B, symbols correspond to sampling surveys 1 to 11, and in panels C and D, symbols correspond to lake types sampled in 4 regions (1–4). In panel B, hydrometric level was measured at the Prefectura Naval gage at Paraná, Argentina. MCL = main channel lakes, SL = scroll lakes of minor channels, AFL = anastomosed floodplain lakes close (AFL_c) or far (AFL_f) from the main channel.

relative abundance in more connected MCL lakes (Fig. 5). Several abundant species like *P. lineatus*, *M. obtusidens*, *H. malabaricus*, *S. brasiliensis*, *P. valenciennis*, *Trachelyopterus* aff. *galeatus*, and *Cynopotamus argenteus*, were situated at the center of the species ordination diagram and did not show clear temporal and spatial abundance patterns (Fig. S1).

In addition to the changes in biomass and species richness, the 2010 extraordinary flood also increased variation in assemblage structure from the rising-water phase (survey 3) to the falling-water phase (survey 4). During this period, sample scores of all lake types sampled from regions 1 and 3 showed abrupt increases in the 1st axis, increasing their similarity with assemblages from the northernmost region 4. The higher similarity among regions was a result of increases in the relative abundances of species commonly limited to northern sites (Fig. 6).

pCCA showed the relative amount of variation explained by geomorphological, hydrological, temporal, and spatial variables. The process of forward selection included 3 geomorphological variables (AFL, MCL, and SL), all 5 hydrological variables (H1–H5), 5 temporal variables (Julian Date, Autumn, Summer, Spring, and Lunar Cycle), and 5 spatial variables (Ln Water distance from main channel, x^2, y, y^3, x^3). pCCA explained 39.1% of the total variation in the matrix of species (TVE). The total variation explained by each set of variables was between 31 and 36%, except for geomorphological variables (21.5%; Table 2). Among the nonoverlapping components of variation, hydrological and temporal variables explained the largest amount of TVE. Geomorphological and spatial variables explained a lower proportion of TVE, but had a relatively large shared component (GS). The components shared by the hydrological and temporal (HT) variables, and the temporal and spatial (TS) variables, also accounted for relatively large fractions of TVE. Third- and 4th-order shared components were small and, in some cases, negative, a common result when >3 sets of variables are considered because of nonlinear relationships among sets of variables (Økland 2003, Legendre and Legendre 2012). For the ecological interpretation of the results, these small and negative values can be considered null (Borcard et al. 2011).

DISCUSSION

Our results indicate that changes in the structure of fish assemblages of the Paraná River floodplain lakes are associated primarily with the interaction between climatic sea-

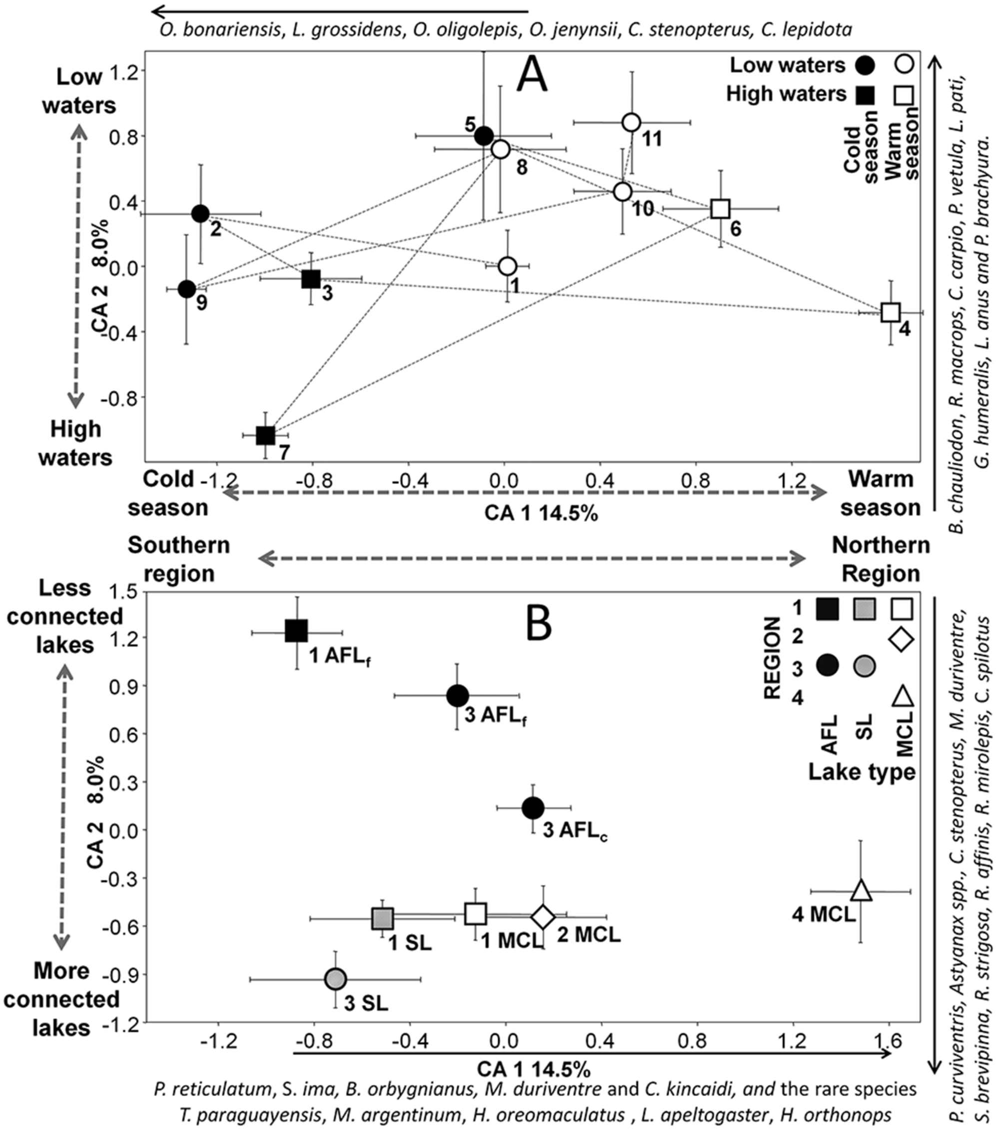

Figure 3. Biplots of mean (±SE) sample scores for the first 2 correspondence analysis (CA) axes obtained from abundance data of 89 fish species collected in the middle and lower reaches of the Paraná River floodplain and showing the % variation explained by each axis. A.—Temporal assemblage variability where symbols represent mean sample scores of sampling surveys (1–11) carried out under different hydrometric conditions (high and low waters) and climatic seasons (cold and warm seasons). Dotted lines connect symbols of consecutive sampling surveys. B.—Spatial assemblage variability where symbols represent mean sample scores for lake types (MCL, SL, AFL) distributed in 4 regions (1–4). Species with extreme lower and higher scores on each axis are shown on the figure margins. Arrows above species names indicate the direction of increase of abundance. See Fig. 1 for lake type abbreviations and Table S1 for genus names.

sonality and hydrologic variability and secondarily with the distribution of geomorphic units along the lateral dimension of the river. The first 2 CA ordination axes explained 22.6% of the total inertia of the species matrix. This fraction is similar to that obtained by other investigators who furnished ecologically interpretable CA axes (Arrington et al. 2005, Arrington and Winemiller 2006). Most of the ecological communities show stochastic variation in species abundance among samples, which introduces noise in the species matrix. Ordination analysis recovers patterns in species composition in the first axes and defers noise to later axes, explaining why ordination can be useful even with a low percentage of variance accounted for by the first axes (Gauch 1982). However, the percentage of total inertia can be a misleading statistic because interpretation of unexplained variation as random noise is inappropriate (Økland 1999). In these cases, congruence between ordination (e.g., CA) and constrained ordination (e.g., CCA) results can be

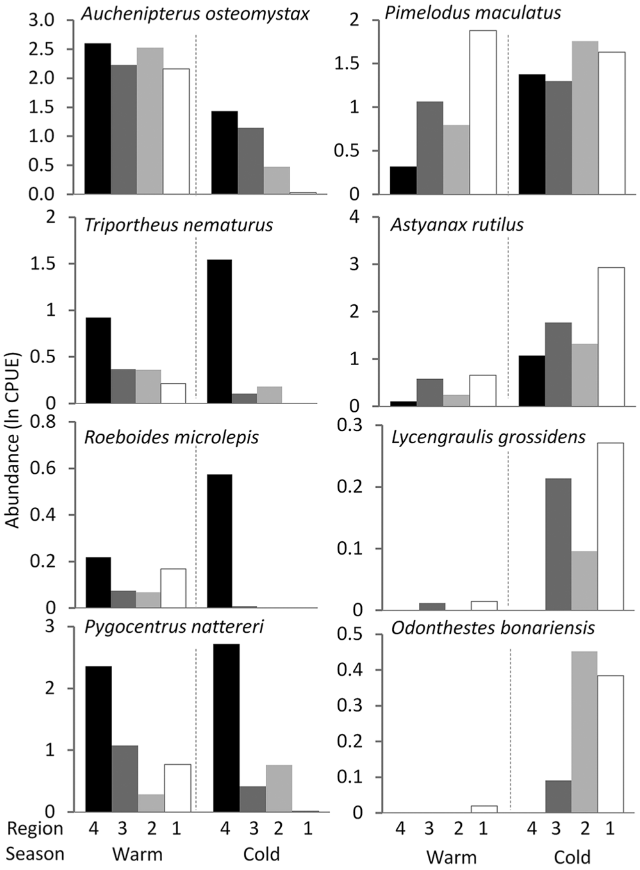

Figure 4. Abundance patterns of representative species during cold and warm seasons along the Paraná River floodplain, from northern (4) to southern regions (1). Species in the left column were more abundant in northern regions and during the warm season, whereas species in the right column were more abundant in the southern regions and during the cold season. CPUE = catch per unit effort.

used as an indicator of the consistency of the patterns observed (Økland 1996). In our study, results of the pCCA were consistent with those of the CA, a result indicating that pattern observed corresponds to spatial and temporal gradients associated with latitude, climate seasonality, hydrological variability, and geomorphology.

Longitudinal dimension: latitudinal climatic gradients and climatic seasonality

CA axis 1 represented the seasonal and latitudinal variations of fish assemblage structure that could be associated with the spatial and temporal variability of thermal conditions of the Paraná River. On one hand, the seasonal variation in water temperature at the study area, from <5°C in winter to >30°C in summer (Drago 2007, Iriondo 2007), can be exploited differently by fish species, based on their life-history strategies (Scarabotti et al. 2011). On the other hand, the longitudinal gradient associated with the north–south latitudinal extension of the river basin causes a gradient in temperature, with differences in mean annual temperatures of 5°C along the last 900 km of the river and 4°C along the section we studied (Iriondo and Paira 2007). These patterns suggest that differences in thermal preferences among species could be the mechanism driving changes in species assemblage composition along longitudinal and seasonal gradients in this system.

Several abundant species seemed not to follow these patterns even though they are regarded as long-distance migratory species. *Prochilodus lineatus*, *M. obtusidens*, and *S. brasiliensis* had species centroids at the center of the ordination diagram and did not show consistent patterns in space or time, and were evenly abundant across seasons and regions. The nonmigratory species, *H. malabaricus* and *P. valenciennis*, also did not exhibit clear patterns. Their lack of response to environmental gradients can be explained by the fact that they are eurytopic and generally exhibit high abundances in a wide range of environmental conditions.

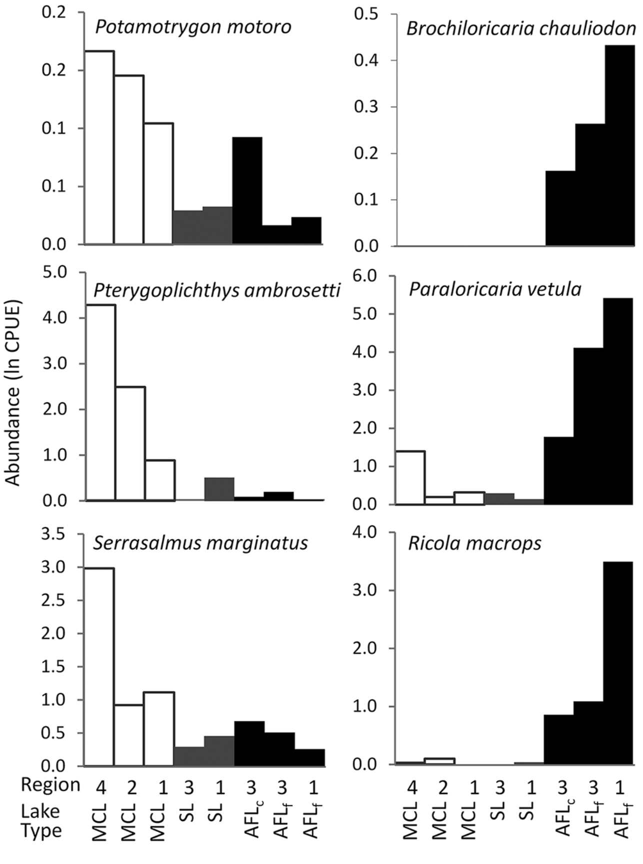

Figure 5. Abundance patterns of representative species showing their preference for different lake types in different regions (1–4) of the middle Paraná River Floodplain. Species in the left column were more abundant in connected main channel lakes (MCL). Species in the right column were more abundant in less connected anastomosed floodplain lakes (AFL) close (c) or far (f) from the main channel. CPUE = catch per unit effort.

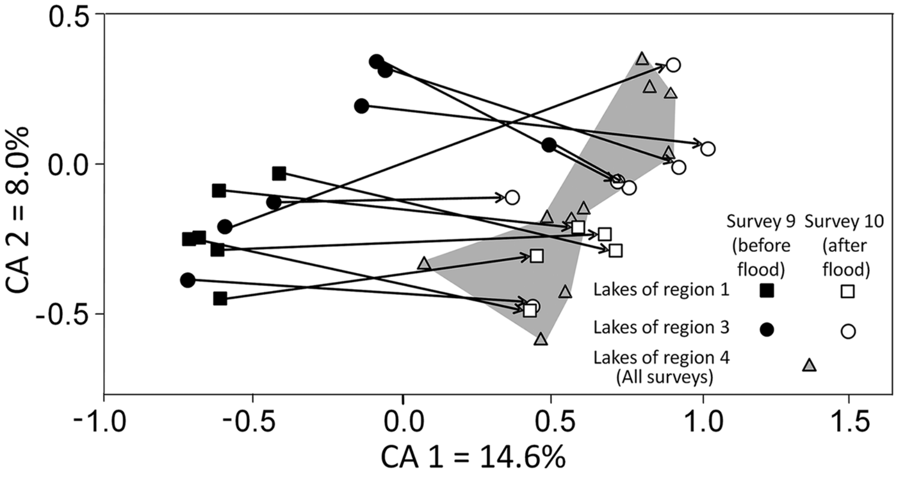

Figure 6. Biplot of the first 2 correspondence analysis (CA) axes of fish assemblage structure showing the displacement of lakes' sample scores during the extraordinary flood of the Paraná River in early 2010 to the position occupied commonly by samples from the northern region (shaded area). Shaded area represents the convex hull occupied by the samples of the northern region (4) from all surveys. Arrows represent the trajectories of assemblage structure variation of lakes from southern (1) and the intermediate (3) regions between surveys 3 (before extraordinary flood, November 2009) and 4 (after extraordinary flood, April 2010).

Table 2. Results of the pCCA showing the total variation explained (TVE) by each of the 4 sets of explanatory variables (top) and the corresponding non-overlapping components of variation: G = geomorphic variables, H = hydrological variables, S = spatial variables, T = temporal variables. %TVE = percentage of total variation explained by each component. Each non-overlapping component is calculated as the variation explained by the intersection of constraining variables that is not explained by the union of covariables. Total inertia = 1.571, sum of all canonical eigenvalues 0.6278, TVE = 40%.

Constraining variables	Covariables	%TVE
Total variation explained by each set of explanatory variables		
G		21.5
H		31.0
S		34.3
T		36.0
Non-overlapping components		
G	HTS	6.24
H	GST	25.57
S	GHT	17.57
T	GHS	26.51
GH	ST	1.83
GS	HT	12.04
GT	HS	0.92
HS	GT	0.51
HT	GS	5.00
ST	GH	5.56
GHS	T	0.30
GHT	S	−0.25
HST	G	−2.23
GST	H	0.05
GHTS		0.38

The species that composed the cold-season assemblage (*Odontesthes bonariensis*, *L. grossidens*, *O. jenynsii*, *R. quelen*, and several *Astyanax* species) were among the few Neotropical fishes inhabiting lakes and rivers of the Pampasic prairies of southern Argentina in zones where mean annual temperatures do not surpass 15°C (Almirón et al. 1997, Gómez et al. 2001). This distribution indicates tolerance to low temperatures. Among these species, *O. bonariensis* and *L. grossidens* undergo downstream migration to the La Plata River estuary and coastal zones, where they remain during the warm season. During winter and spring, they migrate upstream to the northern portions of the middle Paraná River, to reach warmer conditions (Ringuelet et al. 1967, Cervigón et al. 1992, Avigliano and Volpedo 2013). The species that composed the warm-season assemblage (the pimelodid and doradid catfishes *P. reticulatum*, *S. lima*, *H. oreomaculatus*, *O. kenri*, *P. granulosus* and the characids *B. orbignyanus*, *M. duriventre*, and *C. kincaidi*) were more abundant in northern regions of the study area. These species undergo upstream reproductive migration during the winter and downstream feeding migration during the summer (Quirós and Vidal 2000, Carolsfeld 2003). These results indicate that the longitudinal patterns of change in fish assemblages observed along Paraná River mainstem are primarily produced by the interaction between the thermal preferences of species and the thermal gradient observed along their wide latitudinal extent. Although the distribution of fish species in southern South America has been consistently associated with temperature (Cussac et al. 2009), a deeper comprehension of the thermal biology of Neotropical fish will greatly contribute to the understanding of the present and future distribution of species in a context of global warming.

Temporal dimension: hydrological regime and climatic seasonality

Several investigators have found that floodplain environments are more suitable for fish when flood pulses occur during the warm season (Lowe-McConnell 1987, King et al. 2003, Winemiller 2005, Górski et al. 2011). In our study, the association of fish assemblage structure with hydrological variation depended largely on the coincidence of flood pulses during the warm season. Extreme high-water periods during the summer stimulated downstream dispersal of fish species commonly limited to northern regions of the river, and thereby, generated higher than usual similarity in species composition between the southern and northern regions (Fig. 6). After the exceptional flood of 2009–2010, several species, such as *Ageneiosus inermis*, *A. militaris*, and *Brycon orbygnianus*, increased in abundance at all sites. In recent decades, populations of several large-bodied species, such as the herbivorous serrasalmid *Piaractus mesopotamicus* and the giant pimelodid *Zungaro jahu*, were totally depleted in the fisheries of the lower Paraná River (Quirós 1990) but remain abundant in the commercial fisheries in the northern areas of the basin (Vargas 2014). After the extraordinary flood of 2010, juveniles of these species were captured in the study area for the first time after 5 y of sampling. These results indicate that intensive and long-lasting floods during the summer may stimulate juvenile recruitment and adult dispersal producing the recolonization of downstream areas.

Historically, the Paraná River showed seasonal flood pulses in phase with peaks of temperature during late summer (Bonetto et al. 1965). However, changes in rainfall patterns and hydropower development since the mid 1970s have altered the hydrologic regime, and flood pulses now occur at almost any time of the year (Menéndez and Berbery 2005). In spite of these alterations, several large-bodied migratory characiform and siluriform species continue to show regular seasonal variations in abundance in association with changes in temperature (Quirós and Vidal 2000). However, the recruitment success of many of these species depends on the occurrence of flood pulses in phase with the period of warmer temperatures (Bayley 1991, Gomes and Agostinho 1997, Fuentes and Espinach Ros 1998, Bailly et al. 2008). The alteration of the natural flow regime of the river could disrupt the relationship between life-history adaptations and environmental variation (Poff et al. 1997) and, hence, community composition and population size of many ecologically and economically important characiform and siluriform fishes. In the Paraná River, the recent desynchronization between flood peaks and warm water temperatures probably will affect the mean productivity of the system (Winemiller 2004, Caissie 2006) and could produce a shift from a deterministic to a stochastic response of population dynamics, complicating the efficiency of fisheries management.

Lateral dimension: distribution of geomorphic units and hydrological connectivity

The 3rd dimension of variation in assemblage structure was among lake types associated with geomorphic units. Fish assemblages from the same lake types but situated in different river regions were more similar to each other than to assemblages of nearby lakes of a different type (Fig. 3B). Several benthic species, such as Loricariinae (genera *Paraloricaria*, *Brochiloricaria*, *Ricola*, *Loricariichthys*), the pimelodid catfish *L. pati*, the European Carp *C. carpio* (but at very low densities), and the stingray *P. brachyura*, were more abundant in large and shallow lakes situated away from the main channel; whereas, several curimatids (genera *Psectrogaster*, *Potamorhina*, and *Cyphocharax*), *Astyanax* spp., the cichlid *Crenicichla vittata*, and Hypostominae catfishes (genera *Rhinelepis*, *Hypostomus*, and *Pterygoplichthys*) were more abundant in lakes close to the main channel. Large floodplain water bodies like AFL, often have higher turbidity and lower macrophyte cover (Van

Geest et al. 2003) than smaller and elongated lakes like MCL, which are clearer and vegetated (Hamilton and Lewis 1990). Loricarine and pimelodid catfishes generally prefer turbid environments because they orient underwater mainly by mechanoreception, whereas curimatids and cichlids prefer clearer environments because they are visually oriented species (Rodríguez and Lewis 1997, Pouilly et al. 2004, Scarabotti et al. 2011). These patterns of distribution also could be explained by the relationship between species life history and environmental variability (Mims and Olden 2012). For example, Loricariini catfishes and *P. brachyura* have a more extreme equilibrium life-history strategy (large eggs, low fecundity, and parental care) than other fish (Winemiller 1989, Suzuki et al. 2000) that may be favored by the higher stability of environmental conditions observed in lakes distant from main channel (Pouilly and Rodríguez 2004).

A multiscale approach to understanding Paraná River fish assemblages

In Fig. 7, we present a scheme of the processes operating on fish assemblages in the Paraná River at regional and landscape scales. At the regional scale, the river flows along a climatic gradient, from warmer areas in the northern upper region to colder areas in the southern lower region. This thermal pattern makes the Paraná River an uncommon study case, because it is opposite to the longitudinal pattern of temperature variation of most rivers (Caissie 2006). In this river, fish undergo seasonal migrations along different river sections depending on their thermal preferences. By promoting downstream dispersal, flood pulses in phase with warmer temperatures generate an increase in the abundance of species that prefer warmer temperatures in the southern reaches of the river. In this context, our study raises a potentially important management issue,

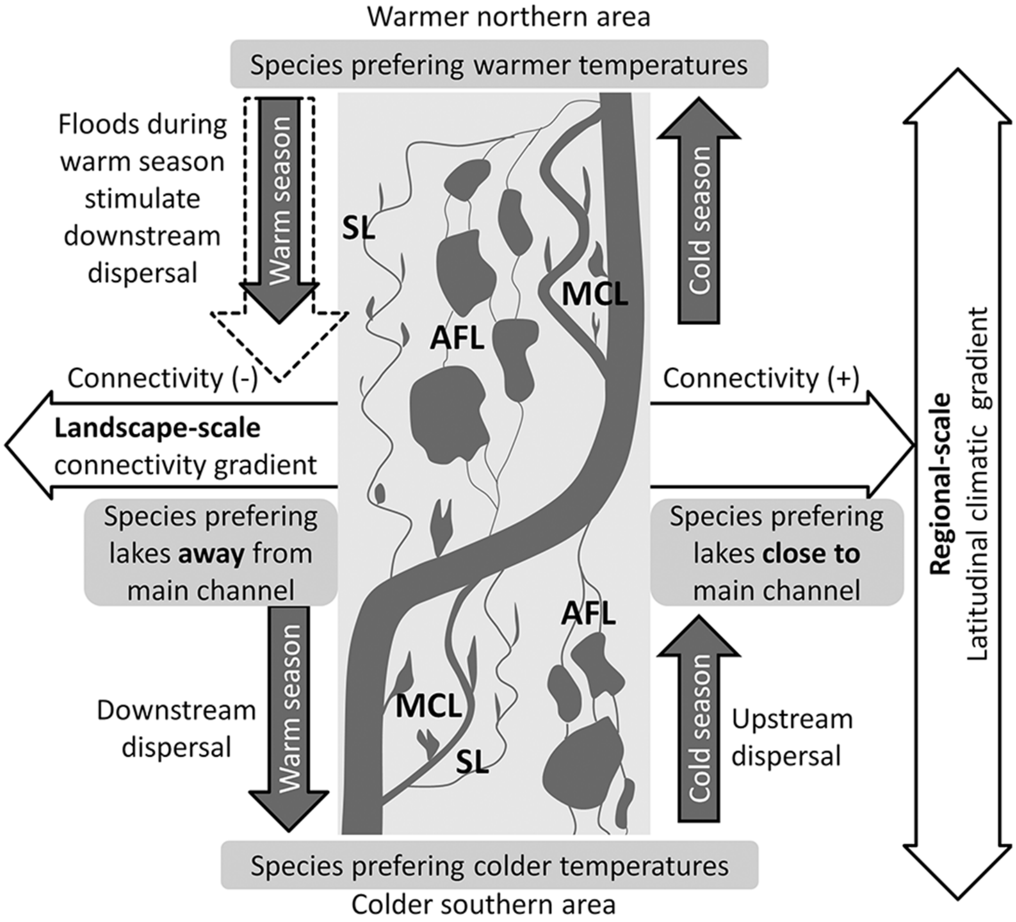

Figure 7. Schematic representation of a section of the Middle Paraná River floodplain showing the processes affecting fish assemblages at different spatial and temporal scales. Fish species are distributed differentially along a latitudinal gradient of temperature and adjust their position through time in response to climatic seasonality (gray arrows). Floods during the warm season stimulate downstream dispersal of species preferring warmer temperatures (dashed arrow). Fish species also are distributed differentially along a lateral gradient of hydrological connectivity mainly determined by the occurrence of geomorphic units of the floodplain. Double-headed white arrows represent the spatial scales at which fish assemblages vary. See Fig. 2 for abbreviations. Note that the occurrence of geomorphic units on the lateral dimension of the river is not completely predicted by the distance to main channel.

suggesting that the recent climate and dam-induced desynchronization of hydrologic variation and temperature seasonality can affect patterns of abundance and recolonization of downstream reaches by migratory species.

At the landscape scale, geomorphic units represent environmental patches that affect the distribution of fish species on the lateral dimension of the river. The geomorphic units of the Paraná River seem to operate like functional process zones (Thoms 2006), i.e., as habitat patches generating environmental discontinuities at the landscape level. The differences in lake morphometry and connectivity between units can determine changes in lake transparency and hydrological disturbances that select different assemblages on the basis of species traits. In this way, the geomorphic heterogeneity of the floodplain generates discontinuous patterns of variation in fish assemblage structure on the lateral dimension of the river.

Elucidation of the mechanisms that affect assemblage structure in large rivers requires multiscale approaches that can handle a high level of environmental variation across different scales of space and time (Boys and Thoms 2006, Kennard et al. 2007, Thorp et al. 2008, Pease et al. 2011). The large spatial and temporal extents included in our study enabled observation of several scales of environmental variation and were essential for understanding the complex relationships between fish assemblages and environmental heterogeneity. Because we included a large spatial extent along the longitudinal dimension of the river, our study contributes to understanding how assemblage structure changes along the latitudinal and seasonal climatic gradients on the basis of the thermal preferences of species. Because we included years with different matching between flood pulse and warm season, our study also provides clues to how the changes in the natural flow regime induced by dams and climate change could affect fish assemblages. Last, consideration of geomorphic units as environmental patches at the landscape scale can help to explain the variation of fish assemblages along the lateral dimension of large rivers with intact floodplains. We consider that the fish–habitat associations we observed will be useful for the development of hypotheses and structured sampling designs to monitoring the ecological functioning of large Neotropical rivers under the present context of global change.

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Author contributions: PAS designed the study, participated in the fieldwork, organized and analyzed the information, and wrote the original manuscript. LDD collaborated in the design of the study, participated in the fieldwork, and organized and processed information. MP collaborated in the analysis and interpretation of the information and supervised the writing of the manuscript.

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