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Multiscale environmental heterogeneity in a large river-floodplain system

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Abstract

River-floodplain systems host very high biodiversity and provide a great variety of ecosystem services due largely to their high environmental heterogeneity, which is strongly dependent on spatial and temporal scales of observation. We aimed to describe the main patterns of environmental variation of the subtropical system of the Middle Paraná River at different scales of analysis using univariate and multivariate statistics. Physical, chemical and biological variables were analyzed during different hydro-sedimentological phases along four consecutive years in 31 aquatic environments. We considered four aquatic habitat types with different degrees of hydrological connectivity and water flow characteristics (major rivers, secondary channels, floodplain lakes permanently connected to the major rivers, and floodplain lakes temporarily connected to the major rivers) from two geomorphologic units with different drainage patterns: anastomosing and meandering. The environmental heterogeneity was mainly associated with the habitat types and relative contributions of lateral tributaries with different water qualities to each unit, in combination with the influence of the

hydro-sedimentological regime. The heterogeneity of the system was significantly higher during low water than during high water phases. However, although the extreme flood reduced dissimilarities between habitat types within each geomorphologic unit, it increased differences between major rivers and between units. In conclusion, at different spatial scales, floods may simultaneously have a homogenization effect due to increased hydrological connectivity and a differentiation effect due to enhanced inputs of water from regions with variable geological characteristics and land uses. Finally, geomorphologic units can play a key role in maintaining the environmental heterogeneity during floods of high magnitude, even when land barriers among aquatic environments disappear.

1. Introduction

Heterogeneity in environmental conditions is one of the most important factors governing biodiversity (Fahrig et al., 2011; Tews et al., 2003). It promotes species persistence and coexistence, and enhances the probability of speciation events (Stein et al., 2014). In turn, high biodiversity favours the provision of essential ecosystem services (Hector and Bagchi, 2007) and the habitat resilience in the face of environmental alterations (Elmqvist et al., 2003).

River-floodplain systems are among the most heterogeneous and biodiverse landscapes around the world. They support a shifting mosaic of different aquatic habitat types characterized by a gradient of hydrological connectivity with the main channel and distinct water flow characteristics (i.e. major rivers, secondary channels and lakes with different connectivity degrees) (Tockner and Stanford, 2002). In addition, river-floodplain systems usually include several contiguous geomorphologic units characterized by different drainage patterns (e.g. braided, meandering, and anastomosing) (Thorp et al., 2006). Therefore, while covering a small portion of the Earth's surface, they are disproportionately important in providing a huge diversity of ecosystem services (Schindler et al., 2014). Although the phenomena involved in the complexity of these systems are strongly scale-dependent (Thorp et al., 2006; Ward et al., 1999), their environmental heterogeneity has been poorly evaluated considering simultaneously different scales of analysis.

The hydro-sedimentological regime is the major determinant of the complexity of river-floodplain systems. It is usually governed by regional factors, i.e. inputs of water and sediments coming from different sections of the upper basin (Junk et al., 1989; Neiff, 1990). Variations in water level regulate the exchanges of materials among aquatic environments, influencing in turn the magnitude of local factors such as point inputs of materials and autogenic processes (e.g., nutrient uptake and release by biota) (Tockner et al., 2000). Local factors are very dynamic in time and space due to their dependence not only on the hydro-sedimentological regime, but also on climatic seasonality, habitat types and position along the floodplain (Bonecker et al., 1998; Hamilton and Lewis Jr, 1990; Mayora et al., 2013; Thomaz et al., 2007), increasing the environmental heterogeneity mainly under isolation conditions (Thomaz et al., 2007; Tockner et al., 2000). In this respect, aquatic habitat types differ markedly during low waters (Cardoso et al., 2012; Maine et al., 2004; Mayora et al., 2017; Unrein, 2002). As the water level rises, the increased hydrological connectivity contributes to the environmental homogenization among water bodies (Thomaz et al., 2007). More isolated habitats are particularly affected, since they can function consecutively as swamps, lakes, and streams, and even become part of the major rivers during periods of extremely high water (Ward et al., 2002).

Despite these general patterns, it is not possible to generalize about the effect of the hydro-sedimentological regime on the environmental heterogeneity in large river-floodplain systems. Floods with high concentrations of suspended sediments may decrease the environmental heterogeneity within the floodplain, but simultaneously increase it across the main channel-floodplain gradient (Mayora et al., 2013). These opposite trends at different spatial extents are attributed to the large sediment retention after the water enters the floodplain, which therefore maintains a particular identity different from that of the main channel (Mayora et al., 2013). Large river-floodplain systems are subject to water inputs from an enormous variety of tributaries (Hamilton, 2009) and support an array of diverse habitat types in combination with different geomorphologic units (Thorp et al., 2006; Tockner and Stanford, 2002). Physical, chemical, ecological, and functional characteristics may change abruptly among adjacent units due to the sharp discontinuities in their hydrographic patterns (Thorp et al., 2008). In sum, the huge complexity and size of these systems demand that different spatial scales should be considered in order to fully understand system environmental dynamics (Dunne and Aalto, 2013).

The objective of this study was to evaluate the environmental heterogeneity of a large river-floodplain system at different scales of analysis. To address this issue, physical, chemical and biological variables were analyzed during four different hydro-sedimentological phases along four consecutive years in the Middle Paraná River system. We sampled four types of aquatic habitats (major rivers, secondary channels, floodplain lakes permanently connected to the major rivers, and floodplain lakes temporarily connected to the major rivers) from two geomorphologic units: an anastomosing and a meandering one. We hypothesized that habitat types are the main responsible for spatial heterogeneity during low waters, whereas geomorphologic units play a major role during high water phases.

2. Study area

The Paraná River is placed in central south America and flows mainly from north to south along 3,800 km, covering a basin area of 3.1 × 10^6 km^2 (Fig. 1). This fluvial system delivers a mean annual discharge and wash load of approximately 16,400 m^3 s^{-1} and a 3,800 kg s^{-1}, respectively (Amsler and Drago, 2009).

The middle stretch of the river is located in a subtropical region. It extends from its confluence with the Paraguay River (27°29′S; 58°50′W) to the city of Diamante (Argentina; 32°4′S; 60°32′W). Nearly 75% of the water discharge is from the Upper Paraná River. About 50% of the water flows through a well‒defined main channel and the remainder through secondary branches. The Paraguay River (the main tributary of the Paraná River) discharges a huge amount of sediments coming from Andean tributaries (mainly the Bermejo River). Therefore, the concentration of suspended solids is high and variable, ranging from 20 to 310 mg L^{-1} (Bonetto et al., 1994). The peak of sediments occurs between late summer and early autumn due to the arrival of the rainy season in the Andean headwaters of the Bermejo River (Amsler and Drago, 2009).

The high sediment load together with the decrease in the general slope in the middle stretch of the Paraná River determines the development of a 10 to 50 km wide floodplain (13,000 km^2). Floodplain lakes have a mean area of 0.32 km^2, a mean maximum depth of 1.46 m and variable degrees of hydrological connectivity. The floodplain drainage network is constituted by secondary channels, which connect floodplain lakes between them and with the main channel (Drago, 2007). Several floodplain geomorphologic units have been identified for the Middle Paraná River floodplain. The units adjacent to the main channel have a higher topographical level because they receive a higher sediment load, and usually show bar-meander morphology (Paira and Drago, 2007). Their fluvial bars and islands that experience frequent floods are characterized by young *Salix humboldtiana* Willd. (willow) forests, including secondarily another pioneer trees such as *Tessaria integrifolia* Ruiz & Pav., *Croton urucurana* Baill., and *Albizia inundata* (Mart.) Barneby & J.W.Grimes. In contrast, their larger islands and river levees support mature willow forests and gallery forests dominated by trees of medium and big size, such as *A. inundata* and *Nectandra angustifolia* (Schrad.) Nees & Mart. (Marchetti et al., 2013). The units located far away from the main channel have a lower topographical level and usually display anastomosing morphology (Paira and Drago, 2007). Terrestrial vegetation of these units is characterized by herbaceous and bushy marshy species (Marchetti et al., 2013). In regard to aquatic macrophytes, emergent and free-floating species are prominent because of their biomass and areal coverage of water bodies in the different geomorphologic units (Schneider et al., 2018).

3. Materials and methods

3.1. Study periods and sites

We studied 31 aquatic environments that covered four habitat types: major rivers (MR), secondary channels (SC), floodplain lakes permanently connected to the MR (LPC), and floodplain lakes temporarily connected to the MR (LTC) (Table 1). MR included the main channel and their secondary branches with higher discharge (1200-1500 m^3 s^{-1}). These have a mean channel width ranging from 330 to 1100 m, flow on the right side of the floodplain, and produce an intense morphogenesis. SC are meandering floodplain channels (discharge < 500 m^3 s^{-1}) that flow between MR and floodplain lakes. They have a channel width between 28 and 137 m. LPC have a surface area between 3.4 and 204 ha and are permanently connected to the MR either directly or through other aquatic environments. LTC have a surface area between 0.01 and 40 ha and are seasonally isolated from the MR.

Aquatic environments were located in two different gemorphologic units (Fig. 1). The first unit is a sand-bar-meandering floodplain island (hereafter MU), which has a higher topographic level than the other studied unit. It is characterized by a major development of meanders and a great number of scroll and irregular lakes. We sampled 2 MR, 4 SC, 4 LPC, and 5 LTC in this unit. The second unit is an anastomosing floodplain island (hereafter AU), which developed at a lower topographic elevation than the MU. It is characterized by a complex anastomosing drainage pattern with a major development of large and irregular interconnected lakes and sinuous, low-energy channels. The last unit is fed not only by the Paraná River system, but also by brackish west tributaries that drain Chacoan plains into the Coronda River. We sampled 2 MR, 4 SC, 3 LPC, and 7 LTC in this unit.

The aquatic environments were sampled four times along four consecutive years corresponding to different hydro-sedimentological phases: an early low water phase (ELW, November–December 2013, in late spring), a late low water phase (LLW, March–April 2014, in early autumn), an ordinary flood (OF, September 2015, early spring), and an extraordinary flood (EF, March 2016, early autumn) (Fig. 2). The LLW was coincident with the sediment peak. Although mean month air temperatures in the study area varied from 12 °C in winter to 26 °C in summer, all sampling surveys were carried out at intermediate temperatures to observe more clearly the effect of the hydro-sedimentological regime. The variation of water temperature along the study period was estimated from air temperature following Drago (1984) (Fig. 2).

In this way, the sampling design integrated the spatial and temporal dimensions at different scales of analysis. The spatial dimension included variations both at the habitat scale (represented by habitat types) and the landscape scale (represented by geomorphologic units). The temporal dimension was focused on the hydro-sedimentological regime (represented by the four surveys).

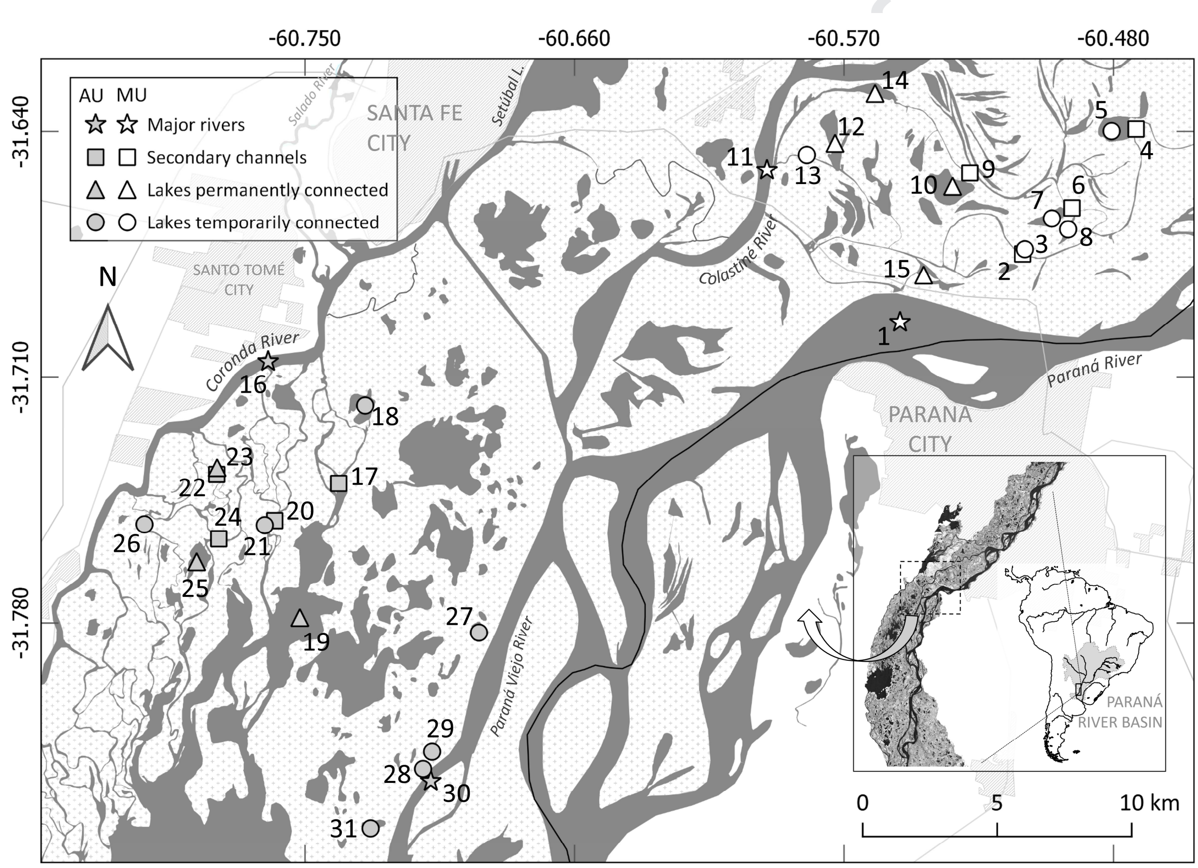

Fig. 1. Location of the study area and sites. Aquatic environments from the meandering unit (white symbols) and the anastomosing unit (grey symbols) are represented by stars (major rivers), squares (secondary channels), triangles (floodplain lakes permanently connected to the major rivers), and circles (floodplain lakes temporarily connected to the major rivers).

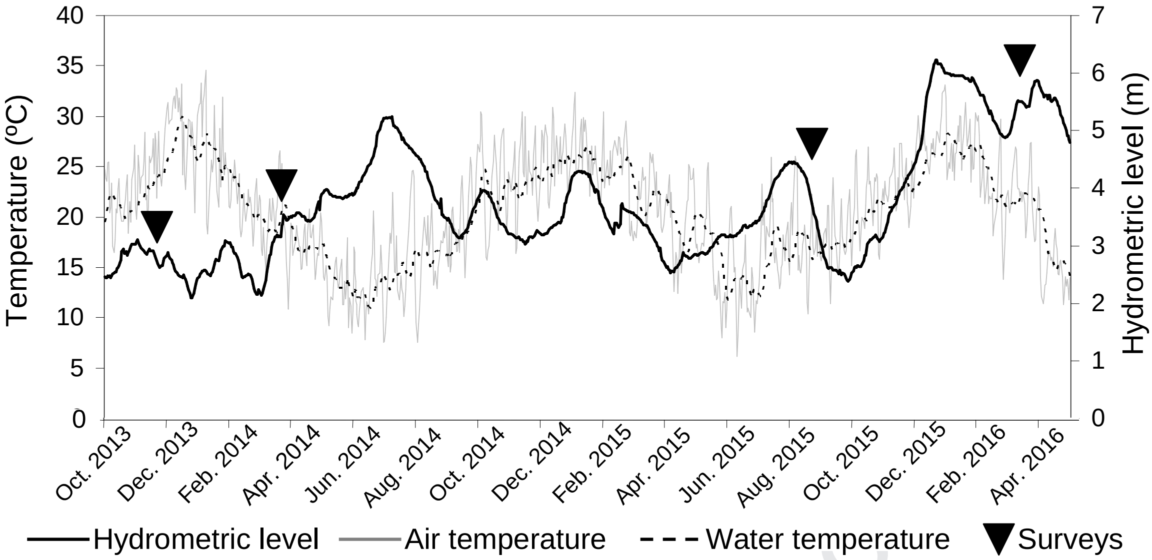

Fig. 2. Hydrometric level of the main channel (Paraná Harbour Station Gauge), air temperature, and water temperature (estimated from air temperature). Survey periods are pointed out.

N°	Aquatic environment	Habitat type	Geomorphologic unit	Geographic coordinates West	South	Distance by water (m)	Width (m)	Area (m^2)
1	Paraná	MR	MU	60°33'04.76"W	31°41'39.53"S	0	1107	-
2	Correntoso A	SC	MU	60°30'37.37"W	01°40'29.31"S	2283	49	-
3	Correntoso B	LTC	MU	60°30'34.68"W	31°40'24.46"S	2376	-	14472
4	Correntoso C	SC	MU	60°28'20.98"W	31°38'21.56"S	4195	49	-
5	Del Medio	LTC	MU	60°28'50.43"W	31°38'23.65"S	4327	-	668542
6	Colastiné de las Cruces	SC	MU	60°29'38.06"W	31°39'42.21"S	3813	30	-
7	El Chajá	LTC	MU	60°30'02.20"W	31°39'52.98"S	3298	-	401314
8	El Chajacito	LTC	MU	60°29'42.65"W	31°40'04.11"S	2851	-	160862
9	Colastiné de las Cruces	SC	MU	60°31'40.74"W	31°39'06.32"S	3876	31	-
10	La Perla	LPC	MU	60°32'01.57"W	31°39'20.02"S	3227	-	846102
11	Colastiné	MR	MU	60°35'44.71"W	31°39'03.48"S	0	408	-
12	La Ferranda	LPC	MU	60°34'22.87"W	31°38'36.05"S	904	-	702199
13	El Escondido	LTC	MU	60°34'56.79"W	31°38'47.89"S	1619	-	1716
14	Moreira	LPC	MU	60°33'34.77"W	31°37'44.75"S	210	-	543600
15	Miní	LPC	MU	60°32'36.36"W	31°40'50.87"S	550	-	195451
16	Coronda	MR	AU	60°45'44.32"W	31°42'19.78"S	0	330	-
17	Cataratas	SC	AU	60°44'19.52"W	31°44'24.91"S	4983	137	-
18	Las Garzas	LTC	AU	60°43'47.68"W	31°43'04.73"S	3686	-	497834
19	Blanca	LPC	AU	60°45'06.23"W	31°46'42.34"S	8922	-	2399070
20	El Cordobés	SC	AU	60°45'36.41"W	31°45'02.99"S	6246	62	-
21	La Chicana	LTC	AU	60°45'48.36"W	31°45'07.64"S	6512	-	56793
22	Pascualito A	SC	AU	60°46'46.09"W	31°44'15.67"S	1610	33	-
23	Pascualito B	LPC	AU	60°46'45.69"W	31°44'8.68"S	1660	-	33970
24	El Pascual	SC	AU	60°46'43.64"W	31°45'21.54"S	5627	50	-
25	El Tuyango	LPC	AU	60°47'10.26"W	31°45'44.92"S	6093	-	449945
26	La Curva	LTC	AU	60°48'13.00"W	31°45'06.76"S	1846	-	79871
27	Los Gansos	LTC	AU	60°41'30.92"W	31°46'57.84"S	15508	-	178953
28	La Escondida	LTC	AU	60°42'38.08"W	31°49'17.44"S	16777	-	6518
29	La Chancha	LTC	AU	60°42'27.26"W	31°48'59.77"S	16677	-	40539
30	Paraná Viejo	MR	AU	60°42'28.78"W	1°49'30.09"S	8733	344	-
31	Los Sauces	LTC	AU	60°43'41.16"W	31°50'18.39"S	19314	-	250637

Table 1. Habitat type, geomorphologic unit, geographical location, distance by water to the Paraná River or Colastiné River (whichever was shorter) (for the meandering unit [MU]) and to the Coronda River (for the anastomosing unit [AU]), width (for channels), and area (for lakes) of the 31 studied aquatic environments. MR: major rivers, SC: secondary channels, LPC: floodplain lakes permanently connected to the MR, LTC: floodplain lakes temporarily connected to the MR.

3.2. Measurement of environmental variables

Hydrometric level of the Paraná River was measured at the Paraná Harbour Gauge by Prefectura Naval Argentina and processed by the Centro de Informaciones Meteorológicas (CIM-Universidad Nacional del Litoral). Subsurface pH, conductivity, temperature, dissolved oxygen (HANNA checkers), and channels' current velocity (current meter AOTT C20) were measured at the center of the lotic environments and in the pelagic zone of the lakes. Additionally, the percentage cover of five macrophyte life forms (emergent, free-floating, rooted-floating stemmed, rooted-floating leaved, and submerged) (Sculthorpe, 1967) was visually estimated in the main macrophyte stands. The percentage of each stand covered by macrophytes was calculated as the sum of the individual percentages of each life form. Due to the scarcity or even absence of aquatic macrophytes, we evaluate the density of macrophyte stands neither in channels nor during the extreme flood. The percentage of the total surface area of each aquatic environment covered by macrophytes was measured using the software Google Earth Pro.

Subsurface water samples were collected by duplicate at each sampling site. They were transported on ice and in darkness to the laboratory to evaluate water quality. Turbidity (formazin turbidity units, FTU) was measured with a HACH DR2000 spectrophotometer at 450 nm wavelength. Subsamples were filtered through Whatman GF/C glass fibre filters, which were stored at −20 °C up to 3 weeks. Chlorophyll−*a* was extracted from the filters with acetone (90%) and spectrophotometrically estimated according to Lorenzen's method (APHA, 2017).

Filtered subsamples were passed through Millipore filters (pore size: 0.45 μm) for colorimetric determination of dissolved components. Nitrate plus nitrite (NO_3^- + NO_2^-) was determined by reduction of nitrate with hydrazine sulfate and subsequent determination of nitrite by diazotizing with sulfanilamide and coupling with N-(1-naphthyl)-ethylenediamine dihydrochloride (Hilton and Rigg, 1983), ammonium (NH_4^+) by the indophenol blue method, soluble reactive phosphorus (SRP) by the ascorbic acid method, and dissolved silica (DSi) by the molybdosilicate method. Dissolved inorganic nitrogen (DIN) was calculated as the sum of NH_4^+ + NO_3^- + NO_2^-. Total phosphorus (TP) and total nitrogen (TN) were estimated from unfiltered water samples by digestion with nitric and hydrochloric acids followed by determination of SRP, and by digestion with potassium persulfate in alkaline medium followed by determination of NO_3^- + NO_2^-, respectively. In all cases, the methods proposed in APHA (2017) were followed.

Chromophoric dissolved organic matter (CDOM) was optically assessed. Absorbance at 440 and 700 nm was measured using 1-cm quartz cuvettes and filtered Milli-Q water as a baseline. The absorbance at 700 nm was subtracted from the absorbance at 440 nm to correct offsets (Green and Blough, 1994). Absorption coefficient (m^{-1}) at 440 nm (a_{440}) was calculated according to Kirk (1994) from the corrected absorbance at this wavelength, and used as a measure of CDOM concentration.

3.3. Data analysis

Data were Ln-transformed (except pH due to its logarithmic nature), centered and standardized before multivariate analyses. The environmental differences between MR was evaluated through a hierarchical cluster analysis using Euclidean distance and Ward agglomerative methods. Cluster analysis identifies groups of samples, so-called ‘clusters’, which share similar characteristics but differ significantly from the others (Hardle and Simar, 2015). High levels of similarity between samples are indicated by a small distance value. The resulting clusters were visually identified on a dendogram.

Lateral river-floodplain gradients across the MU and AU were evaluated using the nonparametric Mann–Kendall method (MK) (Kendall, 1975; Mann, 1945). The temporal gradient was substituted with the spatial gradient, which is an usual practice in environmental sciences (Zhu et al., 2017). Mean values of measured variables in each aquatic environment were ordered in a spatial sequence along the gradients of hydrological connectivity to a MR. They were first ordered from highest to lowest degree of hydrological connectivity as follows: SC > LPC > LTC. Then, environments from the MU were ordered from the shortest to the longest distance by water to the Paraná main channel or the Colastiné River, whichever was shorter; and environments from the AU were ordered from the shortest to the longest distance by water to the Coronda River. These MR are the main water sources for the MU and AU, respectively. MK is commonly used to assess whether a series of values of a water quality variable exhibit a greater monotonic trend than that expected to occur by chance (e.g. Eregno et al., 2014; Kisi and Ay, 2014; Suikkanen et al., 2013; Zeleňáková et al., 2015). A positive value of the MK statistic, S, indicates an ‘increasing trend’, a negative value of S indicates a ‘decreasing trend’, and a zero value of S indicates ‘no trend’. In addition, spatial and spatio-temporal coefficients of variation (CV) were estimated for each geomorphologic unit as the quotient of the standard deviation and mean of each variable. The Fligner-Killeen test (FK) was used to compare the CV of each variable between units.

Finally, we evaluated the patterns of environmental variability contributed by habitat types and geomorphologic units to the river-floodplain system. Principal component analyses (PCA) were used to evaluate the main patters of environmental variation during each hydro-sedimentological phase (Hardle and Simar, 2015). Principal components with eigenvalues higher than 1 were considered as significant (Olsen et al., 2012). Kruskal-Wallis (KW) tests were conducted to examine the significance of differences between MR, SC, LPC and LTC, and between MU and AU, during each hydro-sedimentological phase. Additionally, we used a permutational analysis of multivariate dispersions (PERMDISP) (Anderson et al., 2006) to test for differences in environmental heterogeneity between surveys, geomorphologic units and habitat types. We calculated Euclidean distance matrices between aquatic environments according to the set of environmental variables (for the whole data and for each survey). Then, we tested for differences in multivariate dispersions between the four surveys, between the two geomorphologic units for each survey, and between habitat types of each geomorphologic unit for each survey. Due to the low *n*, MR of both units were grouped for the last comparison. We tested separately the effects of each factor because there are inherent problems with the comparison of multivariate variation for more than one factor simultaneously (Marti Anderson, pers. comm.). The significance of pairwise differences between surveys, geomorphologic units and habitat types were determined for all significant PERMDISP tests ($p<0.05$) through Tukey's honestly significant difference test. The *betadisper* function of the *vegan* package of the R software was used to compare the multivariate dispersions. The remaining statistical analyses were conducted using the software CANOCO version 5 (Ter Braak and Šmilauer, 2012) and PAST Version 3.25 (Hammer et al., 2001).

4. Results

4.1. The main channel and its secondary branches

The hierarchical cluster analysis grouped the major rivers (MR) into four distinctive clusters (Fig. 3). The first three clusters grouped the Paraná main channel and Colastiné River according to the hydro-sedimentological phases. The last cluster comprised the Coronda River, whose most distinctive characteristic was its elevated conductivity (Table 2). In addition, changes in water quality during the EF were stronger in the Coronda River than in the other MR (Fig. 3). This hydrological event largely increased inputs of nutrients and CDOM into this secondary branch (Table 2). Due to the enhanced distinction of the Coronda River, environmental differences between MR was the highest during the EF (Fig. 3).

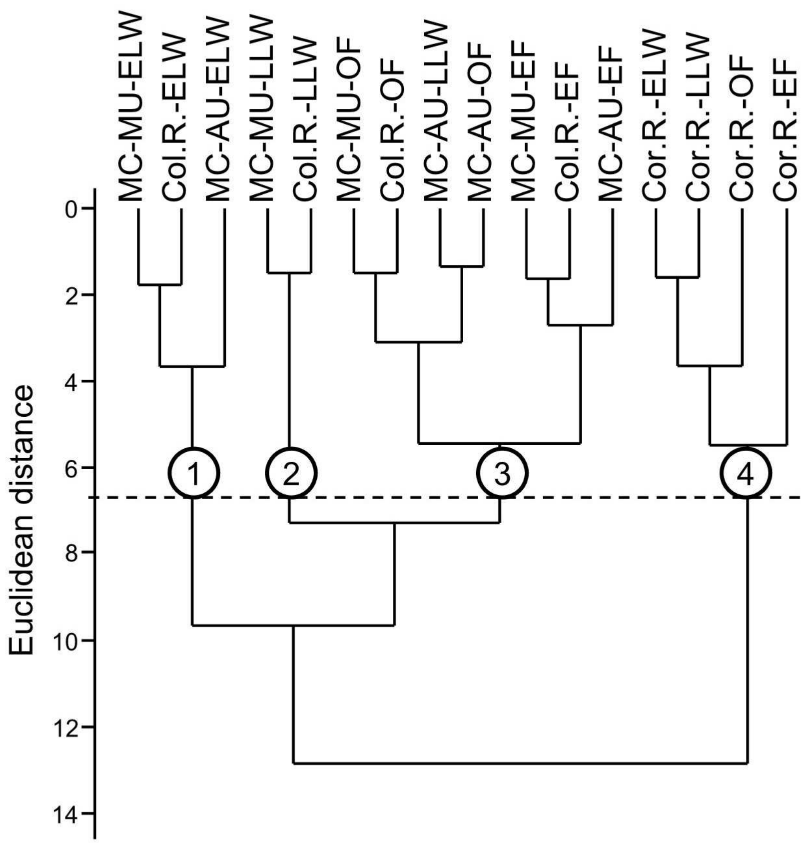

Fig. 3. Cluster dendrogram grouping the main channel of the Middle Paraná River at the meandering and anastomosing units (MC-MU and MC-AU, respectively), Colastiné River (Col.R), and Coronda River (Cor.R.) during the early low water phase (ELW), late low water phase (LLW), ordinary flood (OF), and extreme flood (EF). The analysis was based on subsurface water quality. The dotted horizontal line represents the cutoff criteria for identifying clusters (1, 2, 3 and 4).

		C. Vel.	Cond.	DO	pH	Turb.	DIN	SRP	DSi	TN	TP	a_{440}	Chl-*a*
		m s^{-1}	µS cm^{-1}	%		FTU	µg N L^{-1}	µg L^{-1}	Mg L^{-1}	µg L^{-1}	µg L^{-1}	m^{-1}	µg L^{-1}
ELW	MC-MU	1.23	72	85	7.0	12	517	14	15	1197	42	2.5	3.1
	Col.R.	1.26	79	90	7.8	12	514	24	14	535	62	1.6	3.0
	MC-AU	0.60	72	91	8.1	43	520	26	16	4652	162	2.0	4.8
	Cor.R.	0.89	286	85	7.4	54	234	111	15	645	199	3.9	4.8
LLW	MC-MU	1.14	83	118	7.5	178	337	40	11	808	172	1.4	1.0
	Col.R.	1.17	77	98	7.4	176	321	23	13	333	240	1.6	0.8
	MC-AU	0.71	75	85	6.9	96	337	12	14	1006	180	3.1	3.1
	Cor.R.	1.18	377	87	7.3	86	383	58	13	660	176	3.2	4.5
OF	MC-MU	1.20	66	125	7.1	31	267	45	13	698	194	4.8	1.9
	Col.R.	1.34	69	109	6.8	33	349	17	12	363	213	3.7	1.4
	MC-AU	1.10	68	101	6.7	35	337	18	12	860	139	2.4	3.6
	Cor.R.	1.15	296	91	7.2	23	159	44	8	867	146	5.0	5.3
EF	MC-MU	1.29	65	74	6.4	30	331	25	14	731	106	4.0	1.8
	Col.R.	1.05	66	61	6.3	13	320	41	13	2113	165	4.0	1.4
	MC-AU	1.07	58	68	7.0	17	174	38	13	938	192	4.1	2.3
	Cor.R.	1.39	225	58	7.0	48	296	252	16	3863	467	6.6	7.4

Table 2. Values of physical and chemical variables in the main channel of the Middle Paraná River at the meandering and anastomosing units (MC-MU and MC-AU, respectively), Colastiné River (Col.R), and Coronda River (Cor.R.) during the early low water phase (ELW), late low water phase (LLW), ordinary flood (OF), and extreme flood (EF). C. Vel.: current velocity; Cond.: conductivity; DO: dissolved oxygen saturation; Turb.: turbidity; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DSi: dissolved silica; TN: total nitrogen; TP: total phosphorus; a_{440}: absorption coefficient at 440 nm; Chl-*a*: chlorophyll-*a*.

4.2. The geomorphologic units

Noticeable changes from the MR towards more isolated floodplain environments were observed in both geomorphologic units (Fig. 4). The MU showed significant monotonic trends from the Paraná main channel and Colastiné River towards LTC for turbidity (S=-43), DIN (S=-45), DSi (S=-57) and chlorophyll-*a* (S=35). In the AU, monotonic trends from the Coronda River towards LTC were significant for conductivity (S=-61), turbidity (S=-73), SRP (S=-59), DIN (S=-77), DSi (S=-59), chlorophyll-*a* (S=57), and macrophyte cover of aquatic environments (S=55) (MK test, $p<0.05$). According to FK test, the spatio-temporal coefficient of variation (CV) of conductivity was significantly higher in the AU (48%, in comparison with 19% in the MU, FK: 18, $p<0.0001$); while the CVs were significantly higher in the MU than in the AU for dissolved oxygen saturation (54 vs. 36%, FK = 75), TP (106 vs. 67%, FK = 74), and a_{440} (50 vs. 33%, FK = 72) ($p<0.05$). Spatial CVs of most variables within each unit were the lowest during the EF (FK test, Table 3).

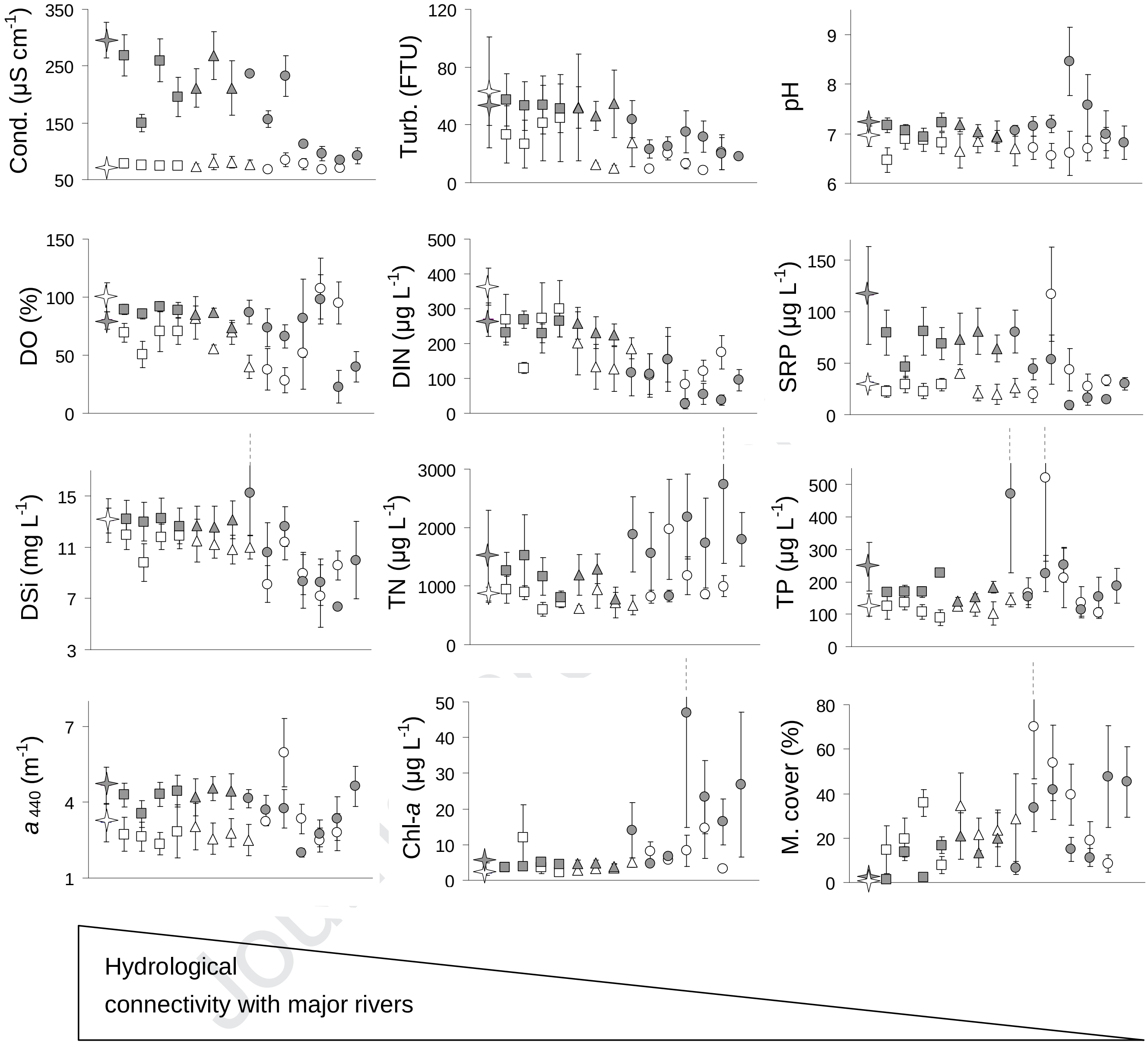

Fig. 4. Mean values of variables measured across the meandering unit (white symbols) and anastomosing unit (grey symbols). Aquatic environments were ordered from the highest to the lowest degree of hydrological connectivity to the major rivers (MR, stars) and are represented by squares (secondary channels), triangles (floodplain lakes permanently connected to the MR), and circles (floodplain lakes temporarily connected to the MR). Error bars represent the standard errors of the means based on the four hydro-sedimentological phases. Cond.: conductivity; Turb.: turbidity; DO: dissolved oxygen saturation; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DSi: dissolved silica; TN: total nitrogen; TP: total phosphorus; a_{440}: absorption coefficient at 440 nm; Chl-*a*: chlorophyll-*a*; M. cover: macrophyte cover of aquatic environments.

		Cond.	DO	pH	Turb.	DIN	SRP	DSi	TN	TP	a_{440}	Chl-*a*	M. cover
MU	ELW	14^{ab}	67^{a}	7	58^{a}	53^{a}	149^{a}	30^{a}	91	202^{a}	56^{ab}	119^{ab}	101^{ab}
	LLW	22^{a}	51^{ab}	5	87^{b}	89^{b}	200^{b}	31^{a}	53	89^{ac}	93^{a}	69^{a}	74^{a}
	OF	8^{b}	41^{ab}	6	47^{a}	85^{ab}	46^{ac}	20^{a}	36	41^{bc}	12^{c}	141^{ab}	117^{a}
	EF	5^{b}	29^{b}	4	44^{a}	33^{c}	16^{c}	4^{b}	49	20^{b}	18^{bc}	36^{b}	237^{b}
AU	ELW	36	37	9^{a}	31	85^{a}	60^{a}	36	69^{a}	108	34^{a}	120	108
	LLW	53	32	4^{ab}	98	61^{ab}	56^{ab}	24	53^{ab}	28	24^{ab}	124	91
	OF	35	24	4^{ab}	23	55^{ab}	27^{b}	12	20^{b}	39	22^{ab}	202	113
	EF	40	18	2^{b}	34	25^{b}	57^{ab}	7	61^{a}	42	15^{b}	32	156

Table 3. Spatial coefficients of variation for the meandering unit (MU) and anastomosing unit (AU) during the early low water phase (ELW), late low water phase (LLW), ordinary flood (OF), and extreme flood (EF). Cond.: conductivity; DO: dissolved oxygen saturation; Turb.: turbidity; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DSi: dissolved silica; TN: total nitrogen; TP: total phosphorus; a_{440}: absorption coefficient at 440 nm; Chl-*a*: chlorophyll-*a*; M. cover: macrophyte cover of aquatic environments. Different letters indicate significant differences between hydro-sedimentological phases according to Fligner-Killeen test ($p<0.05$).

4.3. The river-floodplain system

Four principal components were significant, according to eigenvalues > 1 criterion, in all the PCAs made to interpret the major patterns of spatial heterogeneity during each hydro-sedimentological phase (Table S1, supplementary material). LTC showed the highest dispersion in PC1-PC2 and PC3-PC4 biplots, except during the EF when differences between habitat types were imperceptible and all of them showed a similar dispersion. In contrast, the separation between geomorphologic units increased during the EF (Figs. 5 and 6; A, B, C, and D). This was mainly related to turbidity, conductivity, chlorophyll-*a*, and SRP, whose associations to the AU were intensified.

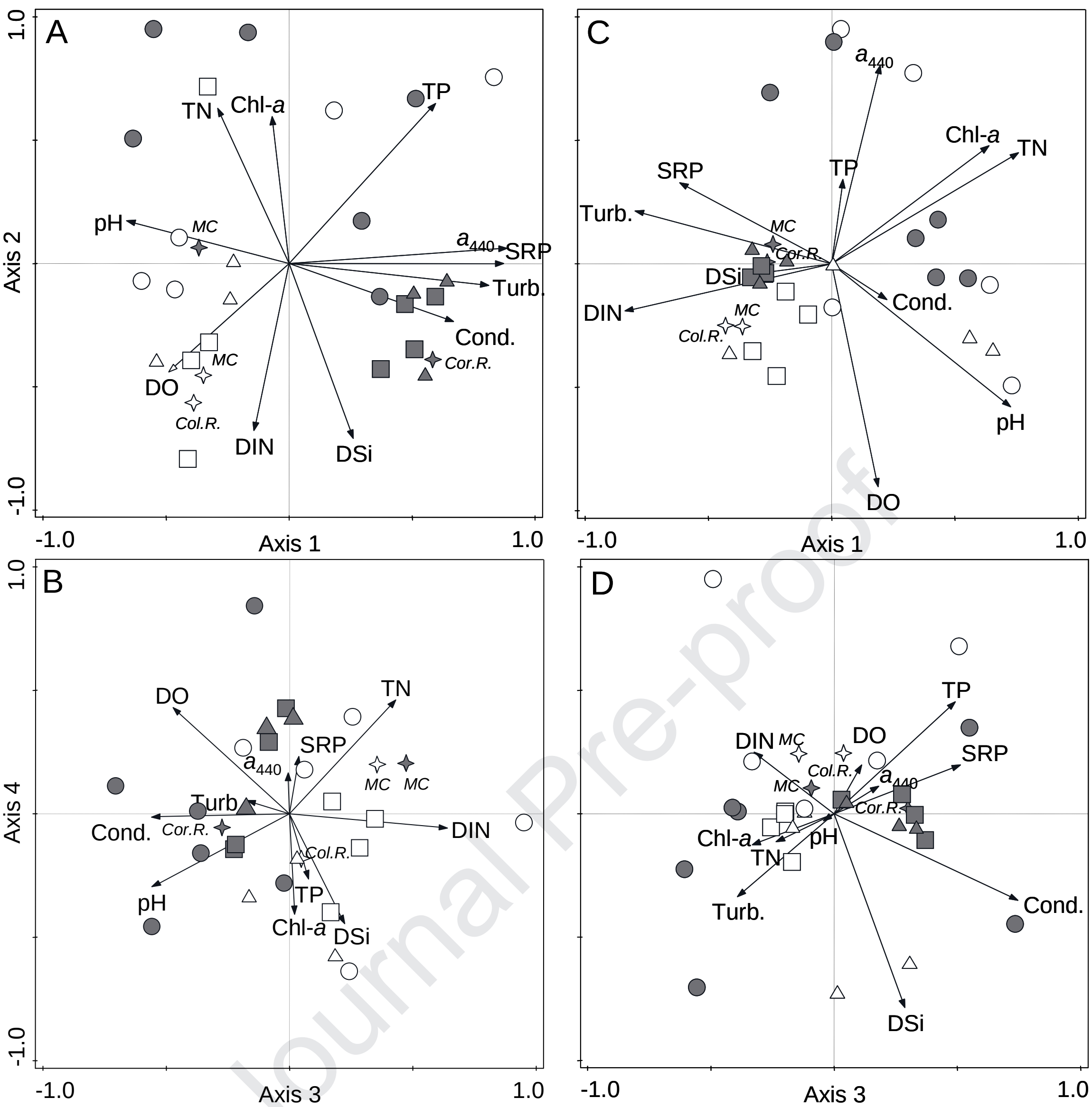

Fig. 5. Principal Component Analysis biplots showing the major patterns of spatial heterogeneity of the river-floodplain system during the early low water phase (A, B) and the late low water phase (C, D). Aquatic environments from the meandering unit (white symbols) and the anastomosing unit (grey symbols) are represented by stars (major rivers [MR]), squares (secondary channels), triangles (floodplain lakes permanently connected to the MR), and circles (floodplain lakes temporarily connected to the MR). Note that the names of MR are spelled out: main channel (MC), Colastiné River (Col.R.), and Coronda River (Cor.R.). Cond.: conductivity; DO: dissolved oxygen saturation; Turb.: turbidity; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DSi: dissolved silica; TN: total nitrogen; TP: total phosphorus; a_{440}: absorption coefficient at 440 nm; Chl-*a*: chlorophyll-*a*.

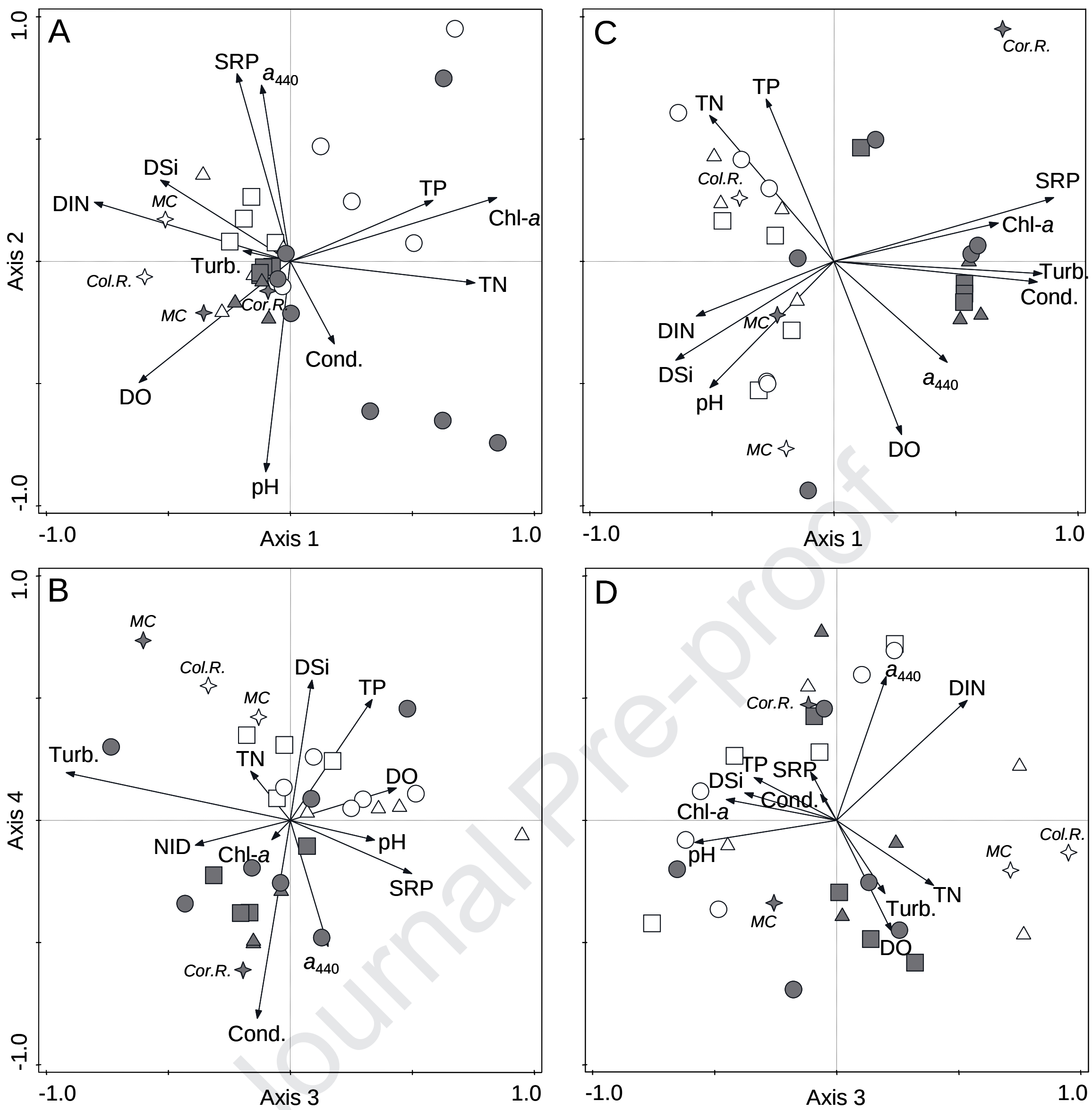

Fig. 6. Principal Component Analysis biplots showing the major patterns of spatial heterogeneity of the river-floodplain system during the ordinary flood (A, B) and the extreme flood (C, D). Aquatic environments from the meandering unit (white symbols) and the anastomosing unit (grey symbols) are represented by stars (major rivers [MR]), squares (secondary channels), triangles (floodplain lakes permanently connected to the MR), and circles (floodplain lakes temporarily connected to the MR). Note that the names of MR are spelled out: main channel (MC), Colastiné River (Col.R.), and Coronda River (Cor.R.). Cond.: conductivity; DO: dissolved oxygen saturation; Turb.: turbidity; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DSi: dissolved silica; TN: total nitrogen; TP: total phosphorus; a_{440}: absorption coefficient at 440 nm; Chl-*a*: chlorophyll-*a*.

Significant differences between habitat types occurred during all the hydro-sedimentological phases (KW test, $p<0.05$, df = 3), with the exception of the EF. LTC differed significantly on DIN (H = 14.7 [ELW], 15.6 [LLW], 15.2 [OF]), DSi (H = 8.6 [ELW], 8.0 [LLW], 14.3 [OF]), TN (H = 11.2 [LLW]) and chlorophyll-*a* (H = 19.9 [LLW], 18.2 [OF]); whereas both PCL and TCL differed significantly from lotic environments in relation to macrophyte cover (H = 17.5 [ELW], 13.4 [LLW], 12.3 [OF]). On the other hand, significant differences between geomorphologic units occurred during all the hydro-sedimentological phases (KW test, $p<0.05$, df = 1). During the EF, units differed significantly on conductivity (H = 6.1), dissolved oxygen saturation (H = 6.1), turbidity (H = 6.1), SRP (H = 6.1), DSi (H = 6.1), TP (H = 5.5), a_{440} (H = 4.9), and chlorophyll-*a* (H = 4.4). Fewer variables differed significantly between units during the ELW (conductivity [H = 16.7], pH [H = 4.3], turbidity [H = 15.4], SRP [H = 7.1], TP [H = 6.4], and a_{440} [H = 9.7]); LLW (conductivity [H = 8.1]); and OF (conductivity [H = 19.1], pH [H = 12.6], turbidity [H = 8.6], and TN [H = 9.3]). In addition, macrophyte stands analyzed in lakes were significantly denser in the AU than in the MU during the ELW (mean values: 120 and 86%, respectively; H = 5.76); whereas the current velocity of SC was significantly higher in the AU than in the MU during the LLW (mean values: 0.75 and 0.14 m s^{-1}, respectively; H = 4.08) and the OF (mean values: 0.89 and 0.41 m s^{-1}, respectively; H = 5.33).

The PERMDISP showed significant differences in environmental heterogeneity across surveys, geomorphologic units (only during the EF), and habitat types (except during the EF) ($p<0.05$) (Table S2, supplementary material). A negative association between environmental heterogeneity and hydrometric level was observed for the whole river-floodplain system: low water phases exhibited more environmental heterogeneity between aquatic environments than high water phases (Tukey's test, $p<0.05$). However, a significantly greater homogenization of the MU in comparison with the AU was observed during the extreme flood (Tukey's test, $p<0.05$). Regarding habitat types, the highest environmental heterogeneity was observed for LTC (Tukey's test, $p<0.05$) (Fig. S1, supplementary material).

5. Discussion

5.1. Spatial patterns of the river-floodplain system

The distinctive water quality of the Coronda River is associated to saline tributaries (mainly the Salado River) coming from the Chacoan plains of Argentina. In addition, creeks coming from urban and rural areas of its basin (José de Paggi and Devercelli, 2011) would increase its values of turbidity, SRP, chlorophyll-*a* and a_{440}, and would decrease its dissolved oxygen saturation. Differences between geomorphologic units would be produced by these tributaries because they flow into the Paraná system, through the Coronda River, upstream the anastomosing unit. In turn, the higher nutrient concentration of the anastomosing unit could lead to denser macrophyte stands at its floodplain lakes. Most plant species show higher rates of growing and vegetative reproduction and a lower rate of mortality when nutrient concentrations are high, which favour a rapid colonization of available areas (Henry-Silva et al., 2008; Junk and Piedade, 1997; Sarneel et al., 2010).

The decreasing trends observed from the major rivers towards more isolated floodplain lakes for turbidity, DIN, and DSi, as well as the increasing trends observed for TN, chlorophyll-*a* and macrophyte cover of aquatic environments are in agreement with previous reports (Cardoso et al., 2012; Maine et al., 2004; Mayora et al., 2017; Unrein, 2002). In contrast, the decreasing trends observed along the gradient of hydrological connectivity of the anastomosing unit for conductivity and SRP are unusual for river-floodplain systems. They would be associated with larger contributions of water rich in salts and nutrients from the Coronda River to nearer aquatic environments. On the other hand, the stronger monotonic trends in physical, chemical and biological variables along the spatial gradient of the anastomosing unit in comparison with the meandering unit would be associated with inputs of water with very different qualities from the right and left sides of the floodplain through the Coronda River and Paraná River, respectively.

5.2. Influence of the hydro-sedimentological regime on environmental heterogeneity at multiple spatial scales

The higher dissimilarities between aquatic environments during the low water phases are likely the result of the higher influence of local driving factors in comparison with high waters (Thomaz et al., 2007). These factors (e.g. point inputs of materials, wind-driven sediment resuspension, and ecological succession) differ in intensity according to habitat type, localization, and morphometry (Bonecker et al., 1998; Mayora et al., 2013). The divergence in environmental conditions during low waters was particularly pronounced at more isolated floodplain lakes, which are known to follow their own succession after isolation (Hamilton and Lewis, 1990; Thomaz et al., 2007). Their persistent distinction during the ordinary flood indicates that the magnitude and/or duration of this phase were not enough to decrease the importance of local factors at these water bodies. In accordance, Weilhoefer et al. (2008) observed that homogenizing more isolated floodplain lakes with the river-floodplain system requires high magnitude floods.

We observed a homogenization effect of the extreme flood when considering all the sampled environments, in accordance with the general pattern proposed for river-floodplain systems. However, this effect varied in accordance with the considered spatial scale. Floods tend to exacerbate the eutrophization of anthropized watersheds, like that of the Coronda River, where the increase in the delivery of nutrients and organic matter from diffuse sources located in flooded areas is much stronger than dilution (Talbot et al., 2018). This can explain the greater environmental differences between major rivers during the extreme flood in comparison to the other phases. Even more, the extreme flood overlapped with rising levels of the Salado River (records of Dirección General de Servicios Técnicos Específicos - Ministerio de Infraestructura y Transporte, Province of Santa Fe), which flows into rural and urban areas before joining the Coronda River (José de Paggi and Devercelli, 2011). The higher supplies of water with different qualities across the meandering and anastomosing units would have in turn pronounced the distinction between them. Simultaneously, the degree of hydrological connectivity within each geomorphologic unit increased as a result of the complete floodplain inundation, which would have contributed to their internal homogenization.

The higher spatio-temporal heterogeneity of the meandering unit in comparison to the anastomosing unit observed for several variables was probably due to the higher levees of the first one and the subsequent longer periods of isolation of its floodplain lakes, which intensify the environmental divergence through local processes (Thomaz et al., 2007; Tockner et al., 2000). However, the spatio-temporal heterogeneity of most variables was similar in both units. The anastomosing unit is mainly fed by the Coronda River and secondary by the Parana River, both of which vary in their relative discharges over time. This could increase the spatio-temporal variability of the anastomosing unit, counteracting partially the effects of its greater hydrological connectivity resulting from its smaller relative relief (Marchetti et al., 2013). Similarly, this can explain the lower homogenization of the anastomosing unit in comparison with the meandering unit during the extreme flood, when the contributions of both the Coronda River and the Parana River increased.

6. Conclusions

As expected, the geomorphologic units played a key role in maintaining the environmental heterogeneity during the extreme flood, when land barriers among aquatic habitats disappeared. However, a detailed analysis of the data allowed us to partially accept our hypothesis. Not only aquatic habitat types, but also geomorphologic units, were major responsible for spatial heterogeneity during low waters; and these roles were not affected by the ordinary flood.

In relation to the previous statements, environmental heterogeneity of the Middle Paraná River system was mainly associated with aquatic habitat types and relative contributions of lateral tributaries with different water qualities to each geomorphologic unit, in combination with the influence of the hydro-sedimentological regime. Both habitat types and geomorphologic units were responsible for spatial heterogeneity during the low water phases and the ordinary flood. In contrast, only geomorphologic units played a major role during the extreme flood, when their differentiation increased as a result of changes in the relative contribution of lateral tributaries.

In conclusion, although the increase in the hydrological connectivity produced by floods has a homogenization effect, floods may also enhance inputs of water from regions with variable geological characteristics and land uses, therefore increasing the environmental heterogeneity. The predominance of one or the other effect depends on the considered spatial scale. It would be beneficial that future management strategies aiming to maintain or restore the functionality of large river-floodplain systems integrate the knowledge about environmental heterogeneity considering the different scales of these complex systems.

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Data Availability

Raw data supporting the findings of this study are available from the corresponding author G. Mayora on request.

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Highlights

- The major environmental heterogeneity at the habitat scale was linked to more isolated floodplain lakes.
- Geomorphologic units maintained the environmental heterogeneity at the landscape scale.
- The effect of floods on the environmental heterogeneity depended on the spatial scales.
- Different interacting scales of variation strengthened the environmental heterogeneity.

Author Statement

All the authors contributed to the study conception and design, acquisition of data, or analysis and interpretation of data; drafted the manuscript or revised it critically for important intellectual content; and finally approved the version to be published.

Conflict of Interest Statement

The authors declare that there is no conflict of interest.