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Macrophyte assemblages in relation to environmental, temporal and spatial variations in lakes of a subtropical floodplain-river system, Argentina

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ABSTRACT

This work analyses the variation in the structure of macrophyte assemblages in relation to environmental (lake morphometry and water physico-chemistry), temporal and spatial variables, in seven floodplain lakes placed in the surrounding of the Salado and the Paraná Rivers confluence in the Paraná floodplain-river system. We recorded the variations in cover of thirteen of the most important macrophyte species among rooted and free-floating life forms. A discriminant analysis of the main coordinates showed significant differences among floodplain lakes (spatial variation), as well as among the 13 months studied (temporal variation). Redundancy analysis indicated that electrical conductivity, maximum depth, shoreline development index, lake area and water temperature had significant influence on macrophyte assemblages. In a partial RDA, environmental and temporal variables accounted for a similar percentage of total explained variation (~50%), whereas spatial variables, including distance to main channel, accounted for 30.6%. Results show that the environmental variables of lakes, temporal descriptors, and the spatial position of lakes along the floodplain can explain a significant fraction of variation of macrophyte assemblages. These results allow us to understand the dynamic of macrophyte assemblages along temporal and spatial scales and their association with flooding regime, considering local (physico-chemical and morphometric) and landscape (spatial) characteristics of the floodplain environments.

1. Introduction

Subtropical floodplain-river systems are among the most biodiverse and productive ecosystems in the world (Lewis et al., 2000; Hamilton et al., 2007). The natural dynamic of these systems is largely driven by the seasonal water level variation that interacts with floodplain geomorphology and determines different degrees of connectivity of floodplain lakes.

The spatio-temporal heterogeneity of floodplain-river systems provides habitats for a wide variety of macrophyte species, which usually appear in multispecific assemblages. Macrophytes are responsible for the high primary productivity, modify nutrient cycling, and affect other organisms like invertebrates and fishes, acting as key elements in the structure and functioning of the entire floodplain-river system (Petr, 2000; Thomaz and Ribeiro da Cunha, 2010; Scarabotti et al., 2011).

Floods have been referred as the most important factor affecting the dynamic of macrophyte assemblages in floodplain-river systems (Junk et al., 1989; Neiff et al., 2014; Morandeira and Kandus, 2015). Flood pulses replenish the nutrient stocks in the floodplain (Junk et al., 1989) and tend to increase environmental similarity among aquatic ecosystems (Thomaz et al., 2007). Additionally, flooding can act as a recurrent disturbance factor that resets the successional process of plant communities and maintains the system in an immature but highly productive and diverse stage (Puckridge et al., 1998; Marchese et al., 2002).

During periods of low water level, lakes become isolated and differentiate in their physico-chemical internal conditions that affect aquatic communities. Perimeter, area and depth have been pointed to affect the macrophyte distribution (Santos and Thomaz, 2007), as well as nutrient availability and conductivity (Neiff and Poi de Neiff, 2003; Schneider et al., 2015). Small changes in the degree of connectivity between water courses and fluvial lakes can strongly affect lake morphometry, physico-chemical variables, and macrophyte assemblage composition (Thomaz et al., 2008).

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Although earlier studies on macrophyte assemblages of the Paraná River included successional changes in the relationship between macrophyte and physico-chemical variables (Neiff, 1975, 1979; Franceschi and Lewis, 1979; Neiff and Neiff, 2003; Sabattini and Lallana, 2007), these relationships have not been studied in combination with hydrological connectivity. A recent contribution shows an association between macrophyte species richness and composition and the degree of connectivity, lake morphometry and abiotic factors (Schneider et al., 2015). However, none of these studies evaluated how the environmental variables and macrophyte assemblages were modified during different periods of connectivity.

This work was conducted to analyze the temporal and spatial variation of macrophyte assemblages in relation to morphometric and physico-chemical changes of floodplain lakes associated with different degree of connectivity of a subtropical floodplain-river system. We separately considered the relationships between macrophyte assemblages and three different dimensions: environmental (including morphometry and physico-chemical), temporal (months during a year) and spatial (location of lakes). This was carried out in order to assess the relative importance of these terms in determining macrophyte assemblage structure.

2. Materials and methods

2.1. Study area

The study area is located in the final reach of the Salado River, three kilometers upstream of the mouth into the Paraná River. The Salado River belongs to the La Plata River basin and it is an affluent of the Middle Paraná River (Fig. 1A-B), with a high conductivity (mean 3000 μScm^{-1}; range 460–7000; Devercelli, 2008) compared to the low conductivity of Middle Paraná River (range between 30 and 120 μScm^{-1}; Depetris and Pasquini, 2007). It originates in northwestern Argentine and flows through 1500 km up to its mouth. In its final reach, it has a meandering channel of about 100 m in width and 7 in depth, which runs in a floodplain being approximately 2.5 km wide with islands, swamps, paleo-channels and oxbow lakes (INCyTH, 1986; FICH, 2006).

The hydrometric regime of the Salado River (Fig. 2) is characterized by high water periods that generally occur in summer and autumn (between December and April) and low water periods at the beginning of spring (between September and October). In the lower reach of the Salado River, the average variation in the water level between both periods is about two meters and it is strongly influenced by the water level of the Paraná River. During high water periods, floodplain lakes become connected with one another and with the Salado River through temporary channels.

The region receives an annual rainfall of 1000 mm, concentrated between December and March, and the monthly mean temperature varies from 11 °C in July to 24 °C in January.

2.2. Sampling

Seven floodplain lakes located in two different locations of the Salado River floodplain were selected for the present study (Fig. 1C). Los Sapos Island (S 31° 39′ 09′′, W 60° 45′ 16′′) is a 200-ha land area situated at the east of the Salado River main channel. The island includes 20 oxbow lakes at their northern end from which five lakes differing in surface area (from 0.52 to 1.76 ha) and distance to the main channel were selected for this study. Santo Tomé swamp (S 31° 39′ 46′′, W 60° 45′ 06′′) is a lowland extension placed on the western bank of the river that communicates with the neighbouring highlands and presents two floodplain lakes (0.76 and 1.61 each), which were also selected as sampling sites (Fig. 1C).

The sampling period spanned 13 months in which the hydrometric levels of the Salado River remained in the average variations. Samples were taken in all lakes within a one-week period every month from August 2004 to August 2005, but they did not start simultaneously in all the lakes: Lakes 1, 2 and 3 were sampled during the whole period; Lakes 4, 5 y 7 in September. Sampling in Lake 6 was initiated in November because it was dry at the beginning of the study. We did not register dry out events in any of the remaining lakes.

We performed monthly sampling transects covering the entire lake perimeter and registered the contour of lakes by means of line drawings on printed and scaled aerial photographs used as reference (1:5000 taken in March 2004 in the low water period). These drawings were then digitalized and georeferenced to measure the surface area, maximum length (fetch), maximum width (breadth) and perimeter for each lake using the software Global Mapper. In order to describe the shape of the lake, we calculated the shoreline development index, i.e. the relation between perimeter (P) and surface area (A), as follows, $P/(4\pi A)^{0.5}$. Additionally, we considered as a measure of spatial connectivity the shortest distance in water from the floodplain lakes. The Salado River hydrometic level was measured in Santo Tomé city and it was provided by the Instituto Nacional de Limnología (INALI). Lakes were weekly visited while hydrometric levels rose, then the overflow level of each lake was determined by recording the date in which they became connected with the river, and observing the hydrometric level of these date. Once overflow level for each lake was obtained, the number of days in which lakes were connected and isolated from the Salado River were calculated by using software PULSO (Neiff and Neiff, 2003). The fluvial connectivity index (FCQ) was also obtained from the ratio between number of the connected days and number of the disconnected days (Neiff and Neiff, 2003). Finally, physico-chemical variables such as water depth, transparency, temperature, electrical conductivity, pH, and dissolved oxygen were measured at the deepest point of each lake and between 9:00 and 13:00 hs, to avoid variation associated to daily cycles of these variables.

Additionally, during the monthly sampling surveys, we registered the contour of all patches of emergent and floating macrophytes. For each patch, we visually estimated the proportion of cover of each species. As described for lake measurements, we used Global Mapper software to measure the surface area of each macrophyte patch. The coverage of each species within each patch was calculated multiplying the surface area of the patch by the visually estimated proportion of coverage of each species. Finally, we calculated the area covered by each species in all the lake summing up their coverage across all patches.

2.3. Quantitative analyses

Macrophyte species occurring in less than 5 samples (<6% occurrence) were not included in the quantitative analyses to avoid biases generated by rare species. These species rarely surpassed 1% of the whole vegetation cover in the samples. For multivariate analysis, species data were transformed by Hellinger-standardization because it offers a better compromise between linearity and resolution for linear ordination methods (Legendre and Gallagher, 2001).

We applied a Canonical Analysis of Principal coordinates (CAP; Anderson and Willis, 2003) based on a linear discriminant analysis, in order to detect differences in floristic composition among floodplain lakes and among months. To use the same ecological distance as in the following linear ordination methods, we used the Euclidean distance together with 1000 random permutations without restrictions (Manly, 1997). Once significant differences in species composition were checked for floodplain lakes and months ($p < 0.05$ obtained from CAP), contrasts between all pairs of lakes and months were evaluated by the Multi-Response Permutation

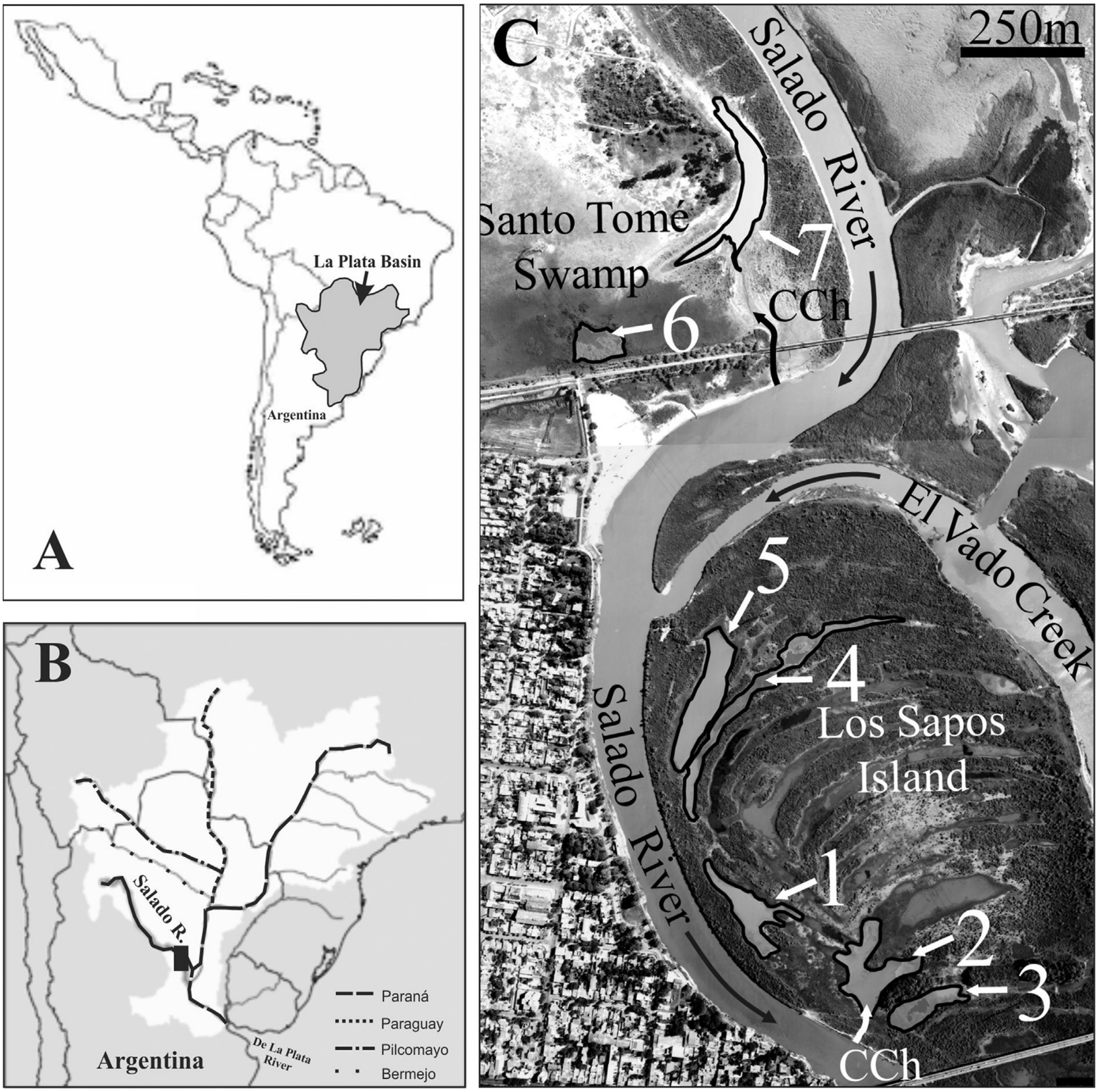

Fig. 1. (A) Study area in the Plata River Basin, (B) the Salado River and main water courses of the basin, (C) Aerial photograph (1:40,000) taken in April 2004 at low waters (hydrometrical level, 2.59 m) showing the location of the floodplain lakes studied, indicated with numbers (1–7). Arrows along channels indicate flow direction; CCh stands for river-floodplain connection channel.

Procedure (MRPP). The MRPP is a nonparametric procedure for testing the hypothesis of no difference between groups (McCune and Grace, 2002). Therefore, the statistical significance for 21 pair-wise contrasts between lakes and for 78 pair-wise contrasts between months was evaluated. We used the Holm procedure to obtain corrected *p*-values in multiple comparisons tests.

To determine the relationship between environmental variables and the spatial and temporal variation in a macrophyte assemblage structure, we performed a series of Redundancy Analyses (RDA; Økland, 2003). Each RDA included a set of explanatory variables (environmental, spatial and temporal) separately, in order to detect only those variables with a significant ($p < 0.05$) association to the species matrix, reducing in this way the degree of multicollinearity within each set of explanatory variables. Environmental variables included transparency, temperature and electrical conductivity of lakes, maximum depth, shoreline development index, fetch, breadth, and lake perimeter.

Spatial variables were generated by the method of Moran Eigenvectors Maps (MEM; Dray et al., 2006). This method starts with two square matrices. The first matrix contains the Euclidean distances among sampling sites calculated from geographic coordinates. The second matrix, called connectivity matrix, contains 1 if sites are neighbors in the space, and 0 if they are not (neighbors). As sites were positioned in an irregular manner in the space, the neighborhood relationships were obtained using the Gabriel graph (Legendre and Legendre, 2012). Then, a weighted matrix of neighbor distances is calculated as the Hadamar product (cell by cell multiplication) between the two matrices. Finally, this matrix is modified replacing the zeros, including cells in the diagonal, by four times the maximum distance between neighbor sites, in a process named truncation. The resulting truncated matrix is used to compute the MEM eigenvectors by the Principal Coordinates Analysis (PCoA). The positive eigenvectors obtained by this method can be used as independent spatial descriptors in multivariate analyses

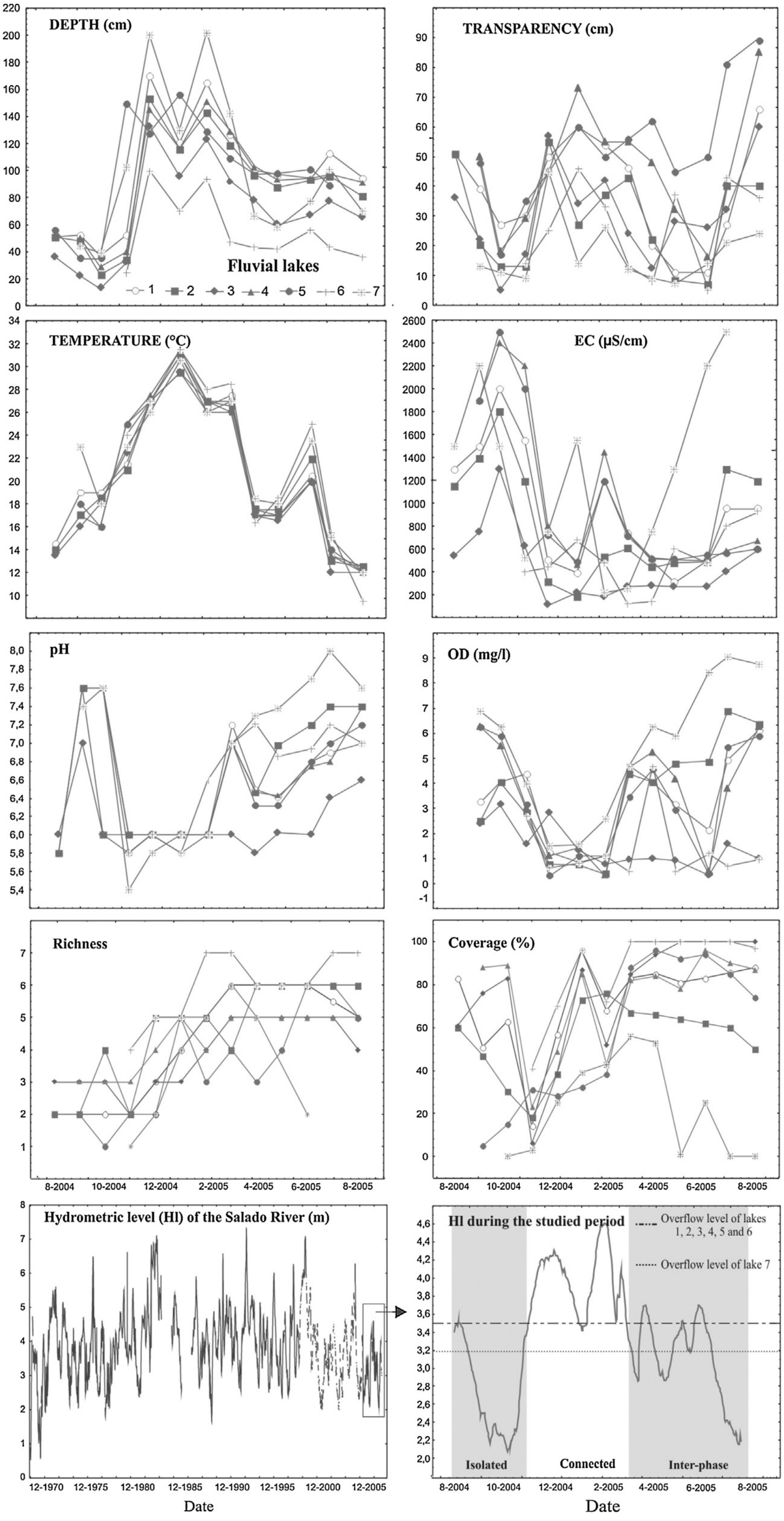

Fig. 2. Temporal variation of water physico-chemistry and macrophyte richness and cover for each floodplain lake, and water level variation of the Salado River during the period studied.

(Borcard and Legendre, 2002). This analysis produced five spatial descriptors from which only one (Spatial Eigenvector 1, SE1) showed a significant ($p < 0.05$) Moranís I spatial correlation coefficient that was used for subsequent analysis. The distance of lakes to main channel (DMC) was also included as a spatial descriptor. These variables modeled different effects of space on macrophyte assemblages: the spatial eigenvector 1 was associated with rela-

Table 1
Median values for the six morphometric variables measured in the seven lakes of the Salado River floodplain and in three hydrological periods (I: Isolation; C: Connection; IF, interphase). Distance to the water course from each lake to main channel is shown in the bottom of the Table Shoreline development index; the relation between perimeter (P) and surface area (A), as follows, $P/(4\pi A)^{0.5}$.

Morphometric variable	Hydrological phase	Lakes						
		1	2	3	4	5	6	7
Maximum Depth (cm)	I	52	41	27	40	35	44	24
	C	165	143	123	145	150	200	94
	IF	96	90	66	94	98	68	43
Area (m^2)	I	611	758	271	1440	604	952	892
	C	823	724	698	1570	822	2410	892
	IF	843	859	472	1455	794	1745	494
Perimeter (m)	I	142	135	85	125	269	225	305
	C	317	263	227	362	322	719	322
	IF	250	203	149	301	302	361	161
Lake Fetch (m)	I	142	135	85	125	269	225	305
	C	317	263	227	362	322	719	322
	IF	250	203	149	301	302	361	161
Maximun Width (m)	I	60	129	28	21	58	42	282
	C	139	158	122	89	82	408	304
	IF	94	154	60	50	72	149	98
Shoreline development	I	1.7	1.5	1.4	1.3	3.1	2.1	2.9
	C	3.1	2.7	2.4	2.6	3.2	4.1	3.0
	IF	2.3	2.0	2.0	2.2	3.0	2.5	2.0
Distance to main channel (m)		395	110	161	619	811	394	452

tionships among neighbor lakes, whereas DMC was associated with relationships between lakes and the main channel.

The MEMs approach was also used to generate temporal descriptors (Legendre and Gauthier, 2014). For this analysis, we used the distance in months among sampling dates (thirteen months). Sampling dates were considered neighbors if they were separated by a distance threshold of one month (consecutive samplings; see Legendre and Gauthier, 2014). Twelve temporal descriptors were obtained and only four (Eigenvectors 1, 2, 3 and 4) exhibited positive eigenvalues and significant Moranís I temporal correlation coefficient, and thus were retained.

Four matrices (macrophyte data, environmental, spatial and temporal variables) were then used in a partial RDA analysis in order to study the amount of variation in the species composition explained by environmental, spatial and temporal variables.

The analysis of partial RDA consisted of a series of RDA runs where all combinations of sets of variables were used as constraining variables and the remaining sets were used as co-variables (Økland, 2003). Then, all remaining fractions of partitioning (unique and shared components of variation) could be obtained by simple subtraction [see Økland (2003) for computation details]. We reported the variation explained by each component as the percentage of total variation explained (TVE), calculated as the ratio between the sum of all canonical eigenvalues and total inertia, as recommended by Økland (1999). Statistical analyses were performed with the free software CAP (Anderson, 2004), CANOCO 5 (ter Braak and Šmilauer, 2012) and the package Spacemaker from the R programming environment (Dray et al., 2006; R Core Team, 2016).

3. Results

3.1. Spatio-temporal variation of environmental features and macrophyte attributes

Environmental variables (morphometric and physico-chemical variables) as well as macrophyte cover and richness showed clear responses to water level variation (Table 1 and Fig. 2). Lakes 1–6 were connected to the river 38% (160 days) of the study period while Lake 7 was connected during 57% (243 days). The Fluvial Connectivity Index was almost twice higher for Lake 7 (1.7) than for Lakes 1–6 (0.8). During the low water phase (which was 62% and 43% for lakes 1–6 and 7, respectively, mainly at the beginning of this study), all fluvial lakes were disconnected from the main channel and their morphometric variables presented the lowest values in the study period. Transparency dropped and conductivity rose following the reduction of the lakeís water surface. The first flood peak occurred in December 2004 and it was associated with the rise of the Paraná River (low conductivity). The second flood happened two months later in February 2005 by the rise of the Salado River (high conductivity). After the first flood, morphometric variables and transparency increased while conductivity dropped. During this period, dissolved oxygen diminished to very low values. From April to September 2005, the Salado River level remained between connection and disconnection levels (inter-phase period, Fig. 2) and the lakes differentiated in relation to macrophyte cover and water characteristics. Completely vegetated lakes (Lakes 3 and 6) showed lower dissolved oxygen and higher transparency, whereas another lake (Lake 7), that was almost without macrophyte cover showed reduced transparency and high dissolved oxygen (Fig. 2).

The fluctuations in macrophyte richness and cover were also associated with seasonal variation in hydrometric level and temperature (Fig. 2). At the beginning of the study (isolated period), species richness was evenly low, whereas macrophyte cover was higher in smaller lakes (1, 2, 3 and 4), and lower in larger ones (5 and 7). After the rapid rise of waters during the November floods (connected period), most of the macrophyte assemblages were completely submerged and cover drastically decreased in almost all lakes. A slight increase in vegetation cover was observed in larger lakes due to the inundation of marginal vegetated areas. During the following period, the Salado River oscillated between connection and disconnection levels (inter-phase period) and lakes differentiated from each other in their macrophyte cover: Lake 7 returned to macrophyte free condition, Lake 2 kept intermediate values, and the rest of the lakes remained almost totally covered.

3.2. Variation in macrophyte floristic composition

The variation in abundance of thirteen macrophyte species −among them rooted and free-floating- was tracked in the studied floodplain lakes. *Ludwigia peploides* and *Azolla filiculoides* were the most frequent species in all lakes (Table 2A), and were present throughout the sampling year (Table 2B). While *Pisita stratiotes* and *Oplismenopsis najada* occured in all the lakes except for the Isolated period, others like *Alternanthera philoxeroides*, *Enydra anagallis*, *Salvinia biloba* and *Eichhornia azurea* occured just in some lakes or under some hydrologic conditions (Table 2, A- B). The floristic composition was significantly different both between floodplain lakes (spatial variation), and among months (temporal variation) as indicated by CAP (Fig. 3). The MRPP showed significant differences in 16 out of 21 pairwise comparisons among lakes; Lakes 1, 2 and 3 did not differ, and Lakes 2 and 3 were also not different from Lake 7. Similarly, significant differences in floristic composition were also found between months of different hydrological periods (Fig. 3B); 37 out of 78 pairwise comparisons were significant (see Results for all pairwise comparisons in Supplementary material). Records performed at the beginning of the sampling period (isolated between August and November 2004) were placed at the first axis on the left (Fig. 3B), whereas records performed at the end of the study (Inter-phase period between March and August 2005) appeared on the opposite side. Records from Connected period (December 2004 to February 2005) positioned at the center of the diagram. At the end of the sampling period, macrophyte assemblages did not return to their original composition and species composition/assemblage

Table 2
Temporal (A) and spatial (B) percentage frequency of occurrence (%FO) of thirteen macrophyte species in the seven floodplain lakes of the Salado River from August 2004 to August 2005. In A, a value of 100%, means that a species was present in that lake throughout that month. In B, a value of 100% means that a species was present in all lakes throughout that month. The hydrological period (Isolated, Connected or Inter-phase) is shown for each sampling month.

		A							B												
MACROPHYTES SPECIES		FLUVIAL LAKES							ISOLATED			CONNECTED					INTER-PHASE				
Species	Family	1	2	3	4	5	6	7	082004	092004	102004	112004	122004	012005	022005	032005	042005	052005	062005	072005	082005
Azolla filiculoides Lam.	Azollaceae	100	100	85	100	83	30	71	100	83	100	57	100	83	83	100	71	71	71	80	83
Ludwigia peploides (Kunth) P.H. Raven ssp. *peploides*	Onagraceae	100	92	100	100	75	100	86	100	83	83	86	100	100	100	100	100	86	86	100	100
Pistia stratiotes L.	Araceae	50	46	15	67	67	70	57				14	50	67	71	100	71	57	100	83	
Oplismenopsis najada (Hack. & Arechav.) Parodi	Poaceae	50	62	69	75	67	80	43				14	71	83	100	100	100	86	57	100	67
Eichhornia crassipes (Mart.) Solms	Pontederiaceae	58	69	69		25	70	43	33	17		26	33	67	71	71	57	57	80	83	
Salvinia biloba Raddi	Salviniaceae	42	38		50	8		29					17		43	43	43	43	40	67	
Sagittaria montevidensis Cham. & Schltdl. ssp. *montevidensis*	Alismataceae		15	15	17		30			17	67	57									
Enydra anagallis Gardner	Asteraceae		8		25	33				33	17	14	33					14	20		
Louisiella elephantipes (Nees ex Trin.) Zuloaga	Poaceae	8	15				100			17	17	14	43	17		14	14	14	14	20	16
Eichhornia azurea (Sw.) Kunth	Pontederiaceae		8	23				14							14		29	29			
Hydrocotyle ranunculoides L. f.	Apiaceae					8	20					14								20	16
Alternanthera philoxeroides (Mart.) Griseb. f. *philoxeroides*	Amaranthaceae			8				14					17								
Schoenoplectus californicus (C.A. Mey.) Soják var. *californicus*	Cyperaceae						100			17	17	14			14	14	14	14	20	16	

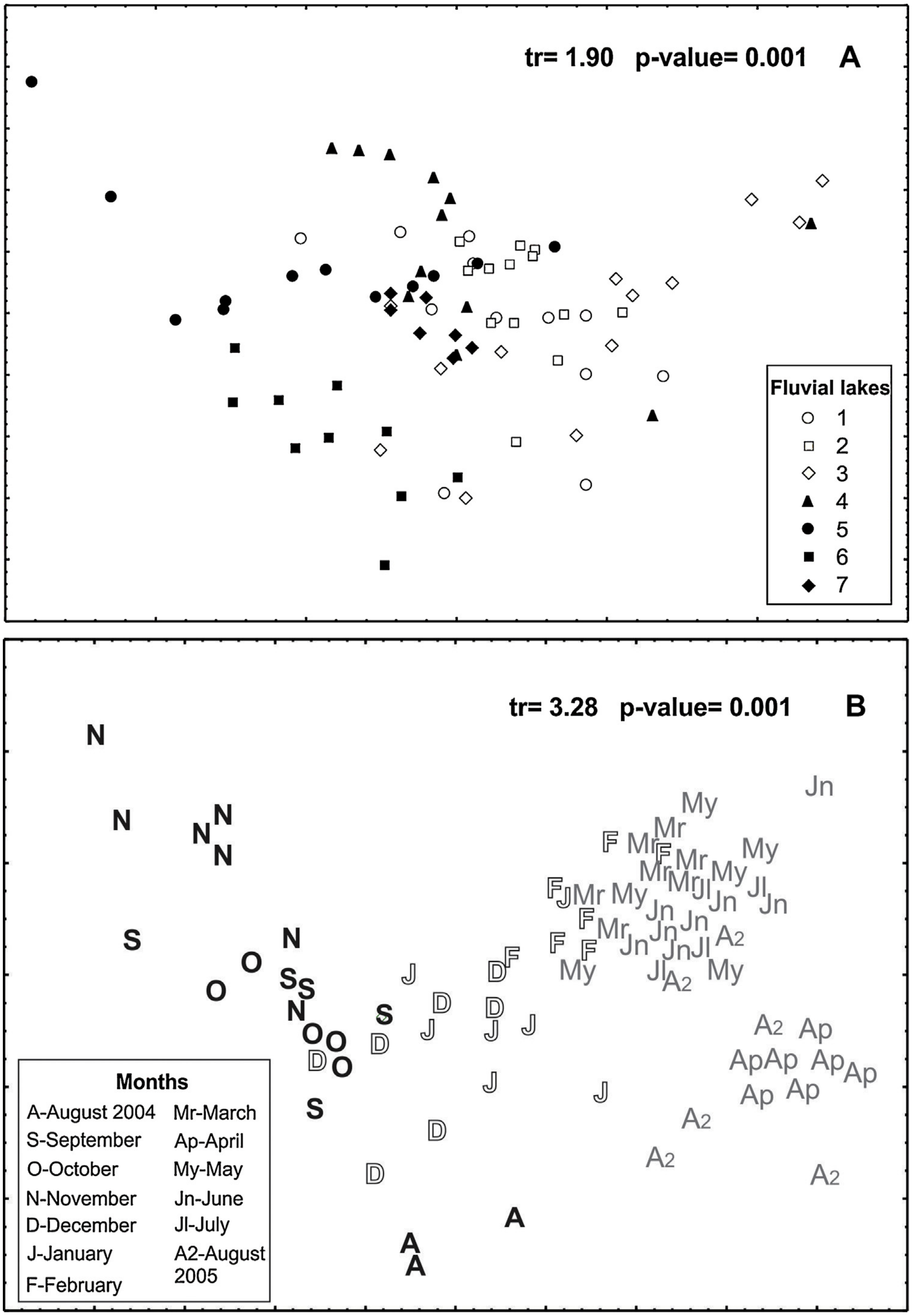

Fig. 3. Canonical Analysis of Principal coordinates (CAP). Spatial (A) and temporal (B) variations in floristic composition of macrophyte assemblages. Symbols represent samples of macrophyte assemblages taken in a particular lake and month. In B, grey, black, and black-white acronyms represent samples taken at different months belonging to inter-phase, isolated and connected periods, respectively. Tr: trace statistic (canonical test statistic).

structures differed in the same month over different years (see August 2004 vs. August 2005 in Fig. 3B and Table 2-B).

3.3. Macrophytes in relation to environmental, temporal and spatial variables

The forward selection procedure included the six environmental variables (electrical conductivity, shoreline development index, maximum depth, lake area, fetch and water temperature), two temporal variables (temporal eigenvectors 1 and 2), and two spatial variables (spatial eigenvector 1 and distance to main channel). The first RDA analysis using only environmental variables showed a significant association between macrophyte assemblages and environmental conditions (Table 3). The first axis was positively associated with lake depth and fetch, and was negatively associated with electrical conductivity (Fig. 4). The second RDA axis was positively associated with temperature and lake area, and negatively associated to shoreline development and conductivity (Fig. 4).

Macrophyte species showed a differential association with these axes (Fig. 4). *Oplismenopsis najada*, *Pistia stratiotes* and *Salvinia*

Table 3
Results of the Redundancy analysis showing the relationship between the abundance of 13 macrophyte species and 6 environmental variables selected by using the forward selection procedure. Results for the process of variables selection and the statistics for the three first canonical axes are shown. Percentage of TVE indicates the amount of the total variation explained by each variable. *Pseudo- F* and *P* values correspond to Montecarlo permutation tests (n = 499 permutations). Total variation is 69.8; explanatory variables account for 29.2%; adjusted explained variation is 23.4%.

Results of forward selection procedure			
Variable	% of TVE	*Pseudo-F*	*P(adjusted)*
Conductivity	25.9	6.5	0.002
Depth	16.3	4.2	0.004
Temperature	22.5	6.2	0.002
Area	11.9	3.4	0.008
Index of shoreline development	10.9	3.2	0.004
Fetch	12.5	3.8	0.008
Summary statistics for ordination axes	Axis I	Axis II	Axis III
Eigenvalues	0.128	0.089	0.017
Cumulative% of the variance of species	12.8	21.7	27.9
Cumulative% of the sp.-env. Correlation	44	74.5	90.1

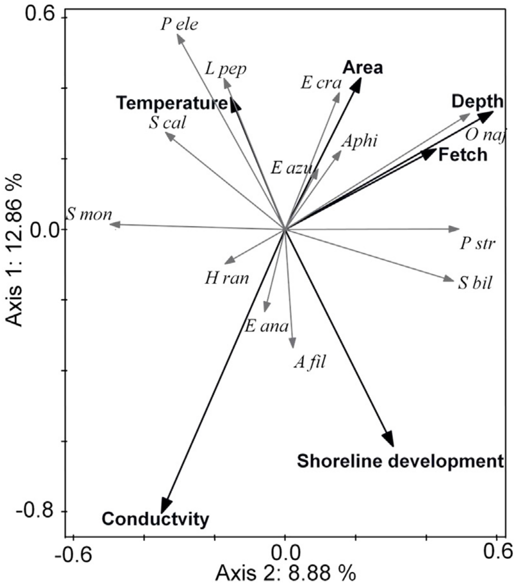

Fig. 4. Biplot of the first two RDA axes showing the relationship between the abundance of 13 macrophyte species and 6 environmental variables selected by the forward selection procedure. Names of environmental variables are indicated in bold, whereas macrophyte species are indicated by italic acronyms (see Table 1 for the correspondence of acronyms with species names).

biloba were more common in larger lakes with low electrical conductivity, whereas *Sagittaria montevidensis* preferred the opposite conditions. *Panicum elephantipes*, *Ludwigia peploides* and *Eichhornia crassipes* preferred conditions of higher temperature and lake area, and lower conductivity and shoreline development index during high water conditions, whereas *Azolla filiculoides* preferred the opposite conditions and was abundant during low waters. The partial RDAs indicated that environmental (lake morphometry and water physico-chemistry), and temporal (monthly variation) variables accounted for a similar percentage of total explained variation (~50% of TVE), whereas the spatial variables only accounted for 30.6% of variation (Table 4). Environmental variables showed component of 15.5% of TVE, whereas temporal and spatial variation showed pure components of 29.3% and 21.8%, respectively. Environmental variables showed a large shared component with temporal variables (24.6%) and a small shared component with spatial variables (9.8%). The shared component of third order was small and negative, a result which is common when three of more set of variables are included in partial ordination analysis (Økland, 2003).

Table 4
Results of the partial RDA showing the total of variation explained by each of the three sets of explanatory variables (top), and the corresponding non - overlapping components of variation: E = Environmental variables, S = Spatial variables, T = Temporal variables. The percentage of TVE indicates the 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 co - variables. Total variation is 69.81; explanatory variables account for 55.0%; adjusted explained variation = 48.5%.

Constrainig Variables	Covariables	% TVE
Enviromental (E)		48.3
Spatial (S)		30.6
Temporal (T)		52.9
Non overlapping components		
E	ST	15.5
S	ET	21.8
T	ES	29.3.
ES	T	9.8
ET	S	24.6
ST	E	0.6
EST		−1.6

4. Discussion

In floodplain-river systems, seasonal variations of levels trigger a homogenization of environmental characteristics of floodplain environments during high waters and a strong differentiation among habitats during low waters (Thomaz et al., 2007; Mormul et al., 2013). This general functioning related to seasonality of water level explains the strong temporal variation detected in environmental variables (physico-chemical and morphometric), as well as in macrophyte richness and cover of floodplain lakes. Most of the recorded variables followed the water level variations over time in association with the variation in connectivity between river and floodplain lakes.

Differences in conductivity and dissolved oxygen among some floodplain lakes were related to morphometric differences in area and depth. In small lakes, for example, rainfall events produce a more pronounced effect of water dissolution than in larger ones, thus reducing conductivity. Similarly, dissolved oxygen values differed spatially between vegetated and open lakes, a fact associated with macrophyte decomposition and wind mixing (Junk, 1997). Besides, after connection with the main channel, macrophyte richness and cover increased in all lakes. In accordance with these results, morphometric and abiotic variables showed a strong correlation with macrophyte richness in aquatic ecosystems of the Paraná River floodplain under different degrees of connectivity (Schneider et al., 2015). Also, hydrology is important in temperate wetlands where the relative importance in determining species composition was estimated in 50% (Thomaz et al., 2008). For example, in an unregulated lowland river from Estonia, the temporal fluctuation of discharge, water level and temperature were identified as the main factors governing the distribution of aquatic plants (Kõrs et al., 2012).

In our study, macrophyte richness and cover increased markedly after the connection period in concordance with high temperatures and reached the highest values during the Inter-phase period. As water levels remained around overflow level during this period, macrophytes continued growing and increased the vegetation cover of lakes during autumn and winter. Although higher productivity values are generally associated with higher temperature in plants, macrophytes can grow in a wide temperature range from 0–40° (Camargo et al., 2003). This indicates that in subtropical systems the temporal variation in macrophyte cover and richnessdepends on the interaction of temperature and hydrometric level variation.

The spatial and temporal differences in the floristic composition of macrophyte assemblages detected by CAP showed that assemblages varied markedly from the beginning to the end of the study period. These differences seem to be associated with the variation of hydrological connectivity during the study period (isolated, connected and inter-phase period). Similar results were obtained for different aquatic ecosystems in the Paraná River floodplain, where macrophyte composition significantly differed according to the degree of connectivity among these ecosystems and the Paraná River (Schneider et al., 2015). In most lakes, macrophyte richness and cover increased from August 2004 to August 2005. At the beginning of the study (Isolated period), *Azolla filiculoides* and some rooted species such as *Alternanthera philoxeroides, Enydra anagallis* and *Sagittaria montevidensis* showed higher relative abundances, but free-floating species such as *Pistia stratiotes, Salvinia biloba* and *Eichhornia crassipes* became dominant towards the end of the hydrological cycle (Connected and Inter-phase period). Dominance of free-floating species after a flood event has been observed in floodplain lakes of the middle Paraná River (Neiff, 1979). The dominance of free-floating species is also common during reservoir filling (Agostinho et al., 1999).

Macrophyte assemblage structure was not recurrent in the same periods of different years, indicating a process of longer time span driving assemblage dynamics. During April 2003, the Salado River experienced an extraordinary century-scale flood event that swept most macrophyte cover from lakes. This event could have initiated a secondary succession, not completed throughout the duration of the present study more than two years after the floods. Understanding the dynamics of macrophyte assemblage variation in floodplain-river systems requires considering both seasonal variation and past flood disturbances that can reset the aquatic ecosystems starting a new successional process (Junk et al., 1989).

Redundancy analysis indicated that electrical conductivity, water temperature, maximum depth, shoreline development index, lake area, and fetch are important factors determining the structure of macrophyte assemblages. These variables have been previously identified as determinants of macrophyte composition for subtropical and temperate aquatic ecosystems. For instance, conductivity and depth (among other variables) significantly influenced macrophyte assemblages in the middle Paraná River floodplain (Schneider et al., 2015). Similarly, deeper lakes of the upper Paraná River showed higher species richness than shallow lakes due to the fact that a greater variety of life forms were replaced along depth gradients (Santos and Thomaz, 2007). This relationship between depth and richness was not found in our study area where the shallowest floodplain Lake 6 presented the highest richness. The low richness of large and deep lakes (e.g. Lake 7) could be associated with its high fetch (Fig. 1C) which probably increased wind and wave disturbance, factors negatively associated with macrophyte cover (Neiff and Poi de Neiff, 2003; Thomaz et al., 2008).

The distance to the main channel is a variable generally associated with connectivity in floodplain studies (Amoros and Bornette, 2000) and has a significant influence on macrophyte composition for temperate floodplain-river systems (Demars and Harper, 2005). In our work, distance to the main channel was associated with changes in macrophyte cover, richness and composition. The highest cover values of species such as *Pistia stratiotes* and *Oplismenopsis najada* were recorded in lakes far away from the main water course (Lakes 6 and 7). The earliest records of these species started during the connection period, reachingmaximum values during the Inter-phase and cold period (April-August).

Colonization by *Ludwigia peploides* seems to be largely triggered by other variables such as temperature and the increase of the lake area during the rising water phase in the summer. The relationship between lake morphometry and macrophyte cover has been previously emphasized for water bodies from Paraguay (Drago et al., 2003), and it is also consistent with our result that the centripetous growth of macrophytes determines small shallow or irregular lakes are covered faster by vegetation than larger and deeper lakes. In correspondence with the results of this study, the shoreline development index has been positively associated with macrophyte richness (Thomaz et al., 2008).

Electrical conductivity of water has been associated with macrophyte distribution in temperate aquatic ecosystems (Kõrs et al., 2012), and with macrophyte diversity patterns in the Itaipú reservoir (Thomaz et al., 2003). In our study, *Azolla filiculoides* and *Enydra anagallis* were positively associated with electrical conductivity. Although *A. filiculoides* was reported to grow at a broad range of conductivity or salinity levels (Rajarathinam and Padhya, 1989; Trindade et al., 2011), it presented its highest cover during the isolated period in which an increase in conductivity was associated with declining lake size. During this process, the floating life style of this species can improve its persistence in water in comparison with rooted species, which rapidly disappear from the lakes. In addition, the low nitrogen availability during low water phases can be a limiting factor in macrophyte growth (Carignan and Neiff, 1992; Neiff and Poi de Neiff, 2003). Symbiotic association of *Azolla filiculoides* with the N_2 fixing cyanobacteria *Anabaena azollae* (Mohamed, 2005) would allow this species to grow in nutritionally poor habitats in which other species could not occur. This idea is also supported by the lack of correlation between water nitrogen and tissue nitrogen in *Azolla caroliniana* (Trindade et al., 2011), suggesting that this nutrient is supplied through symbiosis with Cyanobacteria.

The genus *Salvinia* was pointed as an indicator of connected lakes (Santos and Thomaz et al., 2007), which is consistent with our result since *Salvinia biloba* is associated with deep waters and appeared in the connection period, reaching its maximum cover in the inter-phase period (Table 2).

Partial ordination results showed that environmental (water physico-chemical and lake morphometric variables) and temporal variables accounted for a larger amount of variation in macrophyte assemblages than spatial variables did. Similar to our results, temporal variation in macrophyte composition associated with hydrometric fluctuations was larger in comparison with spatial variation in wetlands of the Llanos of Venezuela (Rial, 2005). The small shared component between environmental and spatial variables was expected since general pattern of environmental variables followed the temporal behavior of the water level, and exhibited a lower degree of spatial differentiation. These analyses suggest that the environmental, temporal and spatial variation of floodplain lakes can explain a significant fraction of variation in macrophyte assemblages for subtropical floodplain-river systems as considered here. These results allows us to understand the dynamic of macrophyte assemblages along temporal and spatial scales and their association with flooding regime, considering local (physico-chemical and morphometric) and landscape (spatial) characteristics of the floodplain environments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.flora.2016.10.004.

References

Økland, R.H., 1999. On the variation explained by ordination and constrained ordination axes. J. Veg. Sci. 10, 131–136.

Økland, R.H., 2003. Partitioning the variation in a plot-by-species data matrix that is related to n sets of explanatory variables. J. Veg. Sci. 14, 693–700.

Agostinho, A.A., Miranda, L.E., Bini, L.M., Gomes, L.C., Thomaz, S.M., Suzuki, H.I., 1999. Patterns of colonization in neotropical reservoirs, and prognoses on aging. In: Tundisi, J.G., Straskraba, M. (Eds.), Theroretical Reservoir Ecology and Its Applications. Backhuys Publishers, The Netherlands, pp. 227–265.

Amoros, C., Bornette, G., 2000. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshw. Biol. 47, 761–776.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.

Anderson, M.J., 2004. CAP: a FORTRAN Computer Program for Canonical Analysis of Principal Coordinates. Department of Statistics, University of Auckland, New Zealand.

Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol. Model. 153, 51–68.

Camargo, A.F.M., Pezzato, M.M., Henry-Silva, G.G., 2003. Fatores limitantes à produção primária de macrófitas aquáticas. In: Thomaz, S.M., Bini, L.M. (Eds.), Ecologia E Manejo De Macrófitas Aquáticas. EDUEM, Maringá, pp. 59–83.

Carignan, R., Neiff, J.J., 1992. Nutrient dynamics in the floodplain ponds of the Paraná River (Argentina) dominated by *Eichhornia crassipes*. Biogeochemestry 17, 85–121.

Demars, B.O.L., Harper, D.M., 2005. Distribution of aquatic vascular plants in lowland rivers: separation the effects of local environmental conditions, longitudinal connectivity and river basin isolation. Freshw. Biol. 50, 418–437.

Depetris, J.P., Pasquini, A.I., 2007. The Geochemistry of the Parana River: An Overview. In: The Middle Parana River: Limnology of a Subtropical Wetland. Iriondo, M.H, Paggi, J.C Parma M.J (eds.), 143–174.

Devercelli, M., 2008. Ecología del fitoplancton en la cuenca inferior del río Salado (Santa Fe, Argentina). In: Desarrollo Algal En Zonas De Retención Hidráulica Y Gradiente Fitoplanctónico En El Flujo Principal. PhD Dissertation. Universidad de Buenos Aires, pp. 161.

Drago, E.C., de Drago, I.E., Oliveros, O.B., Paira, A.R., 2003. Aquatic habitats, fish and invertebrate assemblages of the middle Paraná river. Amazoniana 17, 34–291.

Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modeling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). Ecol. Modell. 3–4, 483–493.

FICH (Facultad de Ingeniería y Ciencias Hídricas), 2006. Estudio de evolución hidráulica, morfológica y dinámica hídrica. In: En: Estudio De Una Interconexión Vial Entre Las Ciudades De Santa Fe Y Santo Tomé. Convenio: Consejo Federal De Inversiones. Universidad Nacional del Litoral – Universidad Tecnológica Nacional (CFI/UNL-UTN), Informe de análisis de alternativas a nivel de prefactibilidad.

Franceschi, E.A., Lewis, J.P., 1979. Notas sobre la vegetación del valle santafecino del Río paraná (República Argentina). Ecosur 6, 55.82.

Hamilton, S.K., Kellndorfer, J., Lehner, B., Tobler, M., 2007. Remote sensing of floodplain geomorphology as surrogate for biodiversity in a tropical river system (Madre de Dios, Peru). Geomophology 89, 23–38.

INCyTH, 1986. Caracterización Hidrológica De La Cuenca Del río Salado. Instituto Nacional de Ciencia y Técnica Hídrica, Centro Regional Litoral Santa Fe.

Junk, J.W., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Can. J. Fish. Aquat. Sci. 106, 110–127.

Junk, W.J., 1997. The Central Amazon Floodplain. Springer-Verlag, New York.

Kõrs, A., Vilbaste, S., Kairo, K., Pall, P., Piirsoo, K., Truu, J., Viik, M., 2012. Temporal changes in the composition of macrophyte communities and environmental factors governing the distribution of aquatic plants in an unregulated lowland river (Emajogi, Estonia). Boreal Environ. Res. 17, 460–472.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., Gauthier, O., 2014. Statistical methods for temporal and space-time analysis of community composition data. Proc. R. Soc. B 281, 0132728, http://dx.doi.org/10.1098/rspb.2013.2728.

Legendre, P., Legendre, L.F.J., 2012. Numerical Ecology, 3rd English edn. Elsevier Science BV, Amsterdam.

Lewis, W.M.J., Hamilton, S.K., Lasi, M.A., Rodríguez, M., Saunders, J.M.I., 2000. Ecological determinism on the Orinoco floodplain. Bioscience 50, 681–692.

Manly, B.F.J., 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, 2nd edn. Chapman & Hall, London.

Marchese, M., Escurra de Drago,I, Drago, E., 2002. Benthic macroinvertebrates and physical habitat relationships in the Paraná River-floodplain system. In: McClain, M. (Ed.), International Association of Hydrological Sciences. Special publication No. 6., pp. 111–131.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach, Oregon, USA.

Mohamed, M., 2005. Role of *Azolla* in Different Ecosystems M.Sc. Degree Thesis. Faculty of Science Al Azhar University, Cairo.

Morandeira, N.S., Kandus, P., 2015. Multi-scale analysis of environmental constraints on macrophyte distribution, floristic groups and plant diversity in the Lower Paraná River floodplain. Aquat. Bot., 13–25, http://dx.doi.org/10.1016/j.aquabot.2015.01.006.

Mormul, R.P., Thomaz, S.M., Soares Vieira, L.J., 2013. Richness and composition of macrophyte assemblages in four Amazonian lakes. Acta Sci. Biol. Sci. 35, 343–350.

Neiff, J.J., Neiff, M., 2003. PULSO, Software Para Análisis De Fenómenos Recurrentes. Dir. Nac. de Derecho de Autor No 236164, Argentina http://www.neiff.com.ar.

Neiff, J.J., Poi de Neiff, A.S.G., 2003. Connectivity processes as a basis for management of aquatic plants. In: Thomaz, S.M., BiniL, M. (Eds.), Ecologia E Manejo De Macrófitas Aquáticas. Editora da Universidade Estadual de Maringá, Maringá, PR, Brazil, pp. 127–144.

Neiff, J.J., Casco, S.L., Mari, E.K.A., Di Rienzo, J.A., Poi, A.S.G., 2014. Do aquatic plant assemblages in the Paraná River change along the river's length? Aquat. Bot. 114, 50–57, http://dx.doi.org/10.1016/j.aquabot.2013.12.005.

Neiff, J.J., 1975. Fluctuaciones anuales en la composición fitocenótica y biomasa de la hidrofitia en lagunas isleñas del Paraná medio. Ecosource 2 (153), 183.

Neiff, J.J., 1979. Fluctuaciones de la vegetación acuática en ambientes del valle de inundación del Paraná medio. Physics 38, 41–53.

Petr, T., 2000. Interactions between fish and aquatic macrophytes in inland waters: a review. FAO Fish. Tech. Pap. 396, 1–185.

Puckridge, J.T., Sheldon, F., Walker, F., Boulton, A.J., 1998. Flow variability and the ecology of large rivers. Mar. Freshw. Res. 49, 55–72.

Rajarathinam, K., Padhya, M.A., 1989. Effect of sodium chloride on composition of *Azolla pinnata*. Curr. Sci. 58, 1250.1251.

Rial, B.A., 2005. Variabilidad espacio-temporal de las comunidades de plantas acuáticas en un humedal de los llanos de Venezuela. Rev. Biol. Trop. 54, 403–413.

Sabattini, R.A., Lallana, V.H., 2007. Aquatic macrophytes. In: Iriondo, M.H., Paggi, J.C., Parma, M.J. (Eds.), The Middle Paraná River: Limnology of a Subtropical Wetland. Springer-Verlag, Berlin, p. 205.226.

Santos, A.M., Thomaz, S.M., 2007. Aquatic macrophytes diversity in lagoons of a tropical floodplain: the role of connectivity and water level. Aust. Ecol. 32, 177–190.

Scarabotti, P.A., López, J.A., Pouilly, M., 2011. Flood pulse and the dynamics of fish assemblage structure from neotropical floodplain lakes. Ecol. Freshw. Fish. 20, 605–618.

Schneider, B., Cunha, E.R., Marchese, M., Thomaz, S.M., 2015. Explanatory variables associated with diversity and composition of aquatic macrophytes in a large subtropical river floodplain. Aquat. Bot. 121, 67–75.

Thomaz, S.M., Ribeiro da Cunha, E., 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurements, causes and consequences on animal assemblages' composition and biodiversity. Acta Limnol. Bras. 22, 218–236.

Thomaz, S.M., Bini, L.M., Pagioro, T.A., 2003. Macrófitas aquáticas em Itaipu: ecologua e perspectivas para o manejo. In: Thomaz, S.M., Bini, L.M. (Eds.), Ecologia E Manejo De Macrófitas Aquáticas. Editora da Universidade Estadual de Maringá, Maringá, PR, Brazil, pp. 319–341.

Thomaz, S.M., Bini, L.M., Bozelli, R.L., 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia 579, 1–13.

Thomaz, S.M., Esteves, F.A., Murphy, K.J., dos Santos, A.M., CAliman, A., Guariento, R.D., 2008. Aquatic macrophytes in the tropics: ecology of populations and comunities, impacts of invasions and use by man, in: encyclopedia of life system support (eolss). Unesco, 1252–1280.

Trindade, C.R.T., Faria Albertoni, E., Palma-Silva, C., 2011. Temporal variation in the biomass and nutrient status of *Azolla filiculoides* Lam: (Salviniaceae) in a small shallow dystrophic lake. Acta Limnol.Bras. 23, 368–375.

Braak, C.J.F., Šmilauer, P., 2012. CANOCO Reference Manual and User's Guide: Software for Ordination (version 5.0). Wageningen UR, The Netherlands.