



# Multi-scale analysis of environmental constraints on macrophyte distribution, floristic groups and plant diversity in the Lower Paraná River floodplain



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## ABSTRACT

The Paraná River floodplain comprises one of the largest wetland systems of South America. In a sector of the Lower Paraná River floodplain (100 km length, 3650 km<sup>2</sup>), floristic composition and species diversity was characterized in 88 sites surveyed during summers 2010–11 and 2011–12. Hierarchical and fuzzy classifications were used to construct 26 floristic groups and 8 associations of floristic groups, and their indicator species were identified. A number of 124 species was distributed with a zonation pattern conforming marshes, salt marshes, wet prairies, bunchgrasses, grasslands and scrublands. We assessed how vegetation is affected by four nested levels of environmental constraints, representing a gradient from a landscape to a local scale, and including hydrological, geomorphological, topographic and edaphic variables. Species richness differed within categories of broad-scale landscape units (level 1) and within topographic positions (level 3). Also, 30 plant species, six floristic groups and five associations of groups responded to levels 1–3. The first two axes of a constrained Outlying Mean Index ordination accounted for 60% of the marginality of 61 common species as a function of soil features and flood frequency (level 4). Thus, the distribution of seven species showed significant marginality in association to soil electrical conductivity, soil silt percent and soil total nitrogen concentration. Multi-scale environmental constraints determined vegetation zones, and emerging floristic and diversity patterns. The multi-scale approach significantly improves the understanding of floristic patterns and plant biodiversity in the study area, and may be extended to other floodplain wetlands.

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## 1. Introduction

The hydrological regime is the main control of plant community development in wetlands. This is particularly true with regard to floodplain wetlands, where plant distribution has been tied to different components of the flood pulse (*sensu* Junk *et al.*, 1989). In South America, the largest wetlands are associated with the floodplains of the Amazonas, Orinoco and Paraná–Paraguay rivers (Junk *et al.*, 2013). From its source in Brazil to its mouth in the Del Plata estuary, the Paraguay–Paraná River floodplain is covered with

mosaics of wetlands with heterogeneous fluvial landforms and flood pulse dynamics. Along the Paraná River (3900 km long), biodiversity changes due to its flux from tropical-subtropical latitudes to temperate ones are expected (Oakley *et al.*, 2005). However, no clear longitudinal pattern was found for aquatic and wetland herbaceous species richness in landscapes located along the Paraná River course and its floodplain (Neiff *et al.*, 2014). A possible explanation for that result can be found in the influence of multi-scale environmental filters (LeRoy Poff, 1997), which may contribute to large scale species patterns.

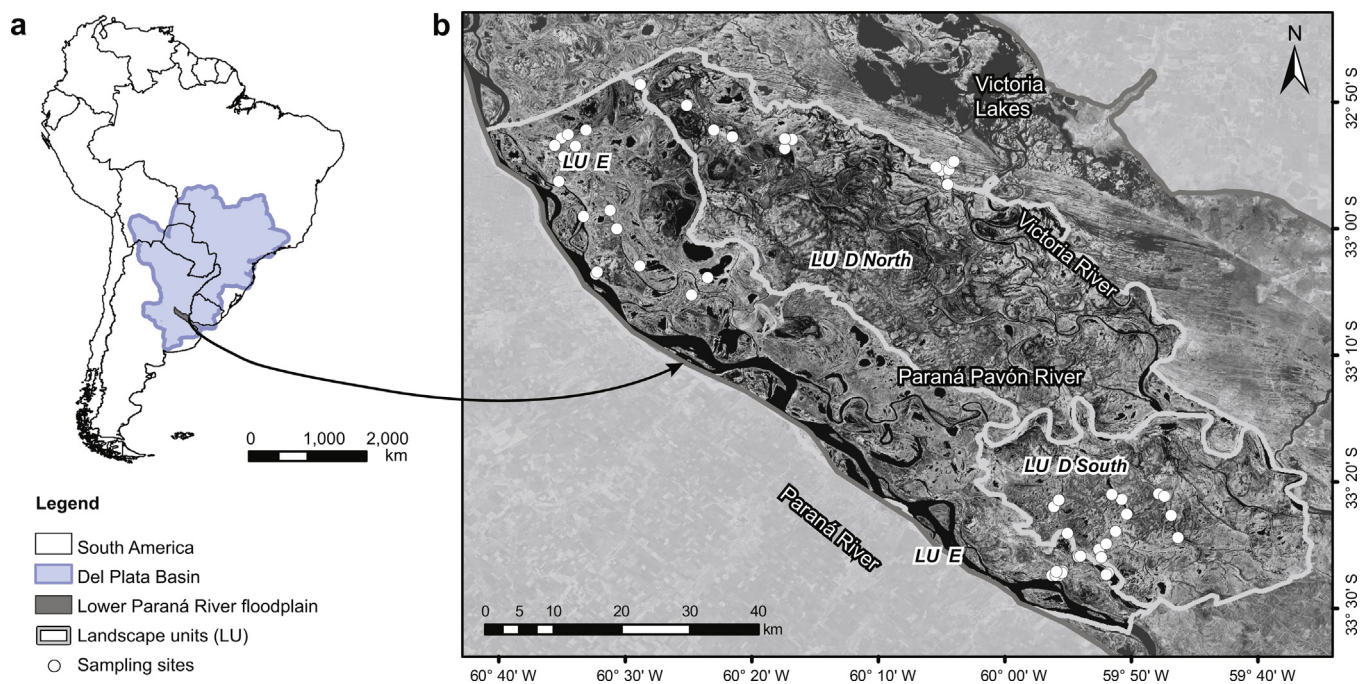
We aimed to analyze multi-scale effects of environment on plant diversity and plant composition in wetlands of the Lower Paraná River floodplain (“section C” in the work by Neiff *et al.* (2014)). In a low water period, we described plant diversity patterns and identified floristic groups. Next, we assessed how vegetation is related to four nested levels of environmental constraints, representing a gradient from a landscape scale to a local scale. Hydrological, geomorphological, topographic and edaphic features were included in

*Abbreviations:* EC, electrical conductivity; IV, indicator value; LU, landscape units; N, nitrogen; NC, noise clustering; Nclass, noise class; OMI, outlying mean index; P, phosphorus; PC, principal component; PCA, principal component analysis.

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**Fig. 1.** Study area. (a) Location of the Lower Paraná River floodplain in South America. (b) Distribution of the sampling sites where vegetation was recorded and soil samples were collected. Landscape units (level 1) are also indicated: D north, D south and E. The background image corresponds to the near infrared band (shown in gray scale) of a Landsat 8 OLI scene (band 5; path-row 226–83; date: 2011/03/21).

the analyses. Plant diversity, floristic groups and dominant species distribution were expected to be related to these levels (prediction 1). The intersection of these four environmental levels was expected to generate mosaics in which zones of vegetation with well-defined limits and few species occur (zonation pattern, prediction 2). Although reciprocal interactions between vegetation and hydrogeomorphic processes usually exist (Corenblit et al., 2007), this work is focused on how hydrology, landforms and soil features affect wetland plant communities.

## 2. Materials and methods

### 2.1. Study area

The study was conducted at a section of ca. 100 km length in the Lower Paraná River Floodplain (sensu Iriondo and Drago, 1972) where freshwater wetlands cover 3650 km<sup>2</sup> (excluding permanent water bodies) (Fig. 1). This section is also known as the Middle Paraná River Delta, and includes the Rosario–Victoria cross-section that Neiff et al. (2014) used to characterize vegetation patterns in their Section C. The climate is temperate humid, with a mean annual temperature of 17.1 °C, July being the coldest month (mean temperature 10 °C) and January the hottest one (mean temperature 24 °C). The mean annual precipitation is 1052 mm, monthly ranging from 132 mm in March to 39 mm in August (1965–2011; Instituto Nacional de Tecnología Agropecuaria (INTA) San Pedro Agrometeorological Station, 33°44'S 59°41'W).

The floodplain under study is a complex littoral area that developed mainly in the last 6000 years, and it comprises river deposits that belong to ancient and present fluvial periods, marine ingression and regression deposits and ancient deltaic deposits (Iriondo, 2004; Ramonell et al., 2012). Nowadays, the area is subject neither to tidal ingressions nor to deltaic deposits, but to the flood pulse of the Paraná River. Herbaceous communities dominate the marshes, whereas forest patches cover ca. 1.5% of the study area (Enrique, 2009). The soils are young and sedimentary, humic gley or subhumic gley (Bonfils, 1962).

### 2.2. Levels of environmental constraints

Four levels of environmental constraints, ordered from a landscape to a local scale were defined:

**Level 1.** Corresponds to three units in which the area was subdivided (hereafter, landscape units, LUs) following Malvárez (1997) and Zóffoli et al. (2008): units D north, D south and E. This level reflects broad features of the hydrological regime, such as connectivity with the main channel of the Paraná River, water drainage and water permanence (see Table 1 for details).

**Level 2.** Comprises landforms with fluvial or fluvial-marine geomorphological origin, which are nested in the first level. Detailed cartography and characterization of the geomorphological settings have been developed by Ramonell et al. (2012), who described units with marine-fluvial history (ancient deltaic deposits, then modified by the action of the Paraná River) and units with fluvial history (fluvial patterns generated by the action of the Paraná River and subsidiaries). Differences in substrate and resources may occur between landforms (Corenblit et al., 2007), as well as water flow variations due to the spatial arrangement of the elements that define each landform (Ramonell et al., 2012).

**Level 3.** Includes relatively high and low topographic positions within each geomorphological setting, with a mean difference in relative height of 65 cm as measured in 17 transects by the authors. These topographic discontinuities may affect water permanence, water column height and sediment dynamics, among other factors (Malvárez, 1997; Steiger and Gurnell, 2002).

**Level 4.** Corresponds to a set of soil variables measured in sampling sites (see Section 2.3), along with information on local flooding frequency published for the area (Borro et al., 2014).

### 2.3. Sampling

Sampling sites were selected with the objectives of representing the four levels, but site selection was limited by accessibility by motorboat or canoe and on foot (Fig. 1, Table 1). Each sampling site was representative of a homogeneous area (with similar vegetation

**Table 1**  
Features of the 88 sampling sites in the Lower Paraná River floodplain. Vegetation censuses were carried out in all the sites and environmental variables of level 4 were recorded in most of them ( $n=84$ ). The sites are described according to their landscape unit (level 1), hydrological regime, geomorphological settings (level 2) and topographical position (level 3).

Level 1. Landscape unit	No. sites	Hydrological regime <sup>a</sup>	Level 2. Geomorphological settings <sup>b</sup>		No. sites <sup>c</sup>	Level 3. Topographic positions	No. sites <sup>d</sup>	
D north	16	Seasonal floods from the Paraná River. Low connectivity with the main channel of the the Paraná River. Flood water enters the floodplain indirectly and slowly drains away. High water permanence	Fluvial	Scroll bars and in-channel levees	11	Low	9	
			Marine-fluvial	Delta lobes (post Holocene transgression)	5	High	2	
D south	31	Seasonal floods from the Paraná River. Low connectivity with the main channel of the the Paraná River, high connectivity with the Paraná Pavón River. Flood water enters the floodplain indirectly from the Paraná River and directly from the Paraná Pavón River, and drains away slowly. Intermediate water permanence	Fluvial	In-channel levees	8	Low	4	
			Marine-fluvial	Delta lobes (post Holocene transgression)	23	High	4	
						Low	12	
E	41	Seasonal floods from the Paraná River. High connectivity with the main channel of the the Paraná River. Flood water enters the floodplain directly and drains away quickly. Low water permanence	Fluvial	Islands of the Paraná main channel	5	Low	4	
				Levees and crevasse sprays of the Paraná main channel		2	High	1
				In-channel levees		15	Low	11
				Scroll bars and in-channel levees		11	High	4
							Low	4
			Marine-Fluvial	Degraded delta lobes (post Holocene transgression)	8	High	7	
						Low	5	
			High	3				

<sup>a</sup> Zoffoli et al. (2008).

<sup>b</sup> Ramonell et al. (2012).

<sup>c</sup> Total number of sites in fluvial settings: 52; in marine-fluvial settings: 36.

<sup>d</sup> Total number of sites in low positions: 52; in high positions: 36.

structure and dominant species) of at least 1000 m<sup>2</sup>. Vegetation and soil sampling was performed in several field-work trips during summers 2010–2011 and 2011–2012. Most sites were sampled once. Those that were revisited had the same vegetation composition as the previous summer, with little changes in species relative abundance-cover. Priority was given to covering different types of wetlands, physiognomies and environments. We only characterized sites dominated by emergent rooted macrophytes, i.e., forest patches and shallow lakes with floating vegetation were excluded.

In 88 sampling sites, three vegetation censuses were carried out in 1 m<sup>2</sup> plots each, and the Braun–Blanquet scale was used to estimate the cover-abundance of the species (Mueller-Dombois and Ellenberg, 1974). Species determination was based on the floristic bibliography of the area (Burkart and Bacigalupo, 2005; Burkart, 1987, 1979, 1974, 1969). Species nomenclature was assigned according to Zuloaga et al. (2009) and plants without reproductive structures were determined to genus level.

To characterize level 4, “flooding frequency”, a continuous variable related to floodability and flooding stress, was extracted from the “flood frequency layer” produced by Borro et al. (2014) (resolution = 30 m) and was assigned to the sampling sites by means of a geographic information system. Also, soil samples were collected in 84 out of the 88 sampling sites where vegetation was sampled. In the four remaining sampling sites, the water column was higher than 80 cm and so soil samples could not be collected. We gathered the samples with a helical manual soil auger (AMS Eijkelkamp Edelman Thread-On Augers), and identified whether one or two soil layers were present in the first 60 cm of each site. The boundary between the first soil layer (maximum depth ranging from 8 to 60 cm) and the second one (maximum depth ranging from 28 to 60 cm) was determined in situ according to structure, texture and color changes. To capture soil heterogeneity in a given site, a composite soil sample of each layer was mixed from three sub-samples.

Soil samples were dried at 60 °C for 72 h to a constant mass. Total nitrogen was quantified with a semi-micro Kjeldahl method (Bremner and Mulvaney, 1982) and extractable phosphorus with a Bray Kurtz I method (Bray and Kurtz, 1945). Soil pH was quantified with a potentiometric method, electrical conductivity with a conductimetric method, organic carbon by dry combustion using an automatic analyzer (LECO CR12) and texture (percent sand, silt and clay) with the pipette method by Robinson. All soil analyses were conducted at the Laboratorio Nacional de Investigación y Servicios N-15 (LANAIS N-15, Universidad Nacional del Sur Bahía Blanca, Argentina).

## 2.4. Data analyses

### 2.4.1. Plant diversity patterns

We estimated the cover of the species of each of the 88 sites as the center of the Braun–Blanquet class for classes 1–5, and as 0.01% and 0.10% for classes *r* and *+*, respectively. To calculate the mean species cover per site, species cover was averaged in the three censuses of each site. Gamma diversity (total richness in the 88 sites) was estimated as the total number of observed species and as Chao and 1st order Jackknife non-parametric indicators (Chao, 1987; Smith and Van Belle, 1984). Species accumulation curves were constructed for all the sites and for subsets corresponding to categories of sites defined in levels 1–3 (subsampling without reposition, 1000 permutations; Gotelli and Colwell, 2001).

Alpha diversity (Shannon (H) and Simpson (D) diversity indexes), site evenness ( $D/D_{\max}$ , where  $D_{\max}$  is the site species richness) (Magurran, 2004) and the number of dominant species (Hill, 1973) were estimated in each site. We analyzed whether these indexes differed between levels 1–3 (prediction 1) by means

of three-way permutation ANOVAs (999 permutations; Wheeler, 2010). Beta diversity between pairs of sites was estimated through Sørensen's dissimilarity index (Magurran, 2004) and differences between categories included in levels 1–3 were tested with a multivariate permutation ANOVA (999 permutations) on Sørensen dissimilarity (Anderson et al., 2006).

### 2.4.2. Floristic classification

We constructed a sites  $\times$  species matrix, and removed the species occurring in less than three sites and those that never accounted for more than 5% cover ( $n=86$  sites remained in the subsequent floristic classification analyses). Chord distances were used to compute dissimilarity between sites (Legendre and Gallagher, 2001). Next, two classification approaches were examined. On the one hand, we carried out a hierarchical cluster analysis. An average linkage method was selected with the cophenetic correlation criterion and the optimum number of clusters ( $k$ ) was defined by means of the maximum silhouette width criterion (Borcard et al., 2011). On the other hand, a non-hierarchical fuzzy noise clustering (NC) analysis was undertaken with 999 permutations, a membership value of 1.2, a minimum distance of 0.8 for a site to be assigned to the noise class (Nclass) and a “defuzzifying” level  $\alpha$  of 0.5 (De Cáceres et al., 2010a). In the NC analysis,  $k$  was defined as the minimum number of classes for which: (a) less than 20% of the sites were included in the Nclass, and (b) the number of sites in the Nclass for  $k$  classes was equal to or lower than the number of sites in the Nclass for  $k-1$  classes.

The resulting classifications were compared through a contingency table. If they differed more than 20%, differences were considered to have arisen from a gradient of plant communities (rather than from a zonation pattern, prediction 2) and the fuzzy NC classification was selected. Otherwise, the hierarchical classification was chosen, since it allows for class association at upper cut levels. To characterize each floristic group, the indicator values (hereafter, IV) of the species were computed (999 permutations to evaluate their statistical significance) (Dufrière and Legendre, 1997). IV ranges from 0 to 1: species with IV equal to 1 had maximum specificity and maximum fidelity to a group (De Cáceres and Legendre, 2009).

### 2.4.3. Relation between plant species and environment

To identify the species that were associated with environmental features of levels 1–3 (prediction 1), we evaluated the indicator value of the species (De Cáceres et al., 2010b). The way in which environmental variables included in level 4 affected the distribution and abundance of plant species (prediction 1) was assessed by the direct ordering analysis Outlying Mean Index (OMI) (Dolédec et al., 2000). OMI is explicitly based on the evaluation of the marginality of species assemblages, i.e., their degree of specialization. OMI does not assume a linear or unimodal response to the environment as Redundancy Analysis (RDA) and Canonical Correspondence Analysis (CCA) do and gives a more even weight to all sampling units, including those which are species poor or individual poor (Dolédec et al., 2000). Also, the marginality of each species can be tested by random permutations. In OMI analyses, the total inertia of a given species was decomposed into three variables: marginality, tolerance and residual tolerance (Dolédec et al., 2000). Marginality expresses the average distance of a given species to the uniform distribution, tolerance is linked to the breadth of environmental features in which the species occur, and residual tolerance is the ratio of the inertia left unexplained by the set of environmental features that are included.

The OMI analysis was undertaken with the sites where soil sampling could be conducted ( $n=84$ ) and with species occurring in three or more sites ( $n=82$  sites remained). Environmental variables were centered and standardized. To avoid redundancy and



collinearity between the environmental variables, we carried out a Principal Component Analysis (PCA) and included the four first Principal Components (PC) in the OMI analysis. To describe the association between the level 4 variables and the marginality axes of the OMI (hereafter OMI axes), we performed Pearson's correlation tests. Also, we evaluated whether the site scores differed between categories of levels 1–3 by means of three-way permutation ANOVAs (999 permutations) (prediction 1).

#### 2.4.4. Software used for data analyses

Data analyses were carried out with the open-source software R (R Core Team, 2013) and the following packages: *vegan* (Oksanen et al., 2013), *ImPerm* (Wheeler, 2010), *cluster* (Maechler et al., 2013), *gclus* (Hurley, 2012), *vegclust* (De Cáceres et al., 2010a), *indicspecies* (De Cáceres and Legendre, 2009) and *ade4* (Dray and Dufour, 2007).

### 3. Results

#### 3.1. Plant diversity patterns and floristic groups

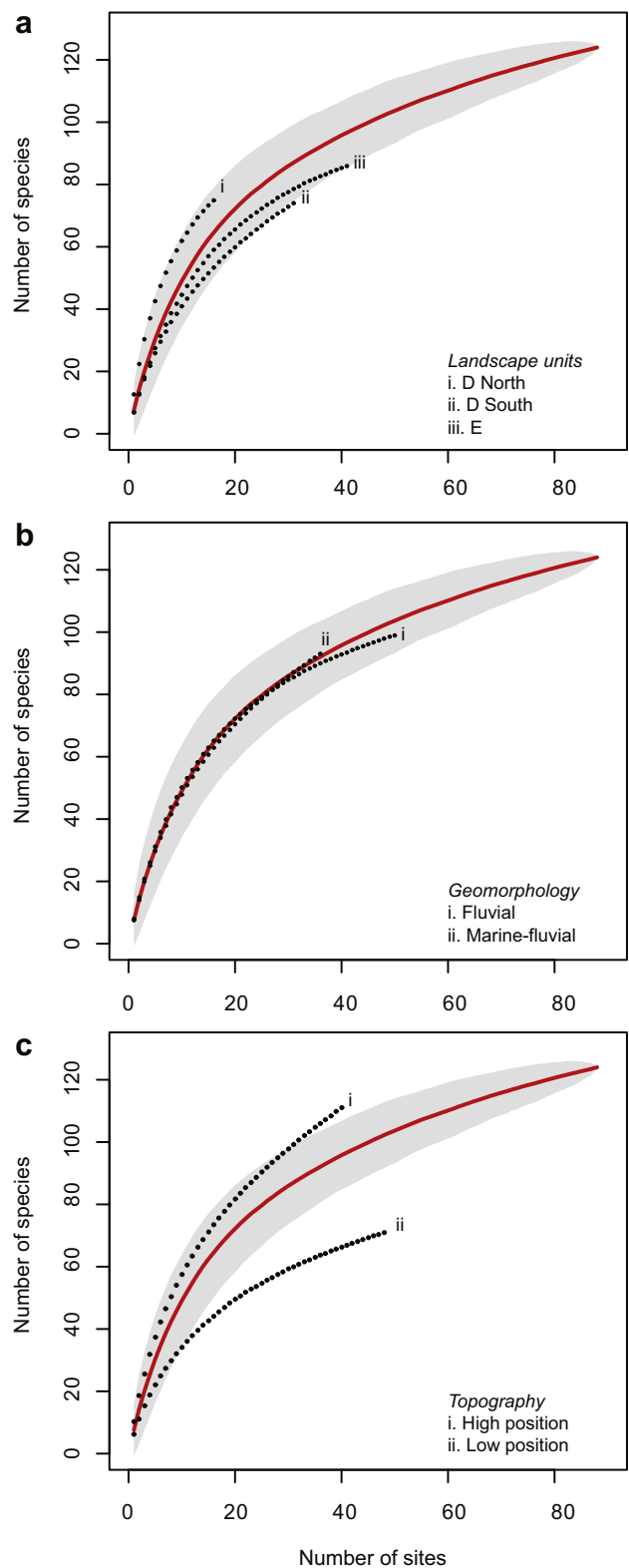
A total of 124 species was observed in the 88 sites (Table S1), with 87% native to the region species and 80% perennial species. The estimated gamma diversity for the study area was higher than the gamma diversity observed (180 and 162 species for the Chao estimator and 1st order Jackknife, respectively). Consistently, the accumulation curves did not reach an asymptote in any of three first levels (Fig. 2). Species diversity per site was low, mainly because both species richness and evenness were low (Table S2). Species richness was higher in LU D north than in D south and E ( $p=0.0083$  and  $0.0015$ , respectively), and was also higher in high topographic positions than in low positions ( $p=0.0060$ ); denoting influences of levels 1 and 3 on plant diversity patterns (Fig. 2, prediction 1). The beta diversity of pairs of sites within the same categories of levels 1–3 was similar to the beta diversity of pairs of sites located in different categories of those levels ( $p<0.01$ ).

After removing low constant species, a matrix of 86 sites  $\times$  63 species was retained. Both the hierarchical and the fuzzy NC classification approaches led to 26 floristic groups. Since the classifications were coincident in 87% (differing mainly in sites assigned to the Nclass in the NC classification), we chose the hierarchical clustering as the final one. The result is consistent with the expected zonation pattern of vegetation (prediction 2). The 26 floristic groups were grouped in 8 associations of floristic groups (Table 2), and 33 indicator species were identified (21 indicating associations of floristic groups and 28 indicating floristic groups, see Table 3). A selection of photographs of the main communities and dominant species is provided as supplementary material (Fig. S1). The association of floristic groups (coded from A to H) (Table 2) can be described as follows:

**A. Short salt marshes.** The short (<10 cm height) halophytic grass *Paspalum vaginatum* was found in almost monospecific communities (group 1).

**B. Tall salt marshes.** Halophytic graminoid herbs of medium height (50–100 cm) dominated. Included two groups, both sharing the presence of *Bolboschoenus robustus*. Besides, group 2 was indicated by the presence of *Echinochloa helodes* and group 3 was indicated by *Leptochloa fusca*. Accompanying halophytic species were *Sesuvium portulacastrum* and *Spergula platensis* var. *platensis*.

**C. Bulrush marshes.** The tall (100–200 cm) equisetoid herb *Schoenoplectus californicus* was typical of this association, and the broadleaf herb *Polygonum punctatum* was generally accompanying. Group 4 featured the highest constancy and cover of *Schoenoplectus californicus*, accompanied by *Polygonum punctatum*, *Cyperus virens* and *Solanum glaucophyllum*. In group 5, bulrush marshes were



**Fig. 2.** Species accumulation curves for levels 1–3. Solid lines show the accumulation curve for all the sampling sites ( $n=88$ ), grey areas display 95% confidence intervals, and dotted lines show accumulation curves for specific subsets of sites. (a) Level 1: landscape units D north ( $n=16$ ), D south ( $n=31$ ) and E ( $n=41$ ). (b) Level 2: fluvial ( $n=52$ ) and marine-fluvial ( $n=36$ ) geomorphological history. (c) Level 3: high ( $n=36$ ) and low ( $n=52$ ) topographic positions.

**Table 2**

Floristic table. The table was constructed with a hierarchical classification using an average linkage method on a 86 sites × 63 species matrix (species with less than 5% constancy were removed). Dissimilarities between sites were estimated with chord distances. For each species, its family and morphological type (MT) (H = broadleaf rooted herb, G = graminoid rooted herb, E = equisetoid rooted herb, F = floating herb, Su = submerged herb, Sh = shrub, V = vine herb) are indicated and it is stated whether it is an indicator species of a floristic group ( $k=26$ ) or of an association of floristic groups ( $k=8$ ) ( $k$  is the number of groups or cut level of the dendrogram). The associations of floristic groups are coded with capital letters (A–H) and the floristic groups are coded with letter G followed by the group number (G1–G26). Below each group name, the number of sampling sites in the floristic group is provided. If one or two asterisks (\* or \*\*) accompany the number of sampling sites per floristic group, one or two sampling sites (respectively), were assigned to the  $N$  class in the fuzzy NC classification. The constancies of the species in the floristic groups are expressed in five categories: I = 0–20% (very low constancy), II = 20.1–40% (low constancy), III = 40.1–60% (intermediate constancy), IV = 60.1–80% (moderately high constancy), V = 80.1–100% (high constancy).

Family	Species	MT	Indicator		A		B		C			D		E				F		G			H						
			$k=8$	$k=26$	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	G13	G14	G15	G16	G17	G18	G19	G20	G21	G22	G23	G24	G25
Poaceae	<i>Paspalum vaginatum</i> Sw.	G	A	G1	V																								
Poaceae	<i>Echinochloa helodes</i> (Hack.) Parodi	G		G2		V				III		I			II	V	III	V							III	I		II	
Cyperaceae	<i>Bolboschoenus robustus</i> (Pursh) Soják	G	B			III	IV																						
Poaceae	<i>Leptochloa fusca</i> (L.) Kunth	G	B	G3	II		IV																						
Aizoaceae	<i>Sesuvium portulacastrum</i> (L.) L.	H			II		IV														I								
Cyperaceae	<i>Eleocharis</i> aff. <i>bonariensis</i> Nees	E					II												III	II									
Caryophyllaceae	<i>Spergula platensis</i> var. <i>platensis</i> (Cambess.) Shinnars	H			II		II																I						
Cyperaceae	<i>Schoenoplectus californicus</i> (C.A. Mey.) Soják	E	C	G4		III	IV	V	IV	II																		II	
Solanaceae	<i>Solanum glaucophyllum</i> Desf.	Sh					II		II							III					III		II		III	II		II	
Polygonaceae	<i>Polygonum punctatum</i> Elliott	H	C				IV			III		I	V								III				III	II	V		
Cyperaceae	<i>Cyperus virens</i> Michx.	G					II															I				I		III	
Azollaceae	<i>Azolla filiculoides</i> Lam.	F		G5				V				I		III	III														
Ceratophyllaceae	<i>Ceratophyllum demersum</i> L.	Su						IV								II													
Polygonaceae	<i>Polygonum acuminatum</i> Kunth	H		G6					V			I					II								III	III			
Polygonaceae	<i>Polygonum stelligerum</i> Cham.	H							II															II					
Poaceae	<i>Phalaris aquatica</i> L.	G	D	G7						V							III												
Apiaceae	<i>Torilis nodosa</i> (L.) Gaertn.	H		G7						V							III					III	II					II	
Capparaceae	<i>Tarenaya hassleriana</i> (Chodat) H.H. Iltis	H								III							III						I		III	I			
Plantaginaceae	<i>Plantago</i> sp.	H		G7						V													II						
Poaceae	<i>Panicum elephantipes</i> Nees ex Trin.	G	D	G8		III				III	V	II				II													
Apiaceae	<i>Hydrocotyle ranunculoides</i> L. f.	H								II		I		II															
Onagraceae	<i>Ludwigia</i> cf. <i>peruviana</i> (L.) H. Hara	H	E	G9		III		III		IV	V	III	V	III	IV	III	IV	V	III				III	IV					
Haloragaceae	<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	H						II			III	III		II															
Salviniaceae	<i>Salvinia</i> cf. <i>biloba</i> Raddi	F								II		III		II															
Poaceae	<i>Echinochloa polystachya</i> var. <i>polystachya</i> (Kunth) Hitchc.	G										I									III						I		
Asteraceae	<i>Mikania micrantha</i> Kunth	V					II					I		II										II			II		
Asteraceae	<i>Enydra anagallis</i> Gardner	H		G10								II	V		II							I	II						
Poaceae	<i>Echinochloa polystachya</i> var. <i>spectabilis</i> (Kunth) Hitchc.	G		G11			II							V				V					II	III	III				
Cyperaceae	<i>Cyperus meyenianus</i> Kunth	G			II										II												I		
Pontederiaceae	<i>Eichhornia azurea</i> (Sw.) Kunth	H	E	G12								II		II	V						III			II					
Apiaceae	<i>Hydrocotyle bonariensis</i> Lam.	H													II														
Polygonaceae	<i>Polygonum</i> aff. <i>hydropiperoides</i> Michx var. <i>hydropiperoides</i>	H		G13						III		III				V	II				III		II	II		I		II	
Apiaceae	<i>Foeniculum vulgare</i> Mill.	H															III												
Asteraceae	<i>Eupatorium</i> sp.	H															III							I	II				
Poaceae	<i>Oplismenopsis najada</i> (Hack. & Arechav.) Parodi	H	E	G14						II	II				II			V	V	III		I							

Table 2 (Continued)

Family	Species	MT	Indicator		A			B			C			D		E				F		G			H					
			k=8	k=26	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	G13	G14	G15	G16	G17	G18	G19	G20	G21	G22	G23	G24	G25	G26
Amaranthaceae	<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	H							III				III					III		III	I		II			III	II		IV	
Asteraceae	<i>Eclipta prostrata</i> (L.) L.	H			G15															V			I							
Asteraceae	<i>Bidens laevis</i> (L.) Britton, Stern & Poggenb.	H					III		II				I		II					V			I							
Cyperaceae	<i>Cyperus giganteus</i> Vahl	E													II					III										
Poaceae	<i>Leersia hexandra</i> Sw.	G			G16								I							V								I	II	III
Poaceae	<i>Cynodon dactylon</i> (L.) Pers.	G	F		G17																V	III	II						III	
Poaceae	<i>Poa pilcomayensis</i> Hack.	G	F								III										I	III					I			
Poaceae	<i>Coleataenia prionitis</i> (Nees) Soreng	G	F		G18																I	V								
Fabaceae	<i>Mimosa tweedieana</i> Barneby ex Glazier & Mackinder	Sh	F																		I	V					II	V		III
Cyperaceae	<i>Eleocharis</i> aff. <i>viridans</i> Kük. ex Osten	E					III	IV													I	III	III			III		V		
Rubiaceae	<i>Borreria dasycephala</i> (Cham. & Schltld.) Bacigalupo & E.L. Cabral	H											III								I	III	I			III				
Asteraceae	<i>Acmella decumbens</i> (Sm.) R.K. Jansen	H																				III	I						II	
Poaceae	<i>Echinochloa crus-galli</i> (L.) P. Beauv.	G	G		G19																		V	IV		III		V		
Alismataceae	<i>Sagittaria montevidensis</i> Cham. & Schltld.	H			G20		III																	V						
Fabaceae	<i>Vigna luteola</i> (Jacq.) Benth.	H																					I	II		I	V			
Polygonaceae	<i>Polygonum lapathifolium</i> L.	H	G		G21				II														II		V	III	I		II	
Commelinaceae	<i>Commelina diffusa</i> Burm. f.	H											I										II		III	III	I			
Asteraceae	<i>Aspilia silphioides</i> (Hook. & Arn.) Benth. & Hook. f.	H													III								I		III	III	II			
Poaceae	<i>Setaria parviflora</i> (Poir.) Kerguelen	G			G22								I								III		II		III	V	I	V	II	
Convolvulaceae	<i>Aniseia argentina</i> (N.E. Br.) O'Donell	V													III											III	I			
Poaceae	<i>Hymenachne pernambucense</i> (Spreng.) Zuloaga	G	H		G23								I													III	III	V		
Poaceae	<i>Setaria geminata</i> (Forssk.) Veldkamp	G																					III	I		III	II		II	
Asteraceae	<i>Plagiocheilus tanacetoides</i> Haenke ex DC.	H																								III	II			
Asteraceae	<i>Pluchea sagittalis</i> (Lam.) Cabrera	H																											III	
Poaceae	<i>Hemarthria altissima</i> (Poir.) Stapf & C.E. Hubb.	G	H		G24																					III	I	V		
Asteraceae	<i>Baccharis salicifolia</i> (Ruiz & Pav.) Pers.	H	H		G25																		I				II	V	V	
Solanaceae	<i>Solanum nigrescens</i> M. Martens & Galeotti	H	H												III											III	II		III	III
Asteraceae	<i>Conyza bonariensis</i> (L.) Cronquist	H	H		G26																								II	V

**Table 3**  
Indicator species for each floristic group (A–H) or association of floristic groups (G1–G26). The indicator values (IV) are indicated, along with their *p*-value (999 permutations).

Species	Indicator values					
	<i>k</i> = 8	IV	<i>p</i> -value	<i>k</i> = 26	IV	<i>p</i> -value
<i>Paspalum vaginatum</i>	A	1.00	0.001	G1	1.00	0.001
<i>Bolboschoenus robustus</i>	B	0.78	0.001	–	–	–
<i>Echinochloa helodes</i>	–	–	–	G2	0.89	0.007
<i>Leptochloa fusca</i>	B	0.73	0.001	G3	0.97	0.001
<i>Schoenoplectus californicus</i>	C	0.80	0.003	G4	0.74	0.011
<i>Azolla filiculoides</i>	–	–	–	G5	0.87	0.001
<i>Polygonum acuminatum</i>	–	–	–	G6	0.92	0.001
<i>Polygonum punctatum</i>	D	0.66	0.036	–	–	–
<i>Phalaris aquatica</i>	D	0.58	0.025	G7	1.00	0.002
<i>Torilis nodosa</i>	–	–	–	G7	0.92	0.033
<i>Plantago</i> sp.	–	–	–	G7	0.93	0.010
<i>Panicum elephantipes</i>	D	0.91	0.001	G8	0.95	0.001
<i>Ludwigia</i> cf. <i>peruviana</i>	E	0.77	0.001	G9	0.63	0.001
<i>Enydra anagallis</i>	–	–	–	G10	0.95	0.001
<i>Echinochloa polystachya</i> var. <i>spectabilis</i>	–	–	–	G11	0.96	0.001
<i>Eichhornia azurea</i>	–	0.61	0.037	G12	0.98	0.001
<i>Polygonum</i> aff. <i>hydropiperoides</i> var. <i>hydropiperoides</i>	–	–	–	G13	0.90	0.010
<i>Oplismenopsis najada</i>	E	0.62	0.031	G14	0.85	0.001
<i>Eclipta prostrata</i>	–	–	–	G15	1.00	0.013
<i>Leersia hexandra</i>	–	–	–	G16	0.89	0.029
<i>Cynodon dactylon</i>	F	0.98	0.001	G17	0.97	0.001
<i>Coleataenia prionitis</i>	F	0.66	0.002	G18	0.98	0.004
<i>Poa pilcomayensis</i>	F	0.53	0.040	–	–	–
<i>Mimosa tweediana</i>	F	0.67	0.007	–	–	–
<i>Echinochloa crus-galli</i>	G	0.85	0.001	G19	0.85	0.001
<i>Sagittaria montevidensis</i>	–	–	–	G20	0.61	0.023
<i>Polygonum lapathifolium</i>	G	0.61	0.023	G21	0.87	0.009
<i>Setaria parviflora</i>	H	–	–	G22	0.82	0.021
<i>Hymenachne pernambucense</i>	H	0.68	0.005	G23	0.92	0.001
<i>Hemarthria altissima</i>	H	0.58	0.032	G24	0.95	0.026
<i>Baccharis salicifolia</i>	H	0.67	0.010	G25	0.87	0.010
<i>Conyza bonariensis</i>	H	0.52	0.038	G26	0.97	0.005
<i>Solanum nigrescens</i>	H	0.61	0.039	–	–	–

flooded with a high water column (>80 cm) and *Schoenoplectus californicus* was accompanied by floating and submerged species. Group 6 had the lowest constancy of *Schoenoplectus californicus* and was dominated by the broadleaf herb *Polygonum punctatum*.

**D. Grass marshes.** Grasses of medium height, typically *Panicum elephantipes*, were dominant. Group 7 was dominated by the grass *Phalaris aquatica* and accompanied by *Ludwigia* cf. *peruviana*, *Torilis nodosa* and *Panicum elephantipes*. Group 8 exhibited more abundance and dominance of *Panicum elephantipes* than group 7 did.

**E. Broadleaf marshes.** The presence and cover of the broadleaf herb *Ludwigia* cf. *peruviana* was the shared feature of the eight floristic groups included in this association. Group 9 had the highest constancy and cover of *Ludwigia* cf. *peruviana*, accompanied by several floating or emergent herbs. Group 10–16 differed in their co-dominant species, being grasses in groups 11 and 16 (*Echinochloa polystachya* var. *spectabilis* and *Leersia hexandra*, respectively), and broadleaf herbs in the remaining groups (*Enydra anagallis*, *Eichhornia azurea*, *Polygonum* aff. *hydropiperoides* var. *hydropiperoides*, *Oplismenopsis najada* (a grass with leaves similar to those of broadleaf herbs) and *Eclipta prostrata*).

**F. Bunchgrasses and grasslands.** Grasses were found to be dominant in this association. Group 17 was dominated by short grasses (<10 cm) of the species *Cynodon dactylon*. In group 18, bunchgrasses of *Coleataenia prionitis* were dominant in a tall stratum, whereas *Cynodon dactylon*, *Poa pilcomayensis* and *Mimosa tweediana*, among other species, occurred in the low stratum.

**G. Mixed wet prairies of grasses and broadleaf herbs.** The presence of the grass *Echinochloa crus-galli* or of the broadleaf herb *Polygonum lapathifolium* was the shared feature of the three floristic groups included in this association. *Echinochloa crus-galli* was dominant in group 19 and was an accompanying species in group 20 (dominated by the broadleaf herb *Sagittaria montevidensis*).

*Polygonum lapathifolium* was dominant in group 21 and was an accompanying species in group 19. Broadleaf species such as *Aspilia silphoides*, *Setaria parviflora* and *Ludwigia* cf. *peruviana* also occurred in these groups.

**H. Mixed grasslands and scrublands.** Groups included in this association showed some variability. Grasses were dominant in groups 22 and 23 (*Setaria parviflora* and *Hymenachne pernambucense*, respectively). Groups 25 and 26 were dominated by tall (>2 m) broadleaf herbs similar to shrubs but with non-lignified stems (*Baccharis salicifolia* and *Conyza bonariensis*). Group 24 was dominated both by grasses (*Hemarthria altissima*, *Setaria parviflora*) and by tall broadleaf herbs (*Baccharis salicifolia*). The broadleaf herb *Solanum nigrescens* occurred in most of the groups of this association.

### 3.2. Relation between plant species and environment

On average, sites had clay loam soils, soil nitrogen (N) concentration was high, soil P concentration was low, pH was moderately acid and electrical conductivity (EC) indicated soils were slightly saline (Table 4). For all the soil variables, except for extractable phosphorus (P), values in the first soil layer were positively and linearly correlated with values in the second soil layer. On the first PC (28% of the total variance), frequently flooded sites, with high percent silt and high EC were ordered along positive values; whereas clay soils with high N and high OC were ordered along negative values. On the second PC (18% of the total variance), sandy soils were ordered along negative values. On the third PC (14% of the total variance), sites with high OC, N and P (and also with high CE) were ordered along negative values. On the fourth PC (11% of the total variance), clay soils were ordered along positive values and silty soils were ordered along negative values. Summarizing, the



**Table 4**

Summary of the environmental features of level 4 ( $n = 84$  sampling sites). For the soil variables, the soil layer is indicated. Pearson's coefficients are shown in each pair of Principal Component (PC) and environmental variable (bold letter for  $r > |0.4|$  and  $p < 0.0001$ ). Based on soil reference values (Moore, 2001; Sainz Rosas et al., 2012), mean total nitrogen was high, mean extractable phosphorus was low, mean pH was moderately acidic and mean EC denoted slightly saline sites.

Level 4 environmental variables	Soil layer	Pearson correlation with Principal Components				Mean	SD	Minimum	Maximum
		PC 1	PC 2	PC 3	PC 4				
Total nitrogen (%)	1	<b>-0.74</b>	-0.08	<b>-0.44</b>	0.09	0.36	0.25	0.02	1.34
	2	<b>-0.63</b>	0.03	<b>-0.57</b>	-0.18	0.19	0.16	0.02	1.03
Extractable phosphorus (%)	1	0.38	-0.30	<b>-0.61</b>	0.08	$3.90 \times 10^{-04}$	$5.33 \times 10^{-04}$	$5.00 \times 10^{-05}$	$4.18 \times 10^{-03}$
	2	0.40	-0.11	<b>-0.50</b>	0.21	$4.48 \times 10^{-04}$	$5.47 \times 10^{-04}$	$4.00 \times 10^{-05}$	$3.29 \times 10^{-03}$
Organic carbon (%)	1	<b>-0.76</b>	-0.18	<b>-0.43</b>	0.15	6.57	5.48	0.26	27.39
	2	<b>-0.72</b>	-0.09	<b>-0.51</b>	-0.14	2.86	2.18	0.16	10.87
pH	1	0.33	<b>0.49</b>	0.15	0.32	4.61	0.51	3.80	7.70
	2	<b>0.53</b>	0.10	0.06	<b>0.63</b>	4.95	0.74	3.90	7.60
EC (dS.m-1)	1	<b>0.45</b>	-0.25	<b>-0.47</b>	<b>0.43</b>	3.88	4.75	0.49	22.10
	2	<b>0.55</b>	-0.30	<b>-0.41</b>	0.35	3.72	4.72	0.41	20.10
Percent clay	1	<b>-0.56</b>	<b>0.45</b>	0.13	<b>0.56</b>	28.35	10.15	4.10	51.30
	2	<b>-0.58</b>	<b>0.46</b>	0.04	<b>0.53</b>	30.77	10.19	3.41	53.70
Percent silt	1	<b>0.50</b>	<b>0.54</b>	-0.33	<b>-0.48</b>	47.06	11.94	23.00	73.94
	2	<b>0.56</b>	<b>0.50</b>	-0.36	-0.38	47.06	12.03	17.60	74.10
Percent sand	1	-0.03	<b>-0.90</b>	0.22	0.01	24.59	12.09	6.70	52.06
	2	-0.06	<b>-0.86</b>	0.31	-0.07	22.17	12.24	6.03	66.03
Flood frequency	-	<b>0.58</b>	-0.22	-0.17	0.16	0.20	0.19	0.00	0.95

first PC was mostly related to salinity and flooding frequency, the second and fourth PCs to soil texture, and the third PC to soil nutrients (Table 4). The OMI analysis was performed with these four PCs on an 84 sites  $\times$  61 species matrix.

The first two OMI axes accounted for 34% and 26% of the total variance, respectively. Principal Components 1, 3 and 4 were the most influential in the OMI sites and species ordination (Fig. 3a). On the first OMI axis, frequently flooded sites, with high EC, high percent silt and high P were ordered along positive values; whereas clay soils were ordered along negative values ( $p < 0.0001$ ). Along the second OMI axis, sites were ordered mainly due to their soil texture, from clay soils to silty soils ( $p < 0.0001$ ).

The average marginality of the 61 plant species included in these analyses was significant (Table 5), denoting a strong association between the composition of the plant assemblage and the environmental variables included, thereby justifying species plotting on an ordination diagram (Fig. 3b). Seven out of the 61 species were associated with a particular range of environmental variables in the scale defined by level 4 (Table 5). The distribution of the species *Paspalum vaginatum*, *Sesuvium portolacastrum*, *Leptochloa fusca* and *Bolboschoenus robustus* was associated with saline soils (high EC) with relatively high P concentration, which took place in frequently flooded sites (Fig. 4). Those species were included in groups 1 and 3 of the Short salt marshes and tall salt marshes associations. The species *L. fusca* and *B. robustus* were associated to fine texture soils and relatively high N and OC, whereas *P. vaginatum* and *S. portolacastrum* show more tolerance in relation to soil texture. The species *Sagittaria montevidensis* (indicating the broadleaf marshes of floristic group 20) was associated with non-saline soils, with relatively high N and OC (Fig. 4). Both *Vigna luteola* and *Solanum nigrescens* were found in non-saline soils. *Solanum nigrescens*, indicating the Mixed grasslands and scrublands association, occurred in soils with low clay content and relatively high sand content.

The first and the second levels affected the ordination of both environmental features and plant species ( $p < 0.01$ ) (Fig. 3a). On the first OMI axis, sites located in LU D south were ordered along higher values than sites located in LU D north or E were, thus presenting sites with comparatively high electrical conductivity and flood frequency. On the second OMI axis, sites located in LU D south were ordered along lower values than sites located in LU

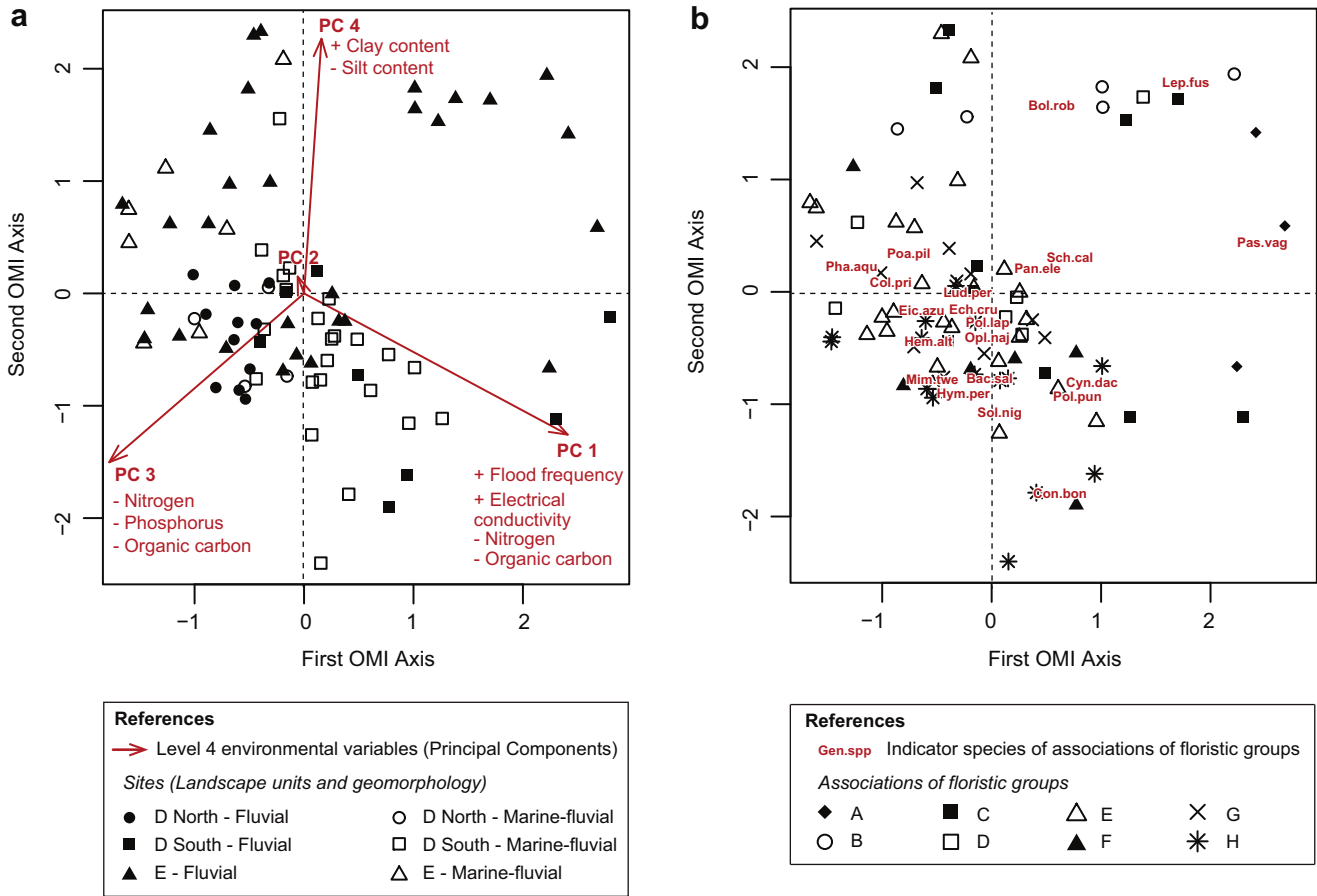
D north or E were, thus presenting siltier soils. Regarding geomorphology, sites with fluvial history were ordered all along the first OMI axis, whereas sites with marine-fluvial history were ordered along a more restricted portion of the first OMI axis and their mean score values were slightly lower than for sites with fluvial history (Fig. 3a).

Most of the floristic groups highly overlapped along the OMI axes, especially in non-saline soils with intermediate nutrient concentrations (Fig. 3b). However, several floristic groups were associated to particular categories of levels 1–3 ( $p < 0.05$ ) (Table 6). In particular, associations of groups C and E are typical in low topographic positions, whereas associations D, F and H are typical in high topographic positions. Except for *Solanum nigrescens*, none out of the 30 species that indicated levels 1–3 (Table 6) showed also significant marginality in the OMI axes representing variations in level 4 (Table 5).

#### 4. Discussion

This is the first detailed floristic characterization for the studied section of the Lower Paraná River floodplain. The wetlands were dominated by native perennial species. This life form goes hand in hand with maintaining reproductive structures between seasons and flood events, and seems well suited for the irregular flood pulse of the Paraná River (Carignan and Neiff, 1992). The most abundant and constant plant families are also abundant upstream in the Middle Paraná River floodplain (Asteraceae, Poaceae, Fabaceae and Solanaceae) (Marchetti and Aceñolaza, 2012) or downstream in the Lower Paraná River Delta (Asteraceae, Cyperaceae, Fabaceae, Polygonaceae and Apiaceae) (Kandus et al., 2003).

In line with prediction 2, vegetation was distributed with a zonation pattern. Several types of communities differing in their physiognomy and indicator species were distributed in zones of vegetation: marshes, salt marshes, wet prairies, bunchgrasses, grasslands and scrublands. These communities had well-defined limits and relatively few species. Their spatial pattern corresponded to mosaics of environmental conditions, accounting for variations in floodability and soil features. The bulrush marshes of *Schoenoplectus californicus* are absent in the Middle Paraná River floodplains (Marchetti and Aceñolaza, 2012) but are typical of the Paraná River



**Fig. 3.** Ordination plots of the Outlying Mean Index (OMI) analysis on the first and second OMI axes. (a) Biplot of sites (symbols,  $n=82$ ) and principal components (PC) derived from environmental variables (arrows). For the sites, the symbols (circles, squares or triangles) represent the landscape unit (level 1) and the colors (black filled or non-filled) represent the geomorphological history (level 2). Principal components 1, 3 and 4 are labeled according to the level 4 environmental variables they are more related to (see the text and Table 4 for details). (b) Biplot of sites (symbols,  $n=82$ ) and species. For the sites, the symbols stand for the association of floristic groups to which they were assigned. Only species that indicated associations of floristic groups are shown (see Table 2), coded as follows. Bac. sal (*Baccharis salicifolia*), Con. bon (*Conyza bonariensis*), Bol. rob (*Bolboschoenus robustus*), Sch. cal (*Schoenoplectus californicus*), Mim. twe (*Mimosa tweediana*), Lud. per (*Ludwigia cf. peruviana*), Col. pri (*Coleataenia prionitis*), Cyn. dac (*Cynodon dactylon*), Ech. cru (*Echinochloa crus-galli*), Hem. alt (*Hemarthria altissima*), Hym. per (*Hymenachne pernambucense*), Lep. fus (*Leptochloa fusca*), Opl. naj (*Oplismenopsis najada*), Pan. ele (*Panicum elephantipes*), Pas. vag (*Paspalum vaginatum*), Pha. aqu (*Phalaris aquatica*), Poa. pil (*Poa pilcomayensis*), Pol. lap (*Polygonum lapathifolium*), Pol. pun (*Polygonum punctatum*), Eic.azu (*Eichhornia azurea*), Sol. nig (*Solanum nigrescens*).

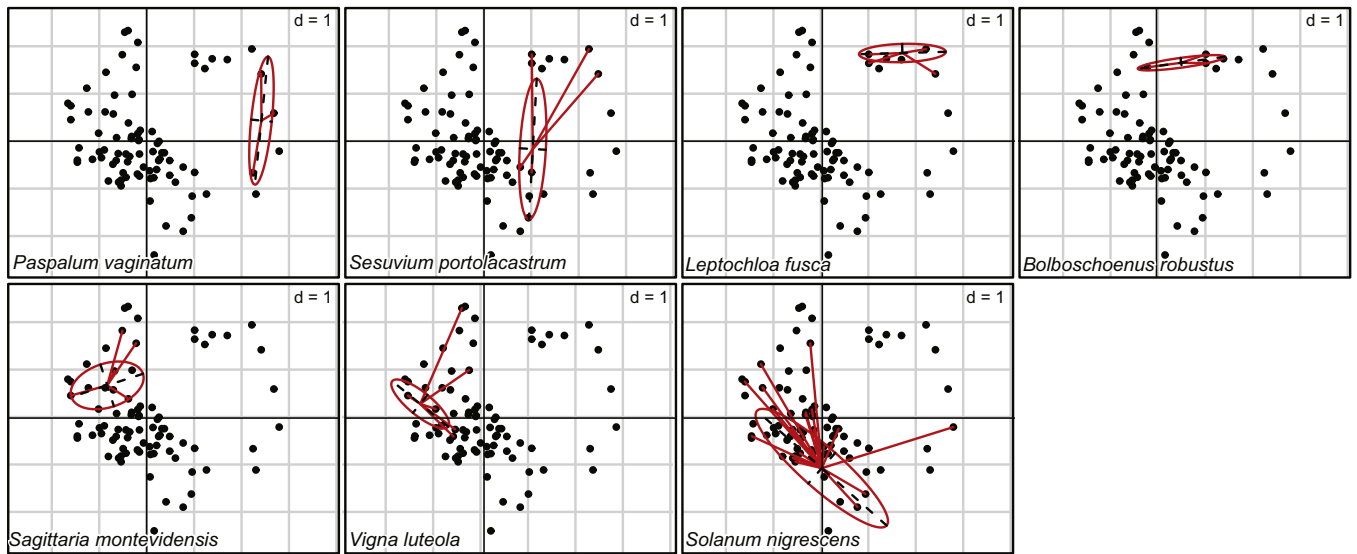
**Table 5** Species with significant marginality according to the OMI analysis. For each species, the total inertia is decomposed into three variables: marginality, tolerance and residual tolerance. The  $p$ -values express the significance of the marginality of each species and of the mean assemblage of species (Monte Carlo tests with 999 permutations).

Species	Inertia	Marginality (%)	$p$ -value	Tolerance (%)	Residual tolerance (%)
<i>Paspalum vaginatum</i>	10.0	69.3	0.0030	2.0	28.7
<i>Sesuvium portolacastrum</i>	12.0	85.3	0.0020	6.0	8.7
<i>Leptochloa fusca</i>	8.7	93.1	0.0030	1.8	5.0
<i>Bolboschoenus robustus</i>	6.5	60.1	0.0260	1.1	38.8
<i>Sagittaria montevidensis</i>	5.6	57.8	0.0340	4.5	37.7
<i>Vigna luteola</i>	6.7	86.2	0.0280	12.1	1.7
<i>Solanum nigrescens</i>	5.1	45.1	0.0160	16.6	38.3
Mean assemblage	4.1	56.4	0.0010	12.4	31.2

Delta downstream the Paraná River (Kandus et al., 2003). Conversely, the bunchgrasses and grasslands of *Coleataenia prionitis* with *Cynodon dactylon* are absent in the Paraná River Delta and are typical of the Middle Paraná River (Marchetti and Aceñolaza, 2012, 2011). Salt marshes of *Paspalum vaginatum* or *Bolboschoenus robustus* had not been described yet for the Middle or Lower sector of the Paraná River floodplain (Kandus et al., 2003; Marchetti and Aceñolaza, 2012).

Regarding plant diversity, per-site alpha diversity was relatively low, but gamma diversity was relatively high due to the high beta diversity (“diversity of habitats” hypothesis, sensu Shmida

and Wilson, 1985). The Shannon-Wiener diversity recorded in this area was always lower than that of the Middle Paraná River floodplain (Marchetti and Aceñolaza, 2012), even when compared to the diversity of islands in an early successional stage after an extraordinary flood (Franceschi and Lewis, 1991; Franceschi et al., 2010). Also, the gamma diversity was lower than upstream (Marchetti and Aceñolaza, 2012) but higher than downstream in the Lower Paraná River Delta (Kandus et al., 2003). This pattern can be attributed to a loss of biodiversity due to the transition from tropical and subtropical latitudes (Oakley et al., 2005). Our result suggests the existence of a downstream longitudinal diversity gradient in the Paraná River,



**Fig. 4.** Plots for the species with significant marginality according to the OMI analysis. Sites are represented as dots. Lines link the center of gravity of each species to each site where the species occurred.

which was not found by Neiff et al. (2014). We observed a higher species richness than in the work by Neiff et al. (2014) (124 vs. 43 species), probably due to sampling effort (88 intensive censuses distributed over the area in this work vs. 22 censuses distributed in a cross-section of the floodplain in Neiff et al., 2014).

Our results are consistent with prediction 1 and indicate that the environmental filters may act at different scales (LeRoy Poff, 1997). Broad-scale hydrogeomorphic features included in level 1 and topographic positions of level 3 seem to be the most important constraining factors of plant diversity, floristic composition and plant species occurrence. The higher species richness in LU D north may be caused by high inputs of propagules with Paraná River floods and a favorable environment for plant establishment and growth (e.g., absence of saline soils). Vegetation differences have already been described for LUs, but based on a few censuses and in qualitative terms (Malvárez, 1997).

Regarding level 2, the reason for its restricted effect on vegetation may be ascribed to the fact that level 1 already summarizes

several of the differences between geomorphological settings. Also, an interplay exists between variables included in level 4 and categories of level 1. Level 3 effects on species richness were important, denoting less restrictive conditions in high than in low topographic positions. The strong influence of topographic positions on both plant community composition and diversity patterns is typical in floodplains (e.g., Franceschi and Prado, 1989; Lenssen et al., 1999; Steiger and Gurnell, 2002).

In relation to level 4, the presence of saline soils was a strong restriction to plant community development and conditioned the presence of salt marshes. Since salinity was found in sites with fluvial history, genetic soil processes are negligible. Instead, salinity may be related to high evapotranspiration rates in high topographic positions with low plant coverage and bare soils (Kirk, 2004). Aside from the water level, the zonation pattern can be explained by salinity: from a gleasonian approach, a zonation pattern can be generated by the specific response of the species to the environmental gradient (Capon, 2005).

**Table 6**

Indicator species and indicator floristic groups of levels 1–3. The groups and species listed are ordered from highest to lowest indicator values with significant indicator values ( $p < 0.05$ ).

Category		Indicators	
		Floristic groups	Species
Level 1. Landscape unit	D North	Groups 21, 22 and 24	<i>Hemarthria altissima</i> , <i>Setaria parviflora</i> , <i>Aspilia silphioides</i> , <i>Polygonum lapathifolium</i> and <i>Plagiocheilus tanacetoides</i>
	D South	Group 26	<i>Conyza bonariensis</i> and <i>Salvinia cf. biloba</i> .
Level 2. Geomorpho-logical unit	Marine-fluvial history	–	<i>Solanum glaucophyllum</i>
	Fluvial history: ‘Levees and crevasse sprays of the Paraná main channel’ Fluvial history: ‘Islands of the Paraná main channel’	Groups 14 and 21 Group 11	<i>Oplismenopsis najada</i> , <i>Polygonum lapathifolium</i> and <i>Commelina diffusa</i> <i>Echinochloa polystachya</i> var. <i>spectabilis</i>
Level 3. Topographic positions	Low	Associations C (“Bulrush marshes”) and E (“Broadleaf marshes”)	<i>Ludwigia cf. peruviana</i> , <i>Oplismenopsis najada</i> , <i>Myriophyllum aquaticum</i> , <i>Schoenoplectus californicus</i> , <i>Enydra anagallis</i> , <i>Azolla filiculoides</i> and <i>Eichhornia azurea</i>
	High	Associations D (“Grass marshes”), F (“Bunchgrasses and grasslands”) and H (“Mixed grasslands and scrublands”)	<i>Aspilia silphioides</i> , <i>Baccharis salicifolia</i> , <i>Conyza bonariensis</i> , <i>Tarenaya hasleriana</i> , <i>Mimosa tweediana</i> , <i>Acmella decumbens</i> , <i>Cynodon dactylon</i> , <i>Hymenachne pernambucense</i> , <i>Setaria geminata</i> , <i>Phalaris aquatica</i> , <i>Solanum nigrescens</i> , <i>Torilis nodosa</i> , <i>Aniseia argentina</i> , <i>Plantago</i> sp. and <i>Borreria dasycephala</i>

Soil texture and nutrients (mean soil total N) also influenced the distribution of some species. These variables can be affected by sediment inputs occurring with intense floods (Trémolières et al., 2009; Willby et al., 2001) and can be a good correlate of vegetation distribution in several floodplain systems (Chacón-Moreno et al., 2004; Higgins et al., 1997; Marchetti and Aceñolaza, 2011; Thomaz and Bini, 2003). The high overlap of most species and of floristic group distribution along level 4 variables was compensated by the vegetation differences in broader scale levels. Other variables can be included in level 4, such as water availability or soil saturation (Lenssen and De Kroon, 2005), or filters acting in a season of the previous year (van Eck et al., 2006).

The study area can be understood as a mosaic of wetlands characterized by different vegetation zones. We suggest that multi-scale environmental constraints determine the limits between vegetation zones as well as the emerging floristic and diversity patterns. Thus, plant composition and distribution respond to several forcing factors: the flood pulse by itself (operating at a landscape scale), the “local control effect” of the flood pulse (Marchetti and Aceñolaza, 2012) and the heterogeneity in soil features (operating at a local scale). Since emphasis was placed on sampling different plant assemblages and environments, phenological or successional dynamics and disturbance factors were not considered. Also, feedbacks between vegetation and environmental features (particularly with landforms) and biotic interactions were not addressed (Corenblit et al., 2007). This multi-scale approach significantly improves the understanding of floristic patterns and plant biodiversity in the Lower Paraná River floodplain, and may be extended to other sections of the Paraná basin or to other floodplain wetlands.

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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.aquabot.2015.01.006>.

## References

- Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* 9, 683–693, <http://dx.doi.org/10.1111/j.1461-0248.2006.00926.x>.
- Bonfils, C.G., 1962. Los suelos del Delta del río Paraná Factores generadores, clasificación y uso. *Revista de Investigaciones Agrícolas. Rev. Investig. Agrícolas T XVI*, 257–370.
- Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology with R*. Springer, New York, United States.
- Borro, M.M., Morandeira, N.S., Kandus, P., Salvia, M.M., Minotti, P.G., Perna, P., 2014. Mapping shallow lakes in a large South American floodplain: a frequency approach on multitemporal Landsat TM/ETM data. *J. Hydrol.* 512, 39–52, <http://dx.doi.org/10.2478/v10104-009-0019-7>.
- Bray, R., Kurtz, L., 1945. Determination of total organic, and available forms of phosphorus in soils. *Soil Sci.* 59, 39–46.
- Bremner, J., Mulvaney, C., 1982. Nitrogen—total. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties*. ASA, Madison, United States, pp. 595–624.
- Burkart, A., 1969. Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte II. Gramíneas. La familia botánica de los pastos. Colección Científica del I.N.T.A., Buenos Aires, Argentina.
- Burkart, A., 1974. Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte VI. Dicotiledóneas Metaclámideas (Gamopétalas) B: Rubiales, Cucurbitales, Campanulales (incluso Compuestas). Colección Científica del I.N.T.A., Buenos Aires, Argentina.
- Burkart, A., 1979. Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte V. Dicotiledóneas Metaclámideas (Gamopétalas) A: Primulales, Plumbaginales, Ebenales, Contortales, Tubiflorales, Callitrichales, Plantaginales. Colección Científica del I.N.T.A., Buenos Aires, Argentina.
- Burkart, A., 1987. Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte III. Dicotiledóneas Arqui-clámideas. A: Salicales a Rosales (incluso Leguminosas). Colección Científica del I.N.T.A., Buenos Aires, Argentina.
- Burkart, A., Bacigalupo, N.M., 2005. Flora ilustrada de Entre Ríos (Argentina). Tomo VI, Parte IV. Dicotiledóneas arqui-clámideas. B: Geraniales a Umbelliflorales. Colección Científica del I.N.T.A., Buenos Aires, Argentina.
- Capon, S.J., 2005. Flood variability and spatial variation in plant community composition and structure on a large arid floodplain. *J. Arid Environ.* 60, 283–302, <http://dx.doi.org/10.1016/j.jaridenv.2004.04.004>.
- Carignan, R., Neiff, J.J., 1992. Nutrient dynamics in the floodplain ponds of the Paraná River dominated by the water hyacinth *Eichornia crassipes*. *Biogeochemistry* 17, 85–121, <http://dx.doi.org/10.1007/BF00002642>.
- Chacón-Moreno, E., Naranjo, M.E., Acevedo, D., 2004. Direct and indirect vegetation-environment relationships in the flooding savanna of Venezuela. *Ecotropicos* 17, 25–37.
- Chao, A., 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43, 783–791, <http://dx.doi.org/10.2307/2531532>.
- Corenblit, D., Tabacchi, E., Steiger, J., Gurnell, A.M., 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth-Sci. Rev.* 84, 56–86, <http://dx.doi.org/10.1016/j.earscirev.2007.05.004>.
- De Cáceres, M., Font, X., Oliva, F., 2010a. The management of vegetation classifications with fuzzy clustering. *J. Veg. Sci.* 21, 1138–1151, <http://dx.doi.org/10.1111/j.1654-1103.2010.01211.x>.
- De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90, 3566–3574, <http://dx.doi.org/10.1890/08-1823.1>.
- De Cáceres, M., Legendre, P., Moretti, M., 2010b. Improving indicator species analysis by combining groups of sites. *Oikos* 119, 1674–1684, <http://dx.doi.org/10.1111/j.1600-0706.2010.18334.x>.
- Dolédéc, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: a new method. *Ecology* 81, 2914–2927, [http://dx.doi.org/10.1890/0012-9658\(2000\)081\[2914:NSICAA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2).
- Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–20.
- Dufrène, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366, [http://dx.doi.org/10.1890/0012-9615\(1997\)067\[0345:SAIIST\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(1997)067[0345:SAIIST]2.0.CO;2).
- Enrique, C., 2009. Relevamiento y caracterización florística y espectral de los bosques de la Región del Delta del Paraná a partir de imágenes satelitales. In: *Degree Thesis in Biological Sciences*. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires.
- Franceschi, E.A., Lewis, J.P., 1991. Early stages in the Parana River tall grassland recovery after an extraordinary flood. *Coenoses* 6, 47–52.
- Franceschi, E.A., Prado, D.E., 1989. Distribution of herbaceous communities of the river Paraná valley along an elevation gradient after a catastrophic flood. *Coenoses* 4, 47–53.
- Franceschi, E.A., Torres, P.S., Lewis, J.P., 2010. Diversidad de la vegetación durante su recuperación tras una creciente extraordinaria del Río Paraná Medio (Argentina). *Rev. Biol. Trop.* 58, 707–716.
- Gotelli, N., Colwell, R., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391, <http://dx.doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Higgins, S.I., Rogers, K.H., Kemper, J., 1997. A description of the functional vegetation pattern of a semi-arid floodplain, South Africa. *Plant Ecol.* 129, 95–101, <http://dx.doi.org/10.1023/A:1009763931832>.
- Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427–432.
- C. Hurlley, gclus: Clustering Graphics. R package version 1.3.1 [www document]. URL <http://cran.r-project.org/package=gclus> 2012.
- Iriondo, M.H., 2004. The littoral complex at the Paraná mouth. *Quat. Int.* 114, 143–154, [http://dx.doi.org/10.1016/S1040-6182\(03\)49-1](http://dx.doi.org/10.1016/S1040-6182(03)49-1).
- Iriondo, M.H., Drago, E.C., 1972. Descripción cuantitativa de dos unidades geomorfológicas de la llanura aluvial del Paraná medio: república Argentina. *Rev. la Asoc. Geológica. Argent.* 27, 143–154.
- Junk, W.J., An, S., Finlayson, C.M., Gopal, B., Květ, J., Mitchell, S.A., Mitsch, W.J., Roberts, R.D., 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquat. Sci.* 75, 151–167, <http://dx.doi.org/10.1007/s00027-012-0278-z>.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 106, 110–127.



- Kandus, P., Malvárez, A.I., Madanes, N., 2003. Estudio de las comunidades de plantas herbáceas de las islas bonaerenses del Bajo Delta del Río Paraná (Argentina). *Darwiniana* 41, 1–16.
- Kirk, G., 2004. The Biogeochemistry of Submerged Soils. John Wiley & Sons, Ltd., Chichester, UK, <http://dx.doi.org/10.1002/047086303X>.
- Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280, <http://dx.doi.org/10.1007/s004420100716>.
- Lenssen, J., Menting, F., van der Putten, W., Blom, K., 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos* 86, 523–534, <http://dx.doi.org/10.2307/3546656>.
- Lenssen, J.P.M., De Kroon, H., 2005. Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. *J. Ecol.* 93, 138–147, <http://dx.doi.org/10.1111/j.1365-2745.2004.00957.x>.
- LeRoy Poff, N., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* 16, 391–409, <http://dx.doi.org/10.2307/1468026>.
- M. Maechler, P. Rousseeuw, A. Struyf, M. Hubert, K. Hornik, cluster: Cluster analysis basics and extensions. R package version 1.14.4 [www document]. URL <http://cran.r-project.org/package=cluster> 2013.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Science, Malden, Massachusetts, United States.
- Malvárez, A.I., 1997. Las comunidades vegetales del Delta del Río Paraná. Su relación con factores ambientales y patrones de paisaje. In: Ph.D Thesis in Biological Sciences. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Thesis.
- Marchetti, Z.Y., Aceñolaza, P.G., 2011. Evaluation of the relationships between floristic heterogeneity of *Panicum prionitis* Ness tall grasslands and the fire history, hydrological regime and soil texture in the Paraná River floodplain, Argentina. *Interciencia* 36, 600–607.
- Marchetti, Z.Y., Aceñolaza, P.G., 2012. Pulse regime and vegetation communities in fluvial systems: the case of the Parana River floodplain, Argentina. *Flora – Morphol. Distrib. Funct. Ecol.* 207, 795–804, <http://dx.doi.org/10.1016/j.flora.2012.09.004>.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley, New York, United States.
- 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>.
- Oakley, L., Prado, D.E., Adámoli, J.M., 2005. Aspectos biogeográficos del Corredor fluvial Paraguay-Paraná. *INSUGEO. Miscelánea* 14, 245–258.
- J. Oksanen, F. Guillaume Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M. Henry, H. Stevens, H. Wagner, Vegan: Community Ecology Package. R package version 2.0-7 [www document]. URL <http://cran.r-project.org/package=vegan> 2013.
- R. Core Team, R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [www document]. URL <http://www.r-project.org/> 2013.
- C.G. Ramonell, P. Kandus, P.G. Minotti, M.M. Borro, N.S. Morandeira, Nueva interpretación geomorfológica del Complejo Fluvioitoral del Río Paraná en su desembocadura, in: V Congreso Argentino de Cuaternario Y Geomorfología. Río Cuarto, Córdoba Argentina. 2012.
- Shmida, A., Wilson, M., 1985. Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20, <http://dx.doi.org/10.2307/2845026>.
- Smith, E.P., Van Belle, G., 1984. Nonparametric estimation of species richness. *Biometrics* 40, 119–129, <http://dx.doi.org/10.2307/2530750>.
- Steiger, J., Gurnell, A.M., 2002. Spatial hydrogeomorphological influences on sediment and nutrient deposition riparian zones: observations from the Garone River, France. *Geomorphology* 49, 1–23, [http://dx.doi.org/10.1016/S0169-555X\(02\)144-7](http://dx.doi.org/10.1016/S0169-555X(02)144-7).
- Thomaz, S.M., Bini, L.M., 2003. *Ecología e Manejo de Macrófitas Aquáticas*. Eduem – Editora da Universidade Estadual de Maringá, Maringá, Paraná Brasil.
- Trémolières, M., Noël, V., Hérault, B., 2009. Phosphorus and nitrogen allocation in *Allium ursinum* on an alluvial floodplain (Eastern France). Is there an effect of flooding history? *Plant Soil* 324, 279–289, <http://dx.doi.org/10.1007/s11104-009-9955-7>.
- van Eck, W.H.J.M., Lenssen, J.P.M., van de Steeg, H.M., Blom, C.W.P.M., de Kroon, H., 2006. Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species. *Hydrobiologia* 565, 59–69, <http://dx.doi.org/10.1007/s10750-005-1905-7>.
- B. Wheeler, lmpPerm: Permutation tests for linear models. R package version 1.1-2 [www document]. URL <http://cran.r-project.org/package=lmpPerm> 2010.
- Willby, N.J., Pulford, I.D., Flowers, T.H., 2001. Tissue nutrient signatures predict herbaceous-wetland community responses to nutrient availability. *New Phytol.* 152, 463–481, <http://dx.doi.org/10.1046/j.0028-646X.2001.00274.x>.
- Zóffoli, M.L., Kandus, P., Madanes, N., Calvo, D., 2008. Seasonal and interannual analysis of wetlands in South America using NOAA AVHRR-NDVI time series: The case of the Paraná Delta Region. *Landscape Ecol.* 23, 833–848, <http://dx.doi.org/10.1007/s10980-008-9240-9>.
- Zuloaga, F.O., Morrone, O., Belgrano, M.J., 2009. Catálogo de las Plantas Vasculares del Cono Sur. Missouri Botanical Garden – Instituto Darwinion, <http://www.darwin.edu.ar>