



Plant functional types and trait values in the Paraná River floodplain: Modelling their association with environmental features



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ABSTRACT

Our aim was to assess whether plant trait values and functional types are associated with environmental features in floodplain wetlands. The study was conducted in the Lower Paraná River floodplain, mostly dominated by marsh communities. In 72 sites, 16 functional traits were screened for 95 plant populations of 44 species. Since the interspecific variability in trait values resulted higher than the intraspecific variability, plant species (and not populations) were hierarchically classified into plant functional types (PFTs). Ten PFTs were identified. Two trade-offs were observed: resource acquisition vs. resource conservation or resource assignment to tissues conferring anoxia or salinity tolerance, and fast growth vs. light interception. Cover-abundance of the PFTs and community-level weighted means (CWMs) of the non-redundant traits were computed for 80 sites. Generalized linear models were used to assess the effect of environmental variables (landscape units, topographic positions, flooding frequency and eight soil variables) on the CWMs and on distribution of PFTs occurring in 15 sites or more. A two-stage modelling process was carried out to account for the presence-absence and cover-abundance of PFTs separately. The association between CWMs and environmental features was relatively weak but significant for six out of the eight traits analysed. Besides, satisfactory models were found for eight out of the nine PFTs assessed. In the studied floodplain, PFTs—interpreted in terms of life strategies—seem to be a better approach than CWMs to understand and characterise functional responses to the environment.

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1. Introduction

Plant establishment and plant community development in floodplain wetland ecosystems are strongly controlled by abiotic factors related to hydrogeomorphic forces, including flood pulses and water permanence (Bornette et al., 2008; Junk et al., 1989). The effect of the environment on species occurrence or dominance can be understood within the conceptual framework of assembly rules (Keddy, 1992). According to this theory, the environment acts as a filter or sieve, selecting species with adequate life history and functional traits for a particular wetland state (Keddy, 1992; Van

der Valk, 1981). In particular, functional traits are of interest for functional and comparative ecology, since they are markers of functions (e.g., specific leaf area (SLA) is a marker of potential growth rate) (Garnier and Navas, 2012; Violle et al., 2007) (see Table 1 for other traits and related functions). Plant individuals respond to the environment according to their trait values, which determine their functional strategy and the environments in which the species can occur. Although biotic relations also shape community structure (Kraft et al., 2015), we here consider that abiotic factors are the strongest constraints to plant distribution and community assembly in floodplain wetlands (Bornette et al., 2008), especially when being studied at broad ecological scales.

Not every combination of trait values can be shared by a plant species or a plant individual. Leaf traits, in particular, are usually restricted by an ecophysiological trade-off between fast resource acquisition and resource conservation in well protected tissues (Díaz et al., 2004; Wright et al., 2004). Plants have developed a reduced number of economically competitive strategies to deal with environmental conditions (Craine, 2005; Grime, 1977; Shipley et al., 2006; Wright et al., 2004). Grime (1977) proposed three main

Abbreviations: AIC, Akaike's information criterion; CV, coefficient of variation; CWM, community-level weighted mean; CSR, competitiveness–stress tolerance–ruderalness; GLM, generalized linear model; PFT, plant functional type; PCoA, principal coordinate analysis; SLA, specific leaf area.

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life strategies for plants (CSR strategies): competitiveness (C), stress tolerance (S) and ruderalness (R), a scheme that has been adapted to wetlands by considering flooding frequency (Menges and Waller, 1983). In the context of assembly rules, a given species cannot possess trait values related to high competitiveness (e.g., high plant height, tough leaves) simultaneously with trait values related to high ruderalness (e.g., high SLA) (Hodgson et al., 1999). Trait values are also constrained by plant species resistance or resilience to different types and dimensions of disturbances (Lavorel et al., 1997), particularly in fluvial systems (Bornette et al., 2008). At a community level, mean trait values of the plant assemblage can be indicators or functional markers of different conditions in sites along an environmental gradient or with different disturbance histories (e.g., Garnier et al., 2004).

Species with a shared set of trait values are usually assumed to have a similar response to environmental conditions (Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Violle et al., 2007) or a similar effect on the functioning of the ecosystem (De Bello et al., 2010; Díaz and Cabido, 2001). The spectrum of trait values can thus be summarized by classifying species (or populations) into plant functional types (PFTs), so that species in each PFT share a set of trait values and, thus, a life strategy (Díaz and Cabido, 2001). This inductive trait-based approach is a pragmatic way that improves the understanding of the presence and distribution of plant strate-

gies, and does not neglect that those strategies and the trait values defining them vary along a spectrum defined by trade-offs (Wright et al., 2004). An inductive trait-based approach for identifying PFTs has been used in several ecosystems, including coastal dunes, semi-arid shrublands and grasslands (e.g., Acosta et al., 2006; Díaz and Cabido, 1997; Leishman and Westoby, 1992). Nevertheless, few studies including traits and/or trait-based PFT classifications have been performed in wetland ecosystems (Boutin and Keddy, 1993; Casanova and Brock, 2000; Díaz Barradas et al., 1999; Kennedy et al., 2006; Shipley and Lechowicz, 2000; Van der Valk, 1981) and, to our knowledge, none in large floodplains such as those of South American rivers.

The present study was conducted at the Lower Paraná River floodplain, surveyed at a broad ecological scale. We aimed to assess how plant strategies vary in relation to substrate features and to other abiotic factors summarizing the effect of flood pulses. A trait-based approach was used and our main hypothesis was that both community-level weighted mean trait values and PFTs are indicators of environmental features. Before identifying the PFTs, we evaluated whether intraspecific variability in trait values (or categories of qualitative traits) was important to be considered. We expected that interspecific variability in trait values was higher than intraspecific variability (Prediction 1), as reported for several ecosystems (Kazakou et al., 2014). If this was supported by our data,

Table 1
Functional traits measured or recorded in 95 dominant populations (belonging to 44 species) in the Lower Paraná River floodplain. Related functions were gathered from the literature.

Functional trait	Measurement	Type	Units or categories	Related functions
Morpho-ecological type	5 individuals or ramets	Categorical	Broadleaf herbs, graminoid herbs, equisetoid herbs	Physiological adaptations to luminic, edaphic and hydric environment; stress and disturbance adaptations; growth forms
Plant height	5 individuals or ramets	Real	cm	Competitiveness; plant fecundity; potential longevity; use of luminic or hydric environment
Anoxia tolerance	5 individuals or ramets; bibliographic compilation	Binary	Presence/absence of aerenchyma or hollow stems	Anoxia tolerance
Salinity tolerance	Bibliographic compilation	Binary	Presence/absence of salinity tolerance or salt exclusion structures	Salinity tolerance
Total leaf area	5 individuals or ramets	Real	m ²	Competitiveness; potential photosynthetic rate per individual
Leaf area	10 leaves (2 leaves × 5 individuals)	Real	cm ²	Growth in shaded vs. sunny sites
Leaf thickness	25 leaves (5 leaves × 5 individuals)	Real	mm	Leaf life span; stress tolerance (drought and nutrients); litter decomposition rate
Specific leaf area	10 leaves (2 leaves × 5 individuals)	Real	m ² /kg	Potential relative growth rate; maximum photosynthetic rate
Leaf shape (Dissection index)	10 leaves (2 leaves × 5 individuals)	Real	-(No units)	Tolerance to drought stress; tolerance to water submersion
Total leaf nitrogen concentration	Leaves from the population	Real	% [(mg N/g dry leaf tissues) × 0.1]	Maximum photosynthetic rate; Palatability; high nutritional quality; litter decomposition rate; soil nutrients
Total leaf phosphorus concentration	Leaves from the population	Real	% [(mg P/g dry leaf tissues) × 0.1]	High nutritional quality
Leaf chlorophyll content	25 leaves (5 leaves × 5 individuals)	Real	SPAD	Maximum photosynthetic rate
Photosynthetic pathway	Bibliographic compilation	Binary	C3 or C4	Photosynthetic efficiency at high temperatures; efficiency in water usage; efficiency in nitrogen usage; efficiency in saline soils; photosynthetic rate stability with low CO ₂ and phosphorus availability
Life cycle	Bibliographic compilation	Binary	Perennial or annual–biannual	Persistence; dispersal; stress tolerance
Clonality	Bibliographic compilation	Binary	Presence/absence of vegetative reproductive structures	Fast colonisation; Invasiveness; Regeneration after disturbances
Seed size	Bibliographic compilation	Real	mm	Resource storage and seedling stress tolerance; persistence in seed bank; long vs. short dispersal

plant species were to be classified into PFTs; if results were contrary to our prediction, plant populations were to be classified into PFTs. The PFTs obtained are interpreted and discussed in terms of CSR strategies.

Next, we modelled how community-level weighted means (CWMs) per each trait and presence–absence and cover–abundance of each PFT were affected by environmental features (edaphic variables, landscape units, topographic position and flood frequency). The CWMs were expected to differ in association with environmental features (Prediction II). Also, each PFT was expected to respond differently to the environment, as expected according to the definition of “functional response groups” in Lavorel and Garnier (2002), especially if assembly rules are operating on species traits (Keddy, 1992). Thus, the probability of occurrence of each PFT and their cover–abundance would vary according to the environment (Prediction III).

2. Materials and methods

2.1. Study area

The study was conducted at a section of ca. 100 km in length and ca. 40 km in width in the Lower Paraná River floodplain where freshwater wetlands cover 3650 km² (Fig. 1). The area is subject to the flood pulse of the Paraná River. The mean annual discharge of the Paraná River is 18,000 m³ s⁻¹ with a drainage area of 2600 × 10³ km² and a length of 3900 km, being the second longest river in South America after the Amazon River and the largest river of the Del Plata basin (Latrubesse et al., 2005; Neiff et al., 2014). The flood pulse of the Paraná River is more irregular than those of the Amazon and the Orinoco (Carignan and Neiff, 1992), with a main flood peak at the end of summer (March) caused by rains in the Upper Paraná River and a second peak during winter (June–July) from the Paraguay River. During strong El Niño events, extended floods affect the whole study area. The climate is temperate humid. Herbaceous communities dominate the marshes and natural forests are restricted to ca. 1.5% of the study area (Enrique,

2009). A total of 124 herbaceous species has been recorded for the study area (Morandeira and Kandus, 2015). The main vegetation units are: short salt marshes, tall salt marshes, bulrush marshes, grass marshes, broadleaf marshes, bunchgrasses and grasslands, mixed wet prairies of grasses and broadleaf herbs, and mixed grasslands and scrublands. The relation between some of the plant species and soil features measured in the field has been documented in Morandeira and Kandus (2015).

2.2. Sampling and measurement of functional traits

The floristic composition of the study area has been described in Morandeira and Kandus (2015), by means of eight field-work trips during the summers of 2010–2011 and 2011–2012, covering a total of 88 sampling sites. In each of the 88 sampling sites, three vegetation censuses were carried out in 1 m² plots each. In the same field trips, the dominant species (i.e., species with maximum coverage in the site or at least twice the coverage than the accompanying species) of each sampling site were identified to measure functional traits. Also, species accumulating at least 80% of the green above-ground biomass present in the site were measured (Grime, 1998). Only emergent rooted macrophyte species were characterised, i.e., trees and floating vegetation were excluded. Species nomenclature was assigned according to Zuloaga et al. (2009); a summarizing Table of plant species and their nomenclature for the study area is available as supplementary material in Morandeira and Kandus (2015).

In the present study, a total of 95 dominant plant populations (belonging to 44 species, one to 11 populations per species) were surveyed in 72 out of the 88 sampling sites of the community study carried out in Morandeira and Kandus (2015). A total of 16 functional traits were recorded in each of the 95 populations. Table 1 summarizes the variable type (real, binary or categorical), the observational unit, and the functions related to the trait. Most traits were measured in the field or in the laboratory from collected leaves, whereas some traits such as photosynthetic pathway, clonality, life cycle, seed size, adaptations to salinity and adaptations

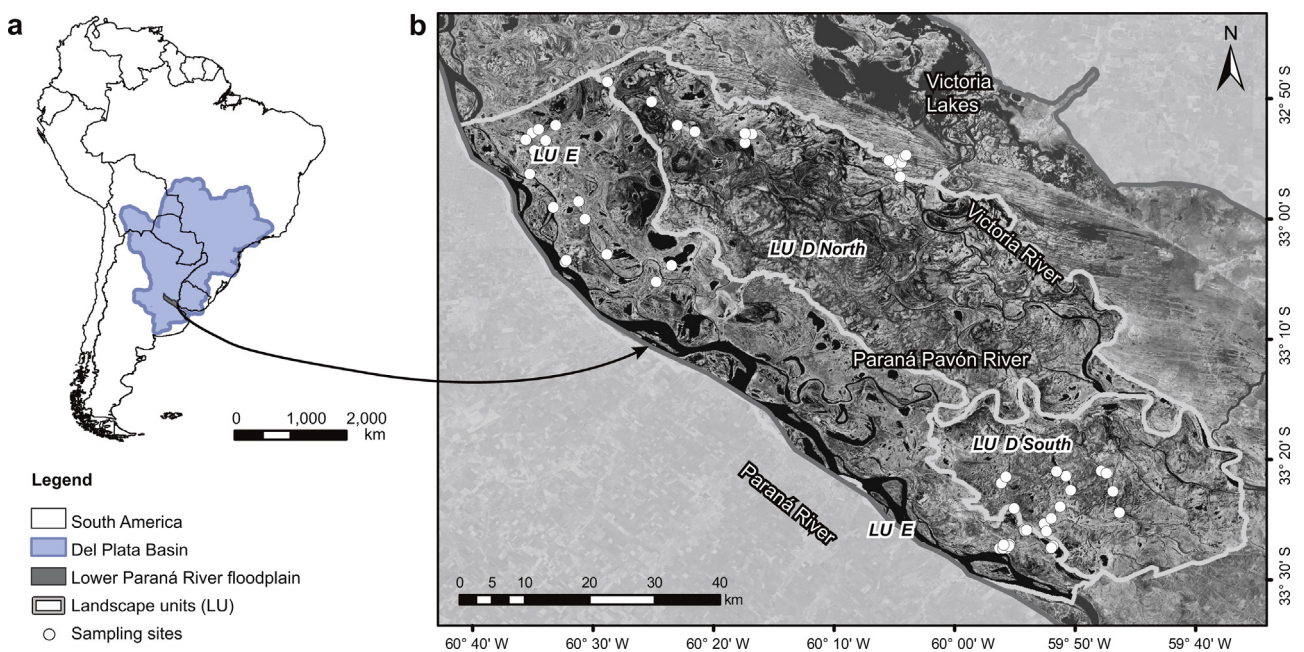


Fig. 1. Study area. (a) Location of the Lower Paraná River floodplain in South America. (b) Distribution of the sampling sites where the community study and environmental characterisation were carried out (Morandeira and Kandus, 2015) and where plant functional traits were recorded. Landscape units (Level 1) are also indicated: D North, D South and E. The background image corresponds to the Near Infrared band (shown in grey scale) of a Landsat 8 OLI scene (Band 5; Path-Row 226-83; date: 2011/03/21). Reproduced with permission of Elsevier.

to floodability were gathered from specific literature. For traits measured at the individual level, five individuals of each population were randomly selected within the homogeneous stand of the sampling site where the three floristic censuses had been carried out. For leaf traits, five leaves completely exposed to sunlight were harvested from each individual. When possible, the handbook in Pérez-Harguindeguy et al. (2013) was followed for trait measurement.

2.3. Intraspecific variability

For species for which more than one population was measured ($n = 21$), the amount of intraspecific variability with respect to interspecific variability in continuous traits was evaluated. In addition, a one-tailed Student's test was used to evaluate whether the coefficient of variation (CV) between trait values in populations of the same species (intraspecific CV) was significantly greater than the CV between species mean trait values (interspecific CV). Since interspecific variability was higher than intraspecific variability for all the traits evaluated (see Section 3), the mean species trait values were used hereafter.

2.4. Species classification into plant functional types

Functional traits were centred by their mean. To remove redundant traits, Pearson's correlations were used for continuous traits. When a pair of traits was correlated ($p < 0.01$; with $|r| \geq 0.4$), we retained the trait that: could be measured in more species, had less measuring error or showed higher variation range between species. Also, measured traits were preferred to those gathered from the literature, and traits mentioned in standardized protocols were prioritized (Pérez-Harguindeguy et al., 2013). The relation between qualitative traits was evaluated with Chi² tests, and the relation between qualitative and continuous traits was evaluated with logistic regressions. If a pair of traits showed a significant association ($p < 0.01$, $|r| > 0.4$ for quantitative traits), one trait of the pair was removed.

A matrix of non-redundant traits \times species was obtained. Next, a distance matrix between species was obtained by computing the generalized Gower's distance (Pavoine et al., 2009), which allows analysing both qualitative and quantitative data. Due to the high influence of categorical variables in Gower's distance (pers. obs.), a weight of 0.5 was assigned to qualitative variables and a weight of 1 to quantitative ones. Hierarchical classifications were computed on this distance matrix. An average linkage method was selected with the cophenetic correlation criterion (Borcard et al., 2011). The optimum number of clusters (k) was defined by means of the maximum silhouette width criterion (Rousseeuw, 1987). If a cluster accounted for more than 15 species, we repeated these clustering analyses and defined sub-groups of PFTs. To assess how strong the clustering is supported by data, a bootstrap analysis was conducted via multiscale bootstrap resampling (Suzuki and Shimodaira, 2006) with 1000 iterations. A cluster was considered to be stable or robust according to the randomization result if the "approximately unbiased" p -value was lower than 0.05 (Suzuki and Shimodaira, 2006).

Next, plant functional types were characterised with a Principal Coordinate Analysis (PCoA) based on the Gower's distance matrix. Pearson's correlation tests were computed between the first three PCoA axes and quantitative traits, whereas logistic regressions were computed between the first three PCoA axes and qualitative traits.

These analyses were carried out with the open-source software R (R Core Team, 2014) and the following packages: ade4 (Dray and Dufour, 2007), ape (Paradis et al., 2004), cluster (Maechler et al., 2013), FD (Laliberté and Shipley, 2011) and gclus (Hurley, 2012). For the multiscale bootstrap resampling, the unofficial version 090824 of pvclust was used (Suzuki and Shimodaira, 2014), so that the

Gower's distance could be defined and given as an argument of the pvclust function.

2.5. Modelling the association between environmental features and trait values and PFT

Species cover–abundance (estimated with a Braun-Blanquet cover–abundance scale in three censuses per site) was extracted from the results of our previous community study (Morandeira and Kandus, 2015). Sites where the PFTs measured did not reach 80% of the total cover were removed from the analysis, so that 80 sites (out of the 88 sites of the community study) remained. The cover of each PFT in each site was computed by adding up the cover–abundance of the species belonging to each site and to each PFT. Based on species cover–abundance, the community-level weighted means (CWMs) of each non-redundant trait was computed (Garnier et al., 2004).

Sites were characterised according to flood frequency (Borro et al., 2014), to their location in landscape units D North, D South or E (Zóffoli et al., 2008), to their topographic position (relatively high or low positions) and to eight soil variables measured in the first two subsurface soil layers (total nitrogen, extractable phosphorus, organic carbon, pH, electrical conductivity, percent clay, percent silt and percent sand) (Morandeira and Kandus, 2015). For soil variables, the mean value in Layers 1 and 2 (weighted by the layer depth) and the difference between soil layer values were computed.

The association between CWMs and PFTs, and environmental features was described by means of generalized linear models (GLM) (Zuur et al., 2009). PFTs occurring in 15 sites or more were modelled individually. We first tested whether the cover–abundance in the 80 sites could be modelled. Since the data had a lot of zeros, the residuals of the fitted models did not show a normal distribution, even when using a compound Poisson-Gamma distribution (Tweedie distribution, see Zhang (2013)). Thus, a two-stage modelling process was conducted. The presence–absence of each PFT in the 80 sites and the abundance of each PFT only in sites where it was present (excluding zeros) were modelled separately.

The presence–absence of PFTs was modelled by assuming a binomial error distribution. A manual upward stepwise multiple regression procedure was performed to find the best models, as described in Cardo et al. (2013). First, explanatory variables were centred and fitted in univariate models. The three variables explaining a higher portion of the total deviance were used in turns as start up of a multivariate model. Each term addition was evaluated with a Chi² test on the change in deviance and a significant reduction (>2) in the Akaike's information criterion (AIC) (Zuur et al., 2009). To avoid collinearity, variables significantly correlated to a previously included term ($|r| > 0.4$, $p < 0.01$) were not included, and terms were restricted to have variance inflation factors <3 (Zuur et al., 2010). Quadratic terms and interactions were tested and, when a soil variable measured in the first soil layer was included, the difference between soil layer values was also tested. Variables in the final GLM models were selected based on the AIC. The ratio of the residual to null deviance was used as an estimation of the explanatory power of the model. We also tested random effect terms by means of generalized linear mixed models (Zuur et al., 2009), to evaluate the contribution of the field trip (differing in dates and locations within the floodplain), of the total cover of the sites, and of the presence of more than one stratum in the plots. However, no random effects explained the variance in any of the fitted models and GLM models were kept.

The procedure to select the best cover–abundance model for each PFT was similar to that described for presence–absence modelling. The cover–abundance was log-transformed to account for the assumptions of normality and homoscedasticity of the residuals, which was assessed with residual plots. As for the community

weighted mean trait values, GLM models assuming a binomial error distribution were fitted for qualitative CWMs (coincidentally to the models fitted for the presence–absence of the PFTs); whereas GLM assuming a normal distribution were fitted for quantitative CWMs. Quantitative CWMs were not transformed since the distribution of the model residuals was consistent with the normality and homoscedasticity assumptions.

Modelling was performed in R (R Core Team, 2014) with the packages lme4 (Bates et al., 2014), cplm (Zhang, 2013), car (Fox and Weisberg, 2011) and boot (Canty and Ripley, 2014).

3. Results

3.1. Functional traits

Regarding the quantitative traits, those with highest interspecific variability were leaf area, leaf thickness and total leaf area (Table 2). In *Schoenoplectus californicus* (C.A. Mey.) Soják and *Cyperus giganteus* Vahl (Cyperaceae), “leaf thickness” had a high value because it was measured in their photosynthetic stems. Since interspecific variability was higher than intraspecific variability for all traits ($p < 0.01$) (Table 2), species mean trait values were used in subsequent analyses. Most species were perennial, broadleaf or graminoid herbs, had aerenchyma or hollow stems, were non-tolerant to salinity, presented a C3 photosynthetic pathway and had clonal structures (Table 3).

As to the results of the correlation tests between functional traits (with $|r| > 0.4$ and $p < 0.01$), plant species with high SLA had low leaf area and low chlorophyll content. Also, thick leaves (or thick photosynthetic stems) had high leaf areas and high dissection indexes. Total leaf nitrogen was positively correlated with total leaf phosphorus, chlorophyll content and seed sizes, and was higher in broadleaf herbs. Plants with high total leaf area had high plant height and high dissection index. Regarding categorical traits, most clonal plants were tolerant to anoxia, and most broadleaf species had a C3 photosynthetic pathway (except for *Sesuvium portulacastrum* (L.) L.). After removing redundant variables, eight traits remained: plant height, SLA, leaf thickness, total leaf nitrogen concentration, life cycle, anoxia tolerance, salinity tolerance and photosynthetic pathway.

Table 2

Quantitative functional traits. The interspecific and intraspecific coefficients of variations, and the p -value of a t -test are indicated ($n = 21$ species for which more than one population was measured). Descriptive statistics were computed on the 95 populations.

Functional trait	Coefficient of variation			Trait values			
	Interspecific	Intraspecific	p value	Mean	Median	Minimum	Maximum
Plant height (cm)	0.59	0.23	<0.0001	92.13	82.00	2.68	227.60
Total leaf area (m ²)	5.42	0.56	<0.0001	0.12	0.02	0.00	6.39
Leaf area (cm ²)	2.34	0.41	<0.0001	36.11	10.17	0.16	676.95
Specific leaf area (m ² kg ⁻¹)	0.64	0.25	<0.0001	20.45	17.88	1.04	64.14
Leaf thickness (mm)	2.76	0.26	<0.0001	1.33	0.18	0.08	17.13
Leaf shape	0.69	0.14	<0.0001	12.55	10.05	3.65	38.94
Total leaf N (%)	0.46	0.18	<0.0001	2.37	2.25	0.55	5.29
Total leaf P (%)	0.38	0.22	0.0024	0.28	0.27	0.06	0.52
Leaf chlorophyll content (SPAD)	0.34	0.14	<0.0001	37.82	40.90	3.30	64.70
Seed size (mm)	0.58	–	–	1.99	2.00	0.75	5.50

Table 3

Proportion of plant species with each category of the qualitative functional traits.

Functional trait	Proportion of plant species
Life cycle	84% perennial, 16% annual or biennial
Morpho-ecological type	24% broadleaf herbs, 17% graminoid herbs, 3% equisetoid herbs
Anoxia tolerance	68% with aerenchyma or hollow stems, 32% without
Salinity tolerance	16% tolerant to salinity, 84% non-tolerant
Photosynthetic pathway	68% C3, 32% C4
Clonality	77% clonal, 23% non-clonal

3.2. Plant functional types

The classification procedure led to ten PFTs (Table 4), which were stable according to the bootstrap analysis ($p < 0.05$). One of the PFTs grouped 20 species and was classified into three sub-PFTs (Table 4, Fig. 2). Plant species were ordered according to their functional trait values (Fig. 3). The first PCoA axis (explaining 19.2% of the total variance) was positively related to leaf thickness or photosynthetic stem thickness (succulent leaves, tough leaves or photosynthetic stems with aerenchyma) and negatively related to total leaf nitrogen concentration and chlorophyll content (more photosynthetic ability). Also, perennial and anoxia-tolerant species were associated with positive values, whereas broadleaf herbs and species with a C3 photosynthetic pathway were associated with negative values. The second PCoA axis (explaining 13.8% of the total variance) was positively related to SLA (high growth rate) and negatively related to plant height, total leaf area, leaf area and chlorophyll content (competitiveness). PFTs can be described according to their trait values and categories (Table 4, Fig. 3). Salinity-tolerant and/or anoxia-tolerant species were grouped in PFTs 1–5, and differed in their photosynthetic pathway and morpho-ecological type, as well as in SLA, leaf area and leaf dissection index. Species ordered along the positive values (or nearly zero values) of the second PCoA axis were grouped in PFTs 1, 2, 3, 6 and 7. Of them, PFTs 1 and 2 were ordered along the positive values of the first and second PCoA axis. On the other hand, species ordered along the positive values of the first and negative values of the second PCoA axes were grouped in PFTs 5 and 10.

3.3. Functional responses to environmental features

The association between CWM of the non-redundant traits and the environmental features was relatively weak: the maximum percentage of the total variance explained by the set of environmental data was 36.4% (Table 5). A high flood frequency was associated with high CWM SLA values (generally related to potential relative growth rate) and to a C4 photosynthetic pathway. Anoxia tolerance was more probable to occur in sites with high water permanence (low topographic positions), in Landscape Unit D North and in soils with relatively low pH. Salinity tolerance was

Table 4
Description of the Plant Functional Types (PFTs) according to their trait values, and plant species classified into each PFT.

PFT	Description	Species
1	Tolerance to salinity. Perennial C4 clonal species. Short broadleaf herbs. Very thick leaves, with succulence. Very low dissection index, total leaf N and total leaf P. Small seeds	<i>Sesuvium portulacastrum</i>
2	Tolerance to salinity and anoxia. Perennial C3 species, mostly clonal. Short graminoid herbs. High specific leaf area, high leaf dissection index, low total leaf P and N. Small seeds	<i>Bolboschoenus robustus</i> , <i>Cynodon dactylon</i> , <i>Echinochloa crus-galli</i> , <i>Leptochloa fusca</i> , <i>Paspalum vaginatum</i> , <i>Phalaris aquatica</i>
3	Tolerance to anoxia. Annual C3 clonal species. Short broadleaf herbs. High specific leaf area, high chlorophyll content and large seeds	<i>Eclipta prostrata</i> , <i>Polygonum punctatum</i>
4a	Tolerance to anoxia. Broadleaf herbs, C3 photosynthetic pathway. Low specific leaf area. Very low dissection index. Low total leaf P	<i>Alternanthera philoxeroides</i> , <i>Eichhornia azurea</i> , <i>Ludwigiacf. peruviana</i> , <i>Ludwigia peploides</i> , <i>Myriophyllum aquaticum</i> , <i>Oplismenopsis najada</i> , <i>Polygonum acuminatum</i> , <i>Polygonum</i> aff. <i>hydropiperoides</i> var. <i>hydropiperoides</i> , <i>Polygonum</i> aff. <i>hydropiperoides</i> var. <i>setaceum</i> , <i>Polygonum lapathifolium</i> , <i>Rumex argentinus</i>
4b	Tolerance to anoxia. Mostly graminoid herbs, mostly C4 photosynthetic pathways. Low leaf area and leaf thickness, low total leaf N and very low chlorophyll content	<i>Echinochloa helodes</i> , <i>Echinochloa polystachyavar. polystachya</i> , <i>Echinochloa polystachya</i> var. <i>spectabilis</i> , <i>Enydra anagallis</i> , <i>Hemarthria altissima</i> , <i>Hymenachne pernambucense</i> , <i>Panicum elephantipes</i> , <i>Setaria geminata</i>
4c	Tolerance to anoxia. Broadleaf herbs, C3 photosynthetic pathway. Very high leaf area and total leaf area, low specific leaf area. Large seeds	<i>Sagittaria montevidensis</i>
5	Tolerance to anoxia. Perennial C3 and C4 clonal species. Tall equisetoid herbs, clonal. Photosynthetic stems and no leaves. Very high photosynthetic area. Low specific photosynthetic area. Very low total leaf N and low total leaf P	<i>Cyperus giganteus</i> , <i>Schoenoplectus californicus</i>
6	Annual C3 species, mostly non-clonal. Short broadleaf herbs. Low specific leaf area. Low total leaf P, high total leaf N, high chlorophyll content	<i>Plagiocheilus tanacetoides</i> , <i>Polygonum stypticum</i> , <i>Tarenaya hassleriana</i>
7	Perennial C3 species, mostly clonal. Short broadleaf, graminoid and equisetoid herbs. High leaf thickness, very low chlorophyll content, low total leaf N and P. Small seeds	<i>Eleocharis</i> aff. <i>bonariensis</i> , <i>Evolvulus sericeus</i> , <i>Leersia hexandra</i> , <i>Poa pilcomayensis</i> , <i>Setaria parviflora</i>
8	Annual C3 non-clonal species. Tall broadleaf herbs. Very high specific leaf area. High leaf area, high total leaf P. Low chlorophyll content, small seeds	<i>Conyza bonariensis</i>
9	Perennial C3 species, mostly non-clonal. Broadleaf herbs with low dissection index and low thickness. High total leaf N and P. Large seeds	<i>Aspilia silphioides</i> , <i>Baccharis salicifolia</i> , <i>Senecio brasiliensis</i>
10	Perennial C4 clonal species. Tall graminoid clonal herbs. Very high leaf area and total leaf area, plants forming tussocks. Very high dissection index. Very low specific leaf area, total leaf N and P. Small seeds	<i>Coleataenia prionitis</i>

Table 5
Models explaining the community-level weighted mean (CWM) values of the non-redundant traits. Only the best models are shown, provided all the explanatory variables had a significant effect ($p < 0.05$; see text for details on the modelling procedure). The positive or negative effect of each variable in the model is indicated with (+) or (–), respectively. For soil variables, the mean value in layers 1 and 2 was used, unless “L1” (Layer 1) is indicated. The explanatory power of the binomial models (computed for binary traits) was estimated as: $((\text{Null deviance} - \text{residual deviance}) / \text{residual deviance}) \times 100$ (equal to R^2 for the models of the continuous traits).

CWM	Type	Best fitted model	
		Variables	% explained
Life cycle	Binary	–	–
Photosynthetic pathway	Binary	Flood frequency (–)	8.2
Anoxia tolerance	Binary	Low topographic positions (+), landscape unit D North (+), pH L1 (–)	36.4
Salinity tolerance	Binary	Electrical conductivity L1 (+)	16.2
Plant height	Real	High topographic positions (+ ^a), electrical conductivity L1 (+ ^a), percent sand (L1) (+), interaction term: electrical conductivity \times percent sand L1 (–)	25.8
Specific leaf area	Real	Flood frequency (+)	7.8
Leaf thickness	Real	–	–
Leaf total phosphorus concentration	Real	Percent silt L1 (+)	10.2

^a Negative univariate effects of both the high topographic positions and the electrical conductivity were found. The effects of these variables turn to be positive in the multivariate model and with the inclusion of the interaction term. See text for details.

more probable to occur in soils with high electrical conductivity (up to 15.3 dS m^{-1}). The CWM of the leaf total phosphorus was higher in soils with high percent silt. The CWM of plant height (usually related to competitiveness) was higher in high topographic positions than in low topographic positions; and was restricted by the soil electrical conductivity and by soil percent sands (univariate models with negative slope, explaining 4.9% and 6.5% of the total variance). In the multivariate model for the CWM of plant height, the coefficients of the electrical conductivity, of plant height and of their interaction term (Table 5) can be interpreted as follows:

provided the soil has high electrical conductivity, coarse textures are associated with tall plants, and vice-versa.

Plant species belonging to PFT 4a were the most constant, followed by species belonging to PFTs 4b and 2. Although some of the presence-absence models explained a relatively low proportion of the total variability in PFT occurrence (Table 6), the explanatory power is generally greater than for the CWM models. Some interesting tendencies arose from presence-absence models. PFT 2, grouping salinity- and anoxia-tolerant species, was consistently associated with soils with high electrical conductivity,

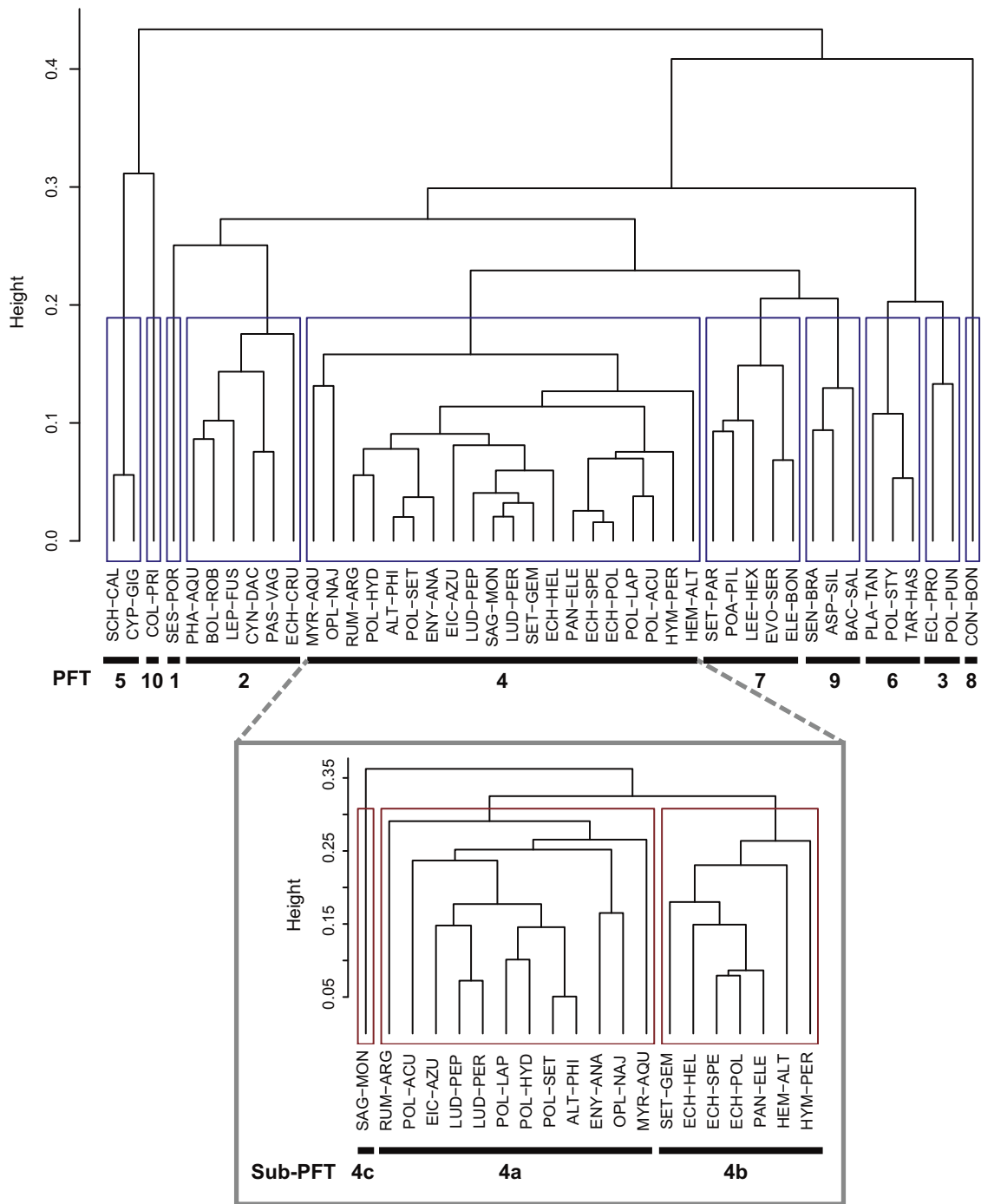


Fig. 2. Hierarchical classification of 44 plant species into 10 plant functional types (PFTs), according to eight functional traits. One of the PFTs was sub-divided into three sub-PFTs. Species names are abbreviated by including the first three letters of the genus and the first three letters of the specific epithet.

mostly sandy soils in high topographic positions. PFT 3 showed a higher probability of being present in sites with low flood frequency, whereas broadleaf herbs in PFT 4a were associated with high flood frequency, in soils with fine textures and low electrical conductivity. Anoxia-tolerant species (mostly graminoid herbs) grouped in PFT 4b had a higher probability of occurrence in soils with high percent clay and low pH (pH ranging between 3.9 and 5.9), and/or in soils with low electrical conductivity and low percent silt. The presence-absence model with the highest explanatory power was obtained for PFT 6, which had a higher probability of occurrence in high topographic positions, of landscape units D North or D South and in soils with low percent silt (54.3% of the

presence-absence explained). However, no satisfactory model of the cover-abundance of PFT 6 species was found.

Lastly, two cover-abundance models had a relatively high explanatory power (Table 6). Bulrushes of PFT 5 had a higher probability of occurrence in silty soils, whereas their abundance was higher in low topographic positions with low percent sand (71.6% of the cover-abundance explained). Tall broadleaf herbs of PFT 9 had a higher of occurrence in high topographic positions and in sites with relatively low pH. This PFT was more frequent in landscape unit D North but reached the highest cover-abundance values when it occurred in landscape unit D South. The cover-4.0% of the cover-abundance explained).

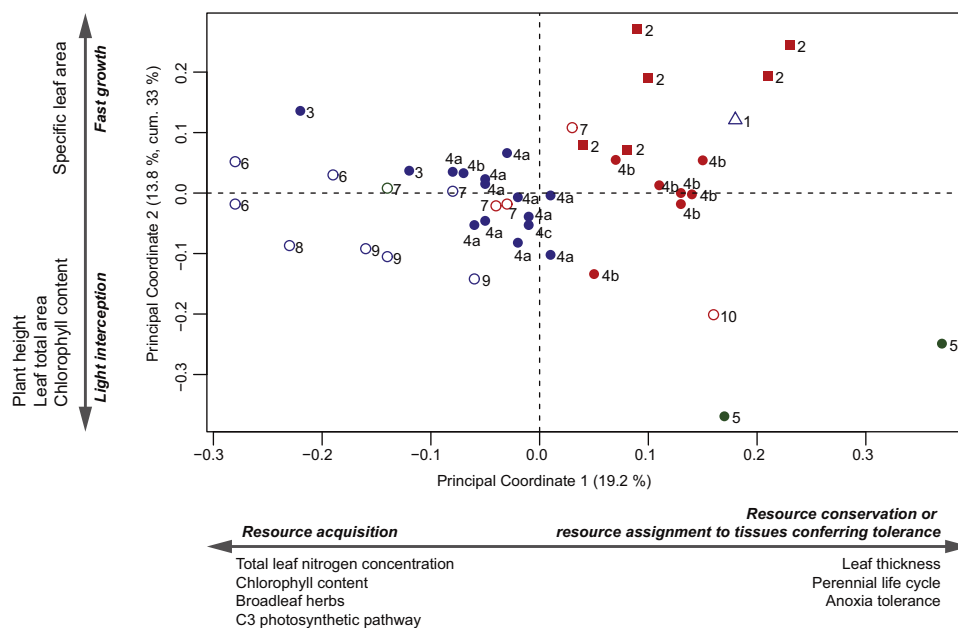


Fig. 3. Ordination of the 44 plant species, according to eight functional traits, along the first two axes of a Principal Coordinate Analysis. The symbol type indicates tolerance to salinity (open triangle), tolerance to anoxia and salinity (filled square), tolerance to anoxia (filled circle), no tolerance to anoxia or salinity (open circle). The symbol colour indicates the morpho-ecological type: broadleaf herbs (red), graminoid herbs (blue), equisetoid herbs (green). Labels next to the symbols are the number of plant functional types. Functional traits significantly correlated to the axes ($p < 0.01$), as well as our interpretation of the main life history trends related to the ordination, are indicated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 6
Models explaining the presence–absence and cover–abundance of the Plant Functional Types (PFTs) occurring in 15 sites or more. Only the best models are shown, provided all the explanatory variables had a significant effect ($p < 0.05$; see text for details on the modelling procedure). For PFT 4b, two models with non-significant differences in the residual deviance and in the Akaike's information criterion are presented. The positive or negative effect of each variable in the model is indicated with (+) or (–), respectively. For soil variables, the mean value in layers 1 and 2 was used, unless “L1” (Layer 1) is indicated. The explanatory power of the presence–absence model was estimated as: $((\text{Null deviance} - \text{residual deviance}) / \text{residual deviance}) \times 100$ (equivalent to R^2 for the cover–abundance model).

PFT	No. sites	Presence–absence model		Cover–abundance model	
		Variables	% explained	Variables	% explained
2	31	Electrical conductivity L1 (+), Percent sand L1 (+), high topographic positions (+), interaction Percent sand L1–high topographic positions (+)	21.5	–	–
3	19	Flood frequency (–), Percent silt (+).	23.2	pH L1 (–)	23.6
4a	64	Flood frequency (+), Sand percent L1 (–), Electrical conductivity L1 (–)	41.2	–	–
4b	46	a) Percent clay (+), pH (–)	18.7	–	–
		b) Electrical conductivity (–), percent silt (–)	17.5		
5	15	Percent silt (+)	11.0	Low topographic positions (+), percent sand (–).	71.6
6	15	High topographic positions (+), landscape unit E (–), percent silt L1 (–)	54.3	–	–
7	25	–	–	–	–
9	15	High topographic positions (+), landscape unit D North (+), pH (–)	45.5	Landscape unit D South (+), pH L1 (–), percent silt L1 (–)	84.0

4. Discussion

Identifying and modelling community-level weighted means (CWM) of trait values and plant functional types (PFTs) based on multiple trait screening is a starting point to understand plant ecology and plant distribution in the Lower Paraná River floodplain wetlands. Our results indicate that the interspecific variability in trait values was higher than the intraspecific variability (Prediction I), consistently with the general trend reported in several studies (e.g., Kazakou et al., 2014). In the context of large floodplains such as the one studied herein, the interspecific variability can be attributed to a variety of plant strategies or to few plant strategies with species being redundant in functional terms. As for the PFTs

identified in this study, ten strategies were distributed along a continuous space defined by eco-physiological constraints that can be described onto the PCoA axes (Fig. 3).

We suggest that the first PCoA axis expressed a trade-off between rapid resource acquisition and resource conservation or resource assignment to tissues conferring anoxia or salinity tolerance (Fig. 3), partially related to the trade-off identified in Diaz et al. (2004). The negative values of this axis were associated with high total leaf nitrogen and leaf chlorophyll content, related to high maximum photosynthetic rate (Wright et al., 2004) and important for rapid resource acquisition. In contrast, the positive values of this axis were associated with perennial species with thick leaves or thick photosynthetic stems. Thick leaves are found in succulent

plants (such as some of the salinity-tolerant species, e.g., *Sesuvium portulacastrum*), in plants with aerenchyma (anoxia-tolerant species) and in long-living plants with tough leaves (associated with resource conservation, low photosynthetic rate and growth rate) and low leaf nitrogen concentration (Pérez-Harguindeguy et al., 2013; Vile et al., 2005).

Regarding the second PCoA axis, we suggest that it expressed a trade-off between fast growth and light interception. The positive values of this axis were associated with high SLA, a trait that is positively related to the potential relative growth rate and to the response to favourable growth conditions (e.g., the period between two floods) and negatively related to leaf life span (Reich et al., 2003; Westoby, 1998; Wright et al., 2004). Although SLA is usually related to high photosynthetic rates (Shipley and Lechowicz, 2000; Wright et al., 2004), a negative relation between SPAD values (estimating chlorophyll content) and SLA was found in this study. This might be explained by the fact that SPAD values are related not only to the transmittance of photosynthetically active radiation through leaves but also to leaf thickness and toughness (Netto et al., 2005). Traits related to the negative values of the second PCoA axis are usually associated with competitiveness. Tall plants, with high total leaf area and high estimated chlorophyll content are expected to effectively intercept and exploit sunlight; and plant height has also been related to plant fecundity and potential life-span (Díaz et al., 2004; Menges and Waller, 1983). In wetland ecosystems, tall plants can also have an advantage for flood resistance because a high proportion of biomass may remain emergent during floods, and plant height is sometimes related to the position in the topographic gradient (Bornette et al., 2008; Keddy, 2010).

The distribution of plants onto the PCoA may also be interpreted in terms of the position of the CSR triangle vertices (Grime, 1977; Menges and Waller, 1983): traits indicating a resource conservation and light interception strategy are related to competitiveness, traits indicating rapid resource acquisition and fast growth are related to ruderalness, and traits conferring anoxia or salinity tolerance to stress tolerance. Following this interpretation, two PFTs grouped species mainly characterized by their stress-tolerance: PFT 1 (species tolerant to salinity) and PFT 2 (species tolerant to salinity and anoxia). Most of the species included in these stress-tolerant PFTs occur in salt marshes (Morandeira and Kandus, 2015). The presence-absence model obtained for PFT 2 was concordant with its stress-tolerant life strategy, since its probability of occurrence was highest in soils with high electrical conductivity.

Resource conservation or competitiveness seems to be a feature of the species grouped in PFTs 5 and 10, which were found in contrasting environments. Bulrushes in PFT 5 (*Schoenoplectus californicus* and *Cyperus giganteus*) are abundant in low topographic positions with fine soils (Table 6). *Schoenoplectus californicus* dominates large lowland areas, covering 17% of the total Lower Paraná River floodplain (Salvia et al., 2009). In contrast, the tussock grass *Coleataenia prionitis* (Nees) Soreng (the only species in PFT 10) is usually related to high topographic positions with coarse soil textures (Marchetti and Aceñolaza, 2011; Morandeira and Kandus, 2015). This suggests that at least two contrasting competitor life strategies exist in the Lower Paraná River marshes, associated with different positions on the topographic gradient and, consequently, with different water permanence and floodability.

Resource acquisition or ruderalness would be the main feature of species grouped in PFTs 3, 6 and 8 (annual species, most with high SLA). Species with an annual life cycle are associated with long dispersal in time and space (Pérez-Harguindeguy et al., 2013), a desirable feature for rapid colonization of growth opportunity sites. In wetlands, Boutin and Keddy (1993) associated ruderalness with an annual life cycle. Similar to that described for competitor PFTs, these groups were associated with different environmental conditions (PFT 3 had a high probability of occurrence in silty soils,

whereas PFT 6 had a low probability) and differed in their tolerance to anoxia. PFT 3 would express a ruderal strategy in sites that are usually disturbed by floods. Although this PFT had a higher probability of occurrence in sites indicated in this work as having low flood frequency, it must be noted that flood frequency was derived from optical remote sensing data (Borro et al., 2014), so that water below high cover vegetation might not be detected (Jakubauskas et al., 2000). In contrast, plant species in PFT 6 occur in high topographic positions and a similar trend is expected for PFT 8 (see Morandeira and Kandus (2015) for *Conyza bonariensis* (L.) Cronquist).

Intermediate life strategies are plausible for the remaining PFTs, ordered near the center of the PCoA plot (Fig. 3). Plant species in PFT 7 were not clearly ordered. Coincidentally, this PFT was the only one not associated with the environmental variables evaluated in the GLM models. Besides, an intermediate ruderalness-competitiveness strategy would be typical of PFT 9, for which we found the cover-abundance model with the highest explanatory power. The effect of landscape units in the models obtained for this PFT (and for PFT 6) may be interpreted in terms of a particular hydrological regime due to geomorphological settings, connectivity to the main rivers and water permanence (Zóffoli et al., 2008). Lastly, PFT 4 seems to be distributed near the center of the PCoA ordination (Fig. 3). This PFT was the most constant and abundant in the area, suggesting that the dominant life strategy in this large floodplain is given by sets of trait values conferring adaptive responses to environmental uncertainty associated with variable flood pulses and disturbances. The large number of plant species included in this PFT, both broadleaf and graminoid herbs, can potentially colonise and establish in different types of sites and respond to disturbances.

The two-stage modelling used, involving presence-absence and cover-abundance separately, led to satisfactory explanations for the distribution of eight out of the nine PFTs assessed. In general terms, the models were able to explain a proportion of the variability in PFT distribution and each PFT was associated with different environmental conditions (Prediction III) (Table 6). This result was consistent with a differential response of the PFT identified to the environment, an emergent process of trait-mediated community assembly (Cornwell and Ackerly, 2009; Keddy, 1992; Martensdóttir and Eriksson, 2014). The variability not accounted for by the GLM models may be related to environmental variables not measured in this study such as burial rate or water energy (Bornette et al., 2008; Corenblit et al., 2007), to biotic factors or to stochasticity in plant colonization, establishment and persistence in the environment (Keddy, 2010). Variables influencing PFT presence-absence were not coincident with those influencing PFT cover-abundance (Table 6), suggesting that the processes of PFT occurrence and abundance may be influenced by different factors, as has been discussed for species distribution (Nielsen et al., 2005). Besides, six out of the eight community-level mean trait values analysed were significantly associated with environmental features (consistently with Prediction II), but the explanatory power of the fitted models was relatively low (Table 5). Thus, in the studied floodplain PFTs are a better approach than CWMs to understand and characterise functional responses to the environment.

Future studies focusing on a small floodplain wetland area or on wetland monitoring should assess the plasticity of plant species and PFTs (as discussed for PFT 4), which may play a crucial role in plant adaptation to wetland states or in disturbance resistance. Distinguishing the potential response to erosion or sedimentation processes associated with flooding or to nutrient excess or limitation (Bornette et al., 2008) may improve the predictive value of our results. Also, the relative importance of stochasticity in PFT presence and abundance should be considered in such a dynamic system. The use of PFTs as indicators seems to be more appropriate

in systems with mosaics of environmental conditions defining plant zonation patterns, such as the floodplain studied herein. Assessments on the distribution of PFTs as environmental indicators can be a valuable tool in line with the need of wetland inventoring and monitoring.

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