




Do taxonomic, phylogenetic and functional plant α - and β -diversity reflect environmental patterns in the Lower Paraná River floodplain?

Natalia Soledad Morandeira & Patricia Kandus


To cite this article: Natalia Soledad Morandeira & Patricia Kandus (2017): Do taxonomic, phylogenetic and functional plant α - and β -diversity reflect environmental patterns in the Lower Paraná River floodplain?, *Plant Ecology & Diversity*, DOI: [10.1080/17550874.2017.1315838](https://doi.org/10.1080/17550874.2017.1315838)

To link to this article: <http://dx.doi.org/10.1080/17550874.2017.1315838>

 View supplementary material 

 Published online: 24 Apr 2017.

 Submit your article to this journal 

 View related articles 

 View Crossmark data 



Do taxonomic, phylogenetic and functional plant α - and β -diversity reflect environmental patterns in the Lower Paraná River floodplain?

Natalia Soledad Morandeira ^{a,b,*} and Patricia Kandus ^a

^aInstituto de Investigación e Ingeniería Ambiental, Universidad Nacional de San Martín. 25 de Mayo y Francia S/N - Campus Miguelete, (1650) General San Martín, Buenos Aires, Argentina; ^bConsejo Nacional de Investigaciones Científicas y Técnicas, Ciudad Autónoma de Buenos Aires, Argentina

(Received 12 September 2016; accepted 2 April 2017)

Background: Floodplain wetlands feature high plant biodiversity, comprising variability in several organisation levels and at different scales.

Aims: In a large river floodplain, we aimed to answer whether taxonomic, phylogenetic and functional α -diversity of herbaceous assemblages responded to hydrogeomorphic features conditioning the local flood pulse and/or to soil features; and to determine the relationship between β -diversity and geographic and environmental distances.

Methods: Taxonomic, phylogenetic and functional α -diversity indices were computed in 82 sites in the Lower Paraná River floodplain. Relationships between α -diversity and environment were explored by generalised linear models. Spatial structure was assessed by semi-variograms. Responses of partitions of β -diversity to geographic or environmental distances were tested through multiple regressions in distance matrices.

Results: Taxonomic and phylogenetic α -diversity showed a similar pattern in relation to environment, especially to hydrogeomorphic features. The regression model fitted to species richness had the highest explanatory power. Regarding functional α -diversity, only the number of plant functional types responded to environmental features. Partitions of β -diversity, particularly the replacement of functional strategies, were better explained by environmental than by geographic distances.

Conclusions: The diversity patterns of plant assemblages in a large river floodplain highlight the importance of heterogeneity conditioning the local effect of flood pulse regimes.

Keywords: autocorrelation; generalised linear models; floodplain wetlands; macrophytes; wetland ecology

Introduction

Floodplains present a shifting mosaic of wetlands strongly conditioned by flood pulses that maintain a highly diverse and dynamic ecosystem (Junk et al. 1989; Ward 1998; Bornette et al. 2008). Herbaceous plants play a key role since they can colonise available patches in the terrestrial or in the aquatic phase of the flood pulse and contribute to primary productivity of these ecosystems (Junk and Piedade 1997). Biomass losses caused by erosional or depositional processes linked to floods tend to be compensated by rapid growth, high reproduction rates and rapid dispersal (Junk et al. 1989; Bornette et al. 1998a). Floods guarantee inflows of propagules, may increase available niches and disrupt competitive dominance interactions, and thus promote diversity (Bornette et al. 1998a, 1998b; dos Santos and Thomaz 2007). Due to the spatial and temporal heterogeneity associated with hydrological dynamics, floodplains present complex gradients of environmental conditions and wetland connectivity, resulting in a high diversity of life histories strategies as well as high taxonomic diversity (α , β and γ) (Amoros and Bornette 2002).

Plant diversity can reflect the environmental conditions of the wetland mosaics, and even more importantly, it is

related to the resistance and/or resilience to changes and disturbances (Loreau et al. 2001; Bornette et al. 2008; Carvalho et al. 2013). In a broad sense, the term diversity refers to the variability in the species composition, the genetic and phylogenetic differences between the species, and variation of the life history traits of the species and individuals (DeLong 1996; Díaz and Cabido 2001; Hamilton 2005). Thus, biodiversity is a complex multifaceted term, addressing entities of different organisational levels (genes, species and traits) as well as several spatial and temporal scales (Meynard et al. 2011; Pavoine and Bonsall 2011). Assessing which are the factors that shape plant diversity patterns can be important to understand how assemblages develop, respond to environmental changes or disturbances and, ultimately, how they affect ecosystem functions (Hamilton 2005; Keddy 2010).

The largest wetlands in South America are associated with the Amazonas, the Orinoco and the Paraná/Paraguay rivers (Junk et al. 2013) comprising wide floodplains with a pulsing water-level. The multifaceted character of diversity (Meynard et al. 2011; Malavasi et al. 2016) has been poorly considered in plant studies in large river floodplains (with few exceptions, e.g., Umaña et al. 2012) and can provide insights into the mechanisms and processes that

*Corresponding author. Email: nmorandeira@unsam.edu.ar

generate diversity patterns at different spatial scales. The indices of taxonomic plant diversity are the most commonly used in ecological studies and summarise the richness and distribution of abundances of the species. Phylogenetic and functional components are less considered and, as well as taxonomic diversity, can be assessed on two spatial scales: α -diversity within sites and β -diversity between sites. Phylogenetic diversity includes the variability in evolutionary histories: the same number of plant species can be close or distant in their phylogeny, with phylogenetic distance being related to different evolutionary adaptations (Webb et al. 2002; Graham and Fine 2008). Functional diversity refers to the variability in trait values and/or in plant functional types. More functional diversity is usually related to complementarity in the use of the resources, more resilience and the ability to respond to a wider range of environmental changes (Diaz and Cabido 2001; Petchey 2004). While the dispersion of propagules is essential for the phylogenetic diversity, niche-based assembly processes structure plant communities through the selection of plant individuals with a given set of functional traits (Fu et al. 2015). A contrasting view to this niche-assembly perspective is provided by Hubbell (2001), who highlights the role of chance and random dispersal in structuring ecological communities.

Since floodplain wetlands of large South American rivers are fully connected at least during severe floods, species pool should be shared at the landscape scale. Thus, we hypothesised that diversity differences would be produced by a local control effect of flood pulses (Marchetti and Aceñolaza 2012) and by environmental conditions that function as a filter “removing all species lacking specified combinations of traits” (assembly rules, *sensu*

Keddy 1992). In this study, we analysed diversity patterns in the Paraná River floodplain, the second South American floodplain in extension after the Amazonas. Our first objective was to answer whether taxonomic, phylogenetic and functional α -diversity responded to hydrogeomorphic features of the floodplain that condition the expression of the flood pulse in the floodplain. Thus, we expected taxonomic, phylogenetic and functional α -diversity to be related to geomorphologic settings and topographic positions (Prediction 1a). We also expected that functional α -diversity varied in response to environmental filtering at a local scale (such as soil features), selecting species with a given set of life history traits (Prediction 1b). Our second objective was to compare the effect of geographic distances and of environmental differences on taxonomic, phylogenetic and functional diversity dissimilarities between plant assemblages. We predicted that environmental variation (rather than geographic distances) could explain both changes in species richness and species replacement (Prediction 2a), especially for functional β -diversity (Prediction 2b).

Materials and methods

Study area and available data

The Paraná River flows from subtropical latitudes in Brazil to temperate latitudes in Argentina (Figure 1(a)), with a drainage area of 2.6×10^6 km², a length of 3900 km and a mean annual discharge in the Del Plata Estuary of $18,000 \text{ m}^3 \text{ s}^{-1}$ (Latrubesse et al. 2005), discharging ca. 200 Tg year⁻¹ of suspended load into the Del Plata Estuary (Iriondo 2004). In its lower section, the river is characterised by an extended floodplain

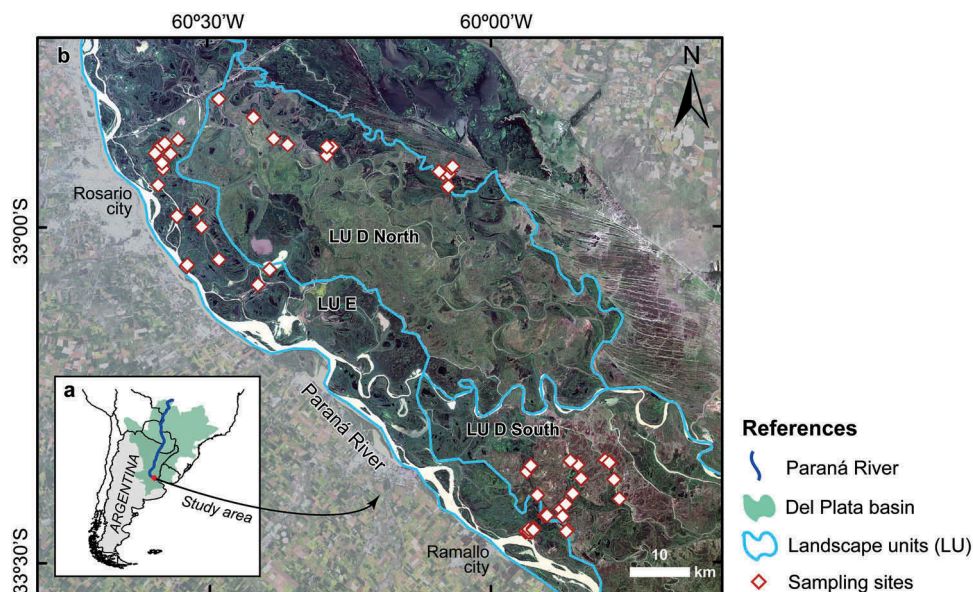


Figure 1. Study area. (a) Location in South America and Del Plata basin. (b) Sampling sites ($n = 82$) in the Lower Paraná River floodplain, where diversity and environmental variables were assessed. Landscape units differing in their geomorphology and hydrology are shown. Background image: Landsat 5-TM scene; 30 March 2011; true colour composite (see electronic paper for the colour version).

(maximum width 40 km) where freshwater wetlands are typically dominated by herbaceous plant communities (marshes, grasslands and meadows) (Morandeira and Kandus 2015), dotted with shallow lakes, streams and rivers (Borro 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; whereas La Niña events lead to dry periods.

A section of ca. 100 km length in the Lower Paraná River floodplain (Figure 1(b)) has been previously sampled for defining vegetation units (Morandeira and Kandus 2015) and for analysing plant traits patterns and identifying plant functional types (Morandeira and Kandus 2016), between December 2010 and March 2012. Weak and moderate La Niña events occurred during these periods. The previous flood event occurred between January and April 2010, during a moderate El Niño event. This section of the floodplain corresponds to three landscape units, with differences in their hydrological regime, such as connectivity with the Paraná River, water drainage, water energy and water permanence (Malvárez 1997; Zoffoli et al. 2008): units D north, D south and E (see Figure 1(b)). Units D north and D south have low connectivity with the main channel of the Paraná River. Flood water enters the floodplain indirectly and slowly drains away. Unit D north has high water permanence, whereas unit D south has intermediate water permanence. Besides, unit E has high connectivity with the Paraná River, and flood water enters the floodplain directly and drains away quickly, so that water permanence is low. For the present study, 82 sites were extracted out of the complete database of the two aforementioned works (Figure 1(b)), including a complete set of species cover-abundance data, trait values, plant functional type (PFT) cover-abundance data, along with environmental variables (soil and hydrogeomorphic features). The main vegetation units of the study area were short salt marshes, tall salt marshes, bulrush marshes, grass marshes, broadleaf marshes, bunchgrasses and grasslands, mixed forb-rich grasslands, and mixed grasslands and scrublands (Morandeira and Kandus 2015).

A total of 123 species of herbaceous plants from 39 families were encountered in the 82 sites (a measure of γ -diversity) (Table S1 in supplementary material). In this study, the environmental and geographic factors conditioning taxonomic, phylogenetic and functional diversity patterns were evaluated at two spatial scales: within sites at a local scale (α -diversity) and between sites at a landscape scale involving the Lower Paraná River floodplain (β -diversity). A scheme of the questions addressed and the analyses conducted is shown in Figure 2.

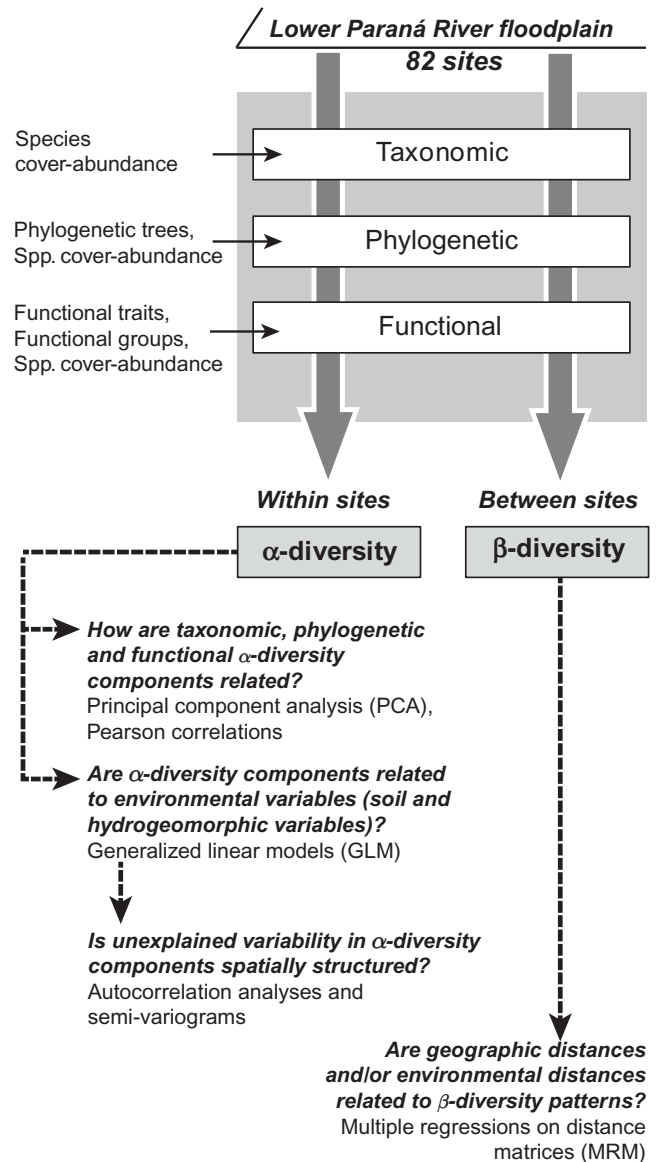


Figure 2. Methods followed analysing α -diversity and β -diversity in the Lower Paraná River floodplain. Three components were assessed: taxonomic, phylogenetic and functional diversity. For each component and diversity descriptor, we state the main questions and the statistics and data analyses used to respond these questions.

Alpha-diversity estimates

Taxonomic α -diversity. After removing highly correlated variables ($|r| > 0.8$ and $P < 0.01$, Pearson's correlation) from the list proposed by Morandeira and Kandus (2015), Simpson's diversity index, Simpson's evenness index, and species richness were retained for this study.

Phylogenetic α -diversity. Out of the 123 species of the 82 sites, only 13 species had not been determined at the species level (with cover-abundance ranging between 0.0003% and 8% per site, that is, always accounting for less than 10% of the total cover of each site). We

constructed a phylogenetic tree by means of the Phylomatic tool version 3 (Webb and Donoghue 2005), using the stored tree R20120829 for plants that showed a better performance than the tree by Zanne et al. (2014). Nomenclature was checked against the Angiosperm Phylogeny Website (Stevens 2012) and corrected to match the nomenclature in the stored tree. Next, the *bladj* function in Phylocom (Webb et al. 2008) was used to assign branch lengths to the phylogenetic tree, following Wikström et al. (2001). The resulting tree was imported into R (R Core Team 2014) and analysed by using functions included in *ape* (Paradis et al. 2004), *phytools* (Revell 2012) and *picante* (Kembel et al. 2010). The phylogenetic tree is included as supplementary material (Figure S1).

Based on the phylogenetic tree, we computed three phylogenetic α -diversity measures that incorporated cover-abundance information. The Faith's phylogenetic diversity index (PD) (Faith 1992) is the sum of the total phylogenetic branch length for taxa occurring in each site. PD tends to increase with the number of taxa, and, for the same species richness, PD is relatively low in communities where taxa are clumped on the phylogeny, thus capturing only a small part of the total phylogenetic diversity present in the species pool. After computing cophenetic distances of the phylogenetic tree (Kembel et al. 2010), we computed the mean pair-wise distance (MPD) between all species in each site and the mean nearest taxon distance (MNTD) (Webb et al. 2002). MPD shows how clumped are the taxa of each community, whereas MNTD summarises the mean distance that separates each species in the community from its closest relative. MPD and MNTD compare the observed phylogenetic relatedness to the pattern expected under a null model in which the distance matrix labels were shuffled across the taxa. The three phylogenetic diversity measures (PD, MPD and MNTD) were not significantly correlated.

Functional α -diversity. Sixteen functional traits were measured or screened for 44 species out of the total of 123 species. These 44 species belong to 95 plant populations that were dominant in the 82 sites (Morandeira and Kandus 2016). Thus, trait measurement was carried out in the dominant plant species of each site (i.e., those with maximum coverage in the site or at least twice the coverage than the accompanying species), as well as species accumulating at least 80% of the green aboveground biomass of the site (following Grime 1998). Eight non-redundant traits were extracted out of the complete data set: life cycle (annual or perennial plants), photosynthetic pathway (C3 or C4), tolerance to anoxia (presence or absence of tolerance structures), tolerance to salinity (presence or absence of salinity tolerance structures), plant height (cm), specific leaf area ($\text{mm}^2 \text{g}^{-1}$), leaf thickness (mm) and leaf total nitrogen concentration (%) (see Morandeira and Kandus (2016) and Pérez-Harguindeguy et al. (2013) for further details on trait screening and for functional implications of these traits).

To compute multi-trait abundance-weighted distance measures, mean species cover-abundances were extracted from the results of Morandeira and Kandus (2015). We computed several functional α -diversity indices: functional richness, functional evenness and functional divergence (Mason et al. 2005; Villéger et al. 2008), functional dispersion index (Laliberté and Legendre 2010) and RaoQ entropy index (Rao 1982). The number of plant functional types (PFTs) was also included as an estimator of functional diversity (one to ten PFTs, derived from the classification of species into PFTs in Morandeira and Kandus 2016). Non-redundant functional indices (Pearson's correlations with $|r| < 0.8$ and $P > 0.01$) were: number of PFTs, functional evenness, functional divergence and RaoQ (correlated to functional dispersion, $r = 0.94$).

Functional evenness (FEve) describes the regularity with which the species cover-abundance is distributed in the multidimensional volume of functional traits and is equal to 1 when the species are regularly distributed in the volume of trait values, with equal cover-abundance (Villéger et al. 2008). Functional divergence (FDiv) represents how the cover-abundance is distributed along the functional space (Mason et al. 2005). For a single-trait analysis, FDiv is low if the most abundant species have trait values near the centre of the trait range and is high if the most abundant species have extreme trait values. For multiple traits, FDiv quantifies the divergence of the species cover-abundance, with regard to their distances to the gravity centre of the functional space (Villéger et al. 2008). Lastly, RaoQ estimates the dispersion of species, weighted by their abundance, in the multidimensional space of functional traits, and expresses the average difference between two randomly selected individuals with replacements (Botta-Dukát 2005).

Functional diversity was computed in R with the library *FD* (Laliberté and Legendre 2010). Note that FEve, FDiv and functional richness can be computed for sites with three or more species ($n = 71$ sites).

Relationship among α -diversity components. The relationship between α -diversity indices was evaluated by means of a Principal Component Analysis and by correlation analyses, with the package *ade4* (Dray and Dufour 2007) in R (R Core Team 2014).

Relating α -diversity and environmental features. Regression models were used to assess whether α -diversity descriptors were associated with environmental variables. For each site, the environmental characterisation included: flood frequency (Borro et al. 2014; related to floodability), location in landscape units D North, D South or E (see description of the study area), topographic position (relatively high or low positions; related to water permanence) and eight soil variables measured in the first two subsurface soil layers up to a maximum depth of 60 cm (total nitrogen, extractable phosphorus, organic carbon, pH, electrical conductivity, per cent clay, per cent silt and per cent sand) (Morandeira and Kandus 2015).

Boundaries between the first and second soil layers were determined according to structure, texture and colour changes. Since soil variables measured in the first and second soil layer showed a high correlation, we avoided redundancy by first addressing the mean value in the two soil layers (weighted by the layer depth) in the regression models. If the mean soil variable value was included in a regression model, we also tested the difference between soil layer values. Interactions and quadratic terms were also evaluated.

For species richness and the number of PFTs (count variables), generalised linear models (GLM) with Poisson distributions were fitted (Zuur et al. 2009). Normality tests were done for the residuals of the fitted models. To discard overdispersion, we checked that the ratios between residual deviance and degrees of freedom were lower than 1.5. For the remaining variables, we first tested a Gaussian linear model, but normality and homoscedasticity assumptions were not satisfied. Thus, a permutation quartile regression was carried out (fitted by the median). Explanatory variables were centred and fitted in univariate models. The three variables explaining the highest portion of the total deviance were used in turns to construct univariate models, and each of these univariate models was used as start up of a multiple regression model. To find the best models, a manual upward step-wise multiple regression procedure was made. A term addition was made if significant reductions (>2) in the Akaike's information criterion (AIC) were observed (Zuur et al. 2009), and if the terms in the model had variance inflation factors <3 (Zuur et al. 2010). Model validity was verified with residuals plots. The explanatory power of the model was estimated with the ratio of the residual to null deviance.

To discard spatial structure in the unexplained variability of the α -diversity descriptor, the residuals of the fitted regression models (or the original variable centred by its mean if no satisfactory model was obtained) were tested by means of semi-variograms. Semi-variograms allow detecting spatial dependence between the diversity indices on both a large scale (spatial trend) and a small scale (spatial autocorrelation) (Cressie 1993). The semi-variance between pairs of sampling sites was plotted against mean separation distances of 2000 m, 1500 m, 1000 m and 500 m (lastly, a lag of 1000 m was chosen). The maximum distance to be evaluated was 50 km (about half the maximum separation distance observed in this study). Isotropic and anisotropic variograms were evaluated, with a minimum of 30 pairs of points and of 10 pairs of points, respectively. In the semi-variograms, a spatial trend is detected as increasing semi-variance with increasing separation distance between pairs of sites. Besides, a variable with an autocorrelation pattern has typically increasing semi-variance up to a separation distance at which the semi-variance reaches a plateau. The portion of semi-variance that is explained by the auto-correlation pattern can be calculated by the ratio between the maximum semi-variance (or *sill*) and the semi-variance at 0 separation

distance (*nugget*, assigned to noise or instrumental errors). Packages *lme4* (Bates et al. 2014) and *Blossom* (Talbert et al. 2016) in R were used for modelling, and S-plus 8.0 was used for performing residuals analyses and fitting semi-variograms.

Beta-diversity estimations

Beta-diversity partitioning. Beta-diversity may be originated by different underlying processes. We partitioned the total β -diversity (β_{total}) into a component of taxa replacement from one site to another (β_{repl}) and a component of taxa loss or gain (richness differences between sites) (β_{rich}) (Cardoso et al. 2014). Cover-abundance data and the Sørensen's dissimilarity index were used for taxonomic, phylogenetic and functional β -diversities. The phylogenetic and functional components of the β -diversity were computed by using trees (a phylogenetic tree and a cluster of species according to their functional traits, respectively). These estimates were made in R with the package *BAT* (Cardoso et al. 2015), by using 1000 permutations and the Sørensen's distance.

Relating beta-diversity to geographic distance and environmental dissimilarity. To assess which factors were associated with changes in diversity and plant communities through the sampling sites, the β -diversity components were related to geographic distances and environmental dissimilarities. Geographic distances were computed by calculating Euclidean distances on the georeferenced position of the sites. Environmental dissimilarity was computed for the sites by using the generalised Gower's distance (Pavoine et al. 2009) on a set of non-redundant environmental variables (flood frequency, landscape units, topographic position and mean total nitrogen, pH, electrical conductivity, per cent clay and per cent silt). The β -diversity dissimilarity matrices (one for each of the diversity components – taxonomic, phylogenetic and functional – and for the partitions of the beta diversity – β_{repl} and β_{rich}) were set as dependent variables, with the geographic distances and the environmental dissimilarities as explanatory matrices. Multiple regressions on distance matrices (MRM) (Lichstein 2007) were computed in R with the package *ecodist* (Goslee and Urban 2007).

Results

Alpha-diversity

The sites showed distinct patterns of α -diversity, with the first two Principal Components explaining 58.2% of the total inertia (Figure 3). Most of the diversity measures were relatively independent ($|r| < 0.6$). However, richness was consistently associated in its three diversity components: taxonomic, phylogenetic and functional ($P < 0.0001$; $r = 0.97$ between species richness and Faith's phylogenetic diversity PD, $r = 0.72$ between species richness and number of PFTs, $r = 0.68$ between number of plant functional types and Faith's

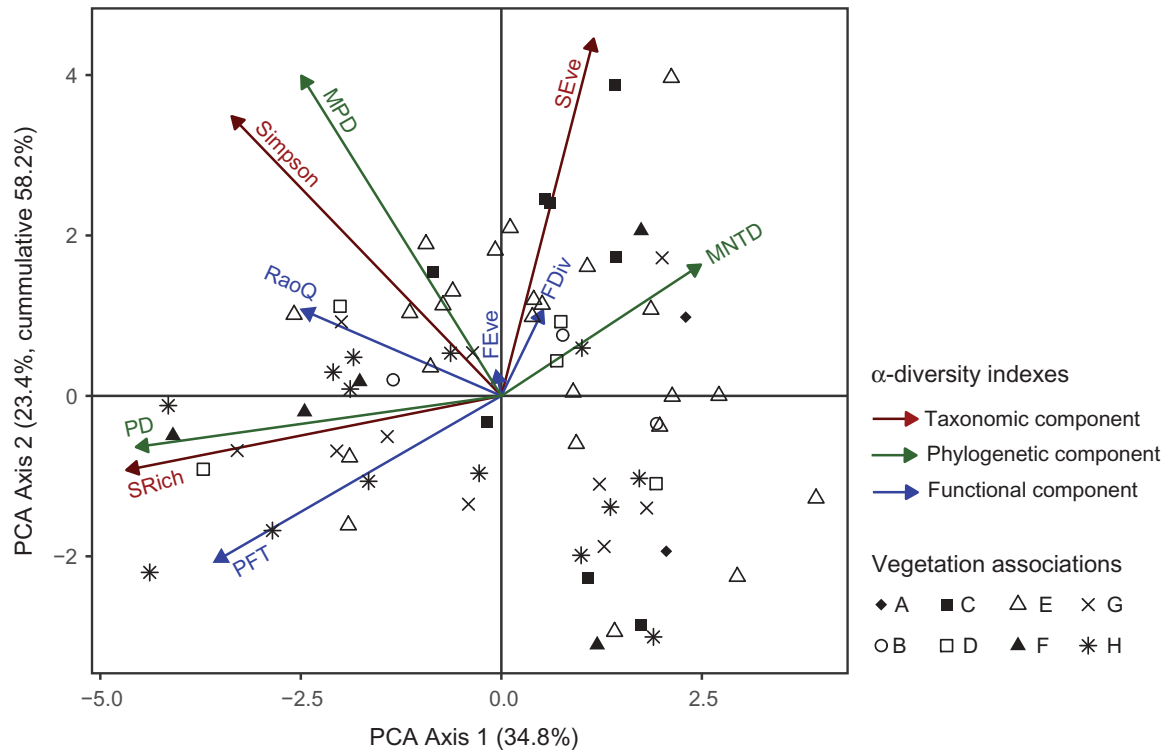


Figure 3. Principal component analysis of the sampling sites (first two axes), ordered according to α -diversity indices. Points represent sites ($n = 71$, for which all the indices could be computed) and arrows diversity indices. Taxonomic component: Simpson's diversity index (Simpson), Simpson's evenness (SEve), species richness (SRich). Phylogenetic component: phylogenetic diversity (PD), mean pairwise distance ("MPD"), mean nearest taxon distance ("MNTD"). Functional component: number of plant functional types (PFT), functional evenness (FEve), functional divergence (FDiv), RaoQ entropy index (RaoQ). The vegetation associations follow the classification by Morandeira and Kandus (2015): A, short salt marshes; B, tall salt marshes; C, bulrush marshes; D, grass marshes; E, broadleaf marshes; F, bunchgrasses and grasslands; G, mixed forb-rich grasslands (In the original study: Mixed wet prairies of grasses and broadleaf herbs); H, mixed grasslands and scrublands.

phylogenetic diversity). Species-rich sites were ordered along Axis 1 negative values and Axis 2 negative values on the PCA (Figure 3). Following the vegetation associations described in Morandeira and Kandus (2015), rich sites were mixed grasslands and scrublands (with more than 20 species and seven plant functional types) dominated by *Hemarthria altissima* and/or *Hymenachne pernambucense* (Poaceae) and including *Baccharis salicifolia* (Asteraceae); Bunchgrasses and grasslands dominated by *Coleataenia prionitis* and *Poa pilcomayensis* (Poaceae) and accompanied by *Eleocharis* aff. *viridans* and other species; or Grass marshes of *Phalaris aquatica* (Poaceae). Some of these sites, such as the Bunchgrasses and grasslands of *Coleataenia prionitis* and *Poa pilcomayensis* that showed a physiognomy with two strata, had also the highest values of the RaoQ entropy index.

Plant assemblages with low species richness, PD and number of PFTs tended to have high MNTD if the taxa at the site were distant in their phylogeny, for example, grasslands dominated by *Cynodon dactylon* (Poaceae) and *Polygonum stypticum* (Polygonaceae) and accompanied by *Sesuvium portulacastrum* (Aizoaceae) or mixed forb-rich grasslands with *Sagittaria montevidensis* (Alismataceae) and *Echinochloa crus-galli* (Poaceae). In addition, sites with high taxonomic evenness and high phylogenetic MNTD were ordered along Axis 1 positive

values and Axis 2 positive values. Two typical communities showing high evenness (maximum scores in the second axis) were bulrush marshes of *Schoenoplectus californicus* (Cyperaceae); and Broadleaf marshes of *Polygonum acuminatum* (Polygonaceae) codominated by *Oplismenopsis najada* (Poaceae); both with a total of four species.

Simpson's taxonomic diversity index and the phylogenetic MPD were positively related ($r = 0.90$, $P < 0.0001$); and sites with positive values of these two indices were ordered along Axis 1 negative values and Axis 2 positive values. Plant assemblages with low diversity, low evenness and low richness were ordered on the opposite side of the plot (Axis 1 positive values and Axis 2 negative values). For example, the broadleaf marshes dominated by *Oplismenopsis najada* or dominated by *Ludwigia* cf. *peruviana* (Onagraceae) and codominated by *Echinochloa polystachya* var. *spectabilis* (Poaceae).

Most of the significant correlations were observed between the taxonomic and phylogenetic components of the diversity. Sites with similar richness and evenness can be ordered according to their RaoQ. For example, a mixed community of bulrushes and grasslands dominated by *Cyperus giganteus* (Cyperaceae), *Eleocharis* aff. *bonariensis* (Cyperaceae) and *Leersia hexandra* (Poaceae) showed a high RaoQ index. With similar taxonomic and phylogenetic

α -diversities, a low RaoQ index was observed in a broadleaf community dominated by *Senecio bonariensis* (Asteraceae) and *Rumex argentinus* (Polygonaceae). The first plant assemblage (bulrushes and grasslands community) showed a wider range of trait values than the second one, leading to higher dispersion of cover-abundances in the multidimensional space of functional traits.

Relationship between α -diversity and the environmental conditions

Environmental variables explained the variability of some of the indices that estimate taxonomic, phylogenetic and functional α -diversity (Table 1). Taxonomic evenness and the mean nearest taxon distance were favoured by low

topographic conditions (with relatively high water permanence), whereas species richness, the number of PFTs and phylogenetic diversity index PD were associated with high topographic positions. Species richness and the phylogenetic diversity index PD were also higher in sites with less flood frequency, especially in landscape unit D North. Also, a model explaining the number of PFTs (alternative to the topographic position) showed that PFTs decreased with increasing mean soil pH.

The regression model with the highest explanatory power was the one fitted for species richness (41% of the total variance was explained by three environmental variables) (Table 1). However, a spatial trend was found in the east–west direction (Figure 4(b)), so that part of the variability was not explained by the environmental variables. In

Table 1. Regression models of taxonomic, phylogenetic and functional α -diversity descriptors, as explained by hydrogeomorphic and soil features in the Lower Paraná River floodplain.

Diversity component	α -diversity index	Model type	Explanatory variables	Explanatory power and P -value	Spatial structure of the residuals
Taxonomic	Simpson's diversity	Median regression	–	–	Isotropic pattern: spatial autocorrelation, up to a range of 4.31 km, explains 20.5% of the total semi-variance.
	Evenness	Median regression	Low topographic positions (+)	14.6% ($P = 0.0001$).	–
	Species richness	GLM, Poisson distribution	High topographic positions (+), flood frequency (–), landscape Unit D_North (+).	41.0% ($P < 0.0001$).	Anisotropic pattern: spatial trend in the East-West direction.
Phylogenetic	Diversity index	Median regression	High topographic positions (+), flood frequency (–), quadratic term of the flood frequency (+), landscape unit D_North (+).	25.7% ($P = 0.0001$).	–
	Mean pair-wise distance	Median regression	–	–	–
	Mean nearest taxon distance	Median regression	Low topographic positions (+)	11.0% ($P = 0.0005$).	–
Functional	Evenness	Median regression	–	–	–
	Divergence	Median regression	–	–	Isotropic pattern: spatial autocorrelation, up to a range of 5.76 km, explains 28.2% of the total semi-variance.
	RaoQ	Median regression	–	–	–
	Number of plant functional types	GLM, Poisson distribution/ Model 1 GLM, Poisson distribution/ Model 2	Mean soil pH (–) High topographic position (+)	13.7% ($P = 0.00753$). 11.7% ($P = 0.00995$).	– Isotropic pattern: spatial trend.

After the manual upward step-wise procedure, the most satisfactory model for each index is shown, based on the explanatory power and on the AIC (AIC is not shown). Two satisfactory models with AIC differences < 2 were found for the number of PFTs. Residuals were tested for their spatial structure and trend or autocorrelation patterns are described (see also Figure 4). For the explanatory variables, positive and negative effects on the diversity descriptors are indicated by (+) and (–), respectively.

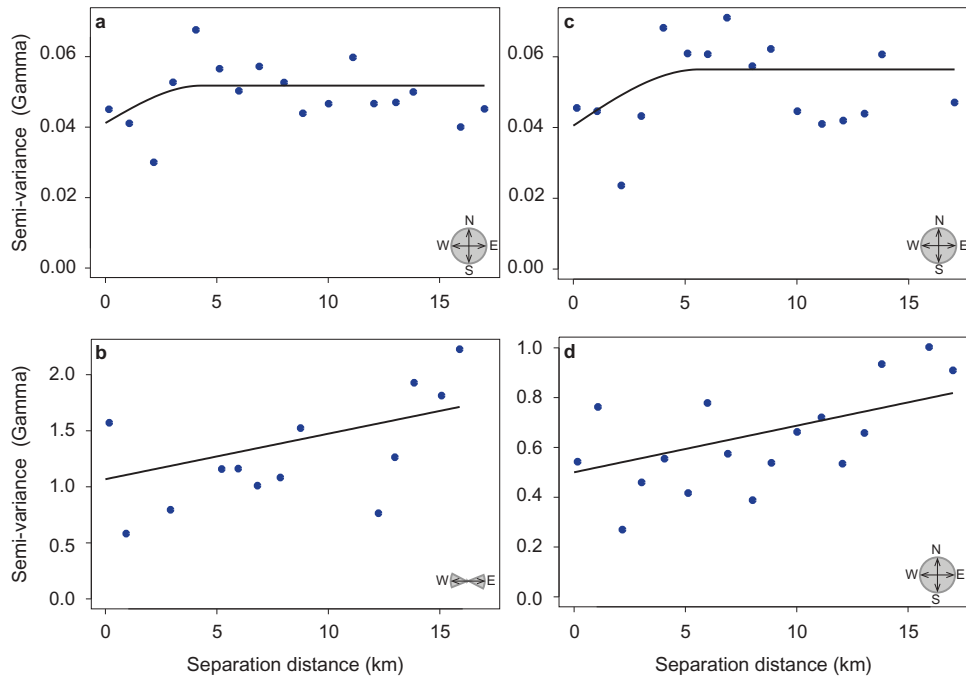


Figure 4. Semi-variograms for the α -diversity descriptors that had spatial structure (trend or autocorrelation patterns) after removing the variance explained by environmental variables. Mean semi-variances for the residuals of pairs of sampling points at a given separation distance are plotted, along with the spherical model fit. (a) Simpson's diversity (centred variable). Isotropic pattern of spatial autocorrelation. (b) Species richness (residuals of the fitted model, see Table 1). Anisotropic pattern of spatial trend in the East-West direction. (c) Functional divergence (centred variable). Isotropic pattern of spatial autocorrelation. (d) Number of plant functional types (residuals of the fitted model 2, see Table 1). Isotropic pattern of spatial trend.

addition, an autocorrelation pattern was found for Simpson's diversity and FDiv up to distances of 4.3 and 5.8 km, respectively (Figure 4(a) and (c), see the separation distances at which the semi-variance reaches a plateau). The autocorrelation patterns for Simpson's diversity and FDiv explained 20.5% and 28.6% of the semi-variance between pairs of sampling sites, respectively. In the case of the number of PFTs, the residuals of the model that explained the decrease in PFT with increasing soil alkalinity (Model 1) showed no spatial structure, whereas the residuals of the model that highlighted that more PFT were found in high topographic positions (Model 2) had an isotropic pattern of spatial trend (Figure 4(d)).

Beta-diversity partitioning and explanatory matrices

The mean taxonomic total β -diversity was higher than the phylogenetic and the functional total β -diversity (Figure 5). For the three diversity components, the partition β_{repl} is in average higher than β_{rich} , and this difference is particularly noticeable for the taxonomic component (Figure 5). Regarding pair of sites, all of them had higher taxonomic than phylogenetic β -diversity (Figure 6(a)), and 95.8% out of the pair of sites had higher taxonomic than functional β -diversity (Figure 6(b)). The maximum phylogenetic and taxonomic β -diversity (and high functional differences) were found between two sites with equal number of PFTs (p1 in Figure 6): a bulrush marsh of *Schoenoplectus californicus* (Cyperaceae) with floating

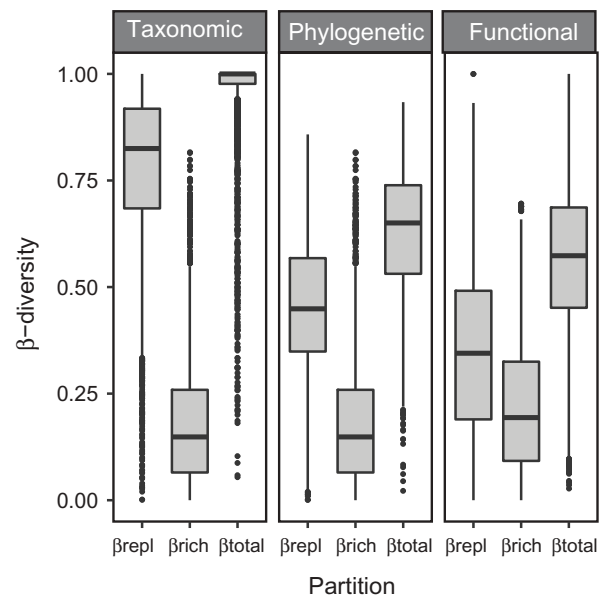


Figure 5. Taxonomic, phylogenetic and functional β -diversity of sites in the Lower Paraná River floodplain. For each component, total-beta diversity (β_{total}) and its two partitions are shown: taxa replacement from one site to another (β_{repl}) richness differences between sites (β_{rich}).

Azolla filiculoides (Azollaceae) and submerged *Ceratophyllum demersum* (Ceratophyllaceae) (seven species, high PD); and a short saltmarsh with very sparse vegetation (low coverage of *Evolvulus sericeus*

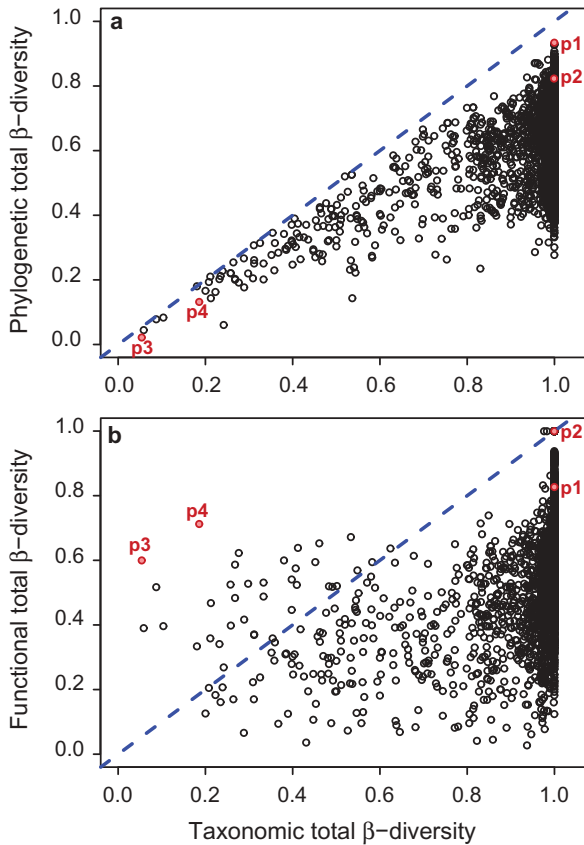


Figure 6. Beta-diversity between pairs of sites for the taxonomic, phylogenetic and functional components. (a) Phylogenetic β_{total} vs. taxonomic β_{total} . (b) Functional β_{total} vs. taxonomic β_{total} . The dashed line shows a 1:1 relation; note that most of the pairs of sites were below this line. Four pair of sites (p1, p2, p3 and p4) are pointed out and used as examples in the text.

(Convolvulaceae) accompanied by *Paspalum vaginatum* (Poaceae) and *Sarcocornia perennis* (Chenopodiaceae)) (four species, low PD). The sites with maximum functional and taxonomic β -diversity and high phylogenetic β -diversity (p2 in Figure 6) were a short salt marsh

dominated by *Paspalum vaginatum* (two species, one PFT, low RaoQ and low PD); and a broadleaf marsh dominated by *Ludwigia cf. peruviana* (Onagraceae) and accompanied by *Myriophyllum aquaticum* (Haloragaceae), *Alternanthera philoxeroides* (Amaranthaceae) and *Enydra anagallis* (Asteraceae) (nine species, two dominant PFTs and relatively high RaoQ and PD).

Between the 47 pairs of sites that showed higher functional than taxonomic β -diversity, we can mention two grassland sites with a high cover of *Cynodon dactylon* (Poaceae) and equal Simpson's diversity, which differ in their accompanying species: one had six species belonging to five different PFTs, whereas the other had three species belonging to only one PFTs (p3 in Figure 6). Another example of high functional but low taxonomic β -diversity was found for two tall grasslands dominated by *Hymenachne perambucense* (Poaceae), both with eight species (p4 in Figure 6). Although their taxonomic and phylogenetic diversity is similar, one of the sites had three PFTs and low RaoQ entropy, while the other had five PFTs and high RaoQ entropy.

The fitted models for explaining the variability in the β -diversity were summarised in Table 2. Geographic distances explained a portion of the variability in taxonomic total β -diversity. Besides, the dissimilarities between the sites due to their environmental conditions could explain several components and partitions of the β -diversity (Table 2): taxonomic β_{total} , phylogenetic β_{rich} and β_{total} and functional β_{repl} and β_{total} .

Discussion

In relation to within-site diversity patterns in the Lower Paraná River floodplain, we found significant correlations mostly between the taxonomic and phylogenetic components of the α -diversity. Although patterns of phylogenetic and functional diversity can be correlated if functional traits are evolutionary conserved (Webb et al. 2002), our results have shown a weak relationship between these two components of α -diversity, except for the number of PFTs.

Table 2. Multiple regression on distance matrices (MRM) models for taxonomic, phylogenetic and functional β -diversity and their partitions in the Lower Paraná River floodplain.

Diversity component	β -diversity index	Univariate models		Bivariate model
		Geographic distances	Environmental distances	Geographic + environmental distances
Taxonomic	β_{repl}	0.7746	0.2827	–
	β_{rich}	0.1654	0.0544	–
	β_{total}	0.0017 (R^2 0.7%)	0.0001 (R^2 3.6%)	0.0001 (R^2 3.8%)
Phylogenetic	β_{repl}	0.3170	0.2733	–
	β_{rich}	0.1606	0.0485 (R^2 0.9%)	–
	β_{total}	0.4838	0.0004 (R^2 2.5%)	–
Functional	β_{repl}	0.4810	0.0013 (R^2 4.9%)	–
	β_{rich}	0.4293	0.0667	–
	β_{total}	0.8853	0.0001 (R^2 9.0%)	–

Geographic distances and environmental distances were set as explanatory variables of β -diversity. P values of the fitted models are shown; for P values <0.05 (bold letter), R^2 is informed. The results of the bivariate model are shown when a significant model was obtained, with higher explanatory power than the explanatory power of the univariate models.

Novel information about within-site diversity patterns was added by considering the functional component of the α -diversity, for example, by the RaoQ index that shows high values for sites that with intermediate species richness (Figure 3). Thus, we suggest addressing functional diversity for studying plant assemblages in large river floodplains. In line with our results, recent studies have pointed out that phylogenetic diversity is a poor surrogate for functional diversity (Pavoine et al. 2013; Malavasi et al. 2016) and that these two components may respond differently to environmental heterogeneity (Meynard et al. 2011). For a given level of taxonomic diversity, environmental filtering tends to decrease functional α -diversity (Arnan et al. 2017), what can also promote functional β -diversity between patches with different environmental conditions. Our results were consistent with the expected according to assembly rules based on life history traits of the species.

The variation of life strategies and of the mean trait values per community in relation to environmental features – which has been described for the Lower Paraná River floodplain by Morandeira and Kandus (2016) – seems to be reflected in diversity patterns. Some of the indices of α -diversity responded to geomorphology (landscapes with different origin, fluvial or marine-fluvial history), topography (high and low positions in each geomorphologic setting, i.e., variability at a geographic scale of more detail than landscape units) and flood frequency. In the first place, this emphasises the need to include more than one index for quantifying a complex concept such as diversity. Secondly, results were consistent with our Prediction 1a and with the fact that the more important factor conditioning plant diversity in a large floodplain wetland is the local control effect of the flood pulse (Marchetti and Aceñolaza 2012): both topography and geomorphologic settings are related to variations in overflow levels, water permanence, water energy and flux types, and this effect was reflected by the variation of several α -diversity indices (Table 1), consistent with patterns described in other floodplains or herbaceous wetlands (Franceschi and Prado 1989; Lenssen et al. 1999; Steiger and Gurnell 2003; Zelnik and Čarni 2008).

Taxonomic and phylogenetic α -diversity patterns were similar and related to hydrogeomorphic features. This suggests that species richness and species evenness can be proxies for phylogenetic diversity (PD) and mean nearest taxon distance (MNPD), respectively, in the studied floodplain and at a local scale. However, environmental variables were better predictors of the variation in taxonomic α -diversity than of variation in phylogenetic α -diversity. The spatial structure observed for Simpson's richness may be related to the local dispersion of the species, with the local flooding regime or sedimentation patterns. The scale at which this taxonomic diversity index showed an autocorrelation pattern (up to 4.3 km, Figure 4 (a)) is in the order of the distance between the main streams and rivers that act as corridors in the landscape (see Figure 1 and the distance between lotic waterbodies

that flow from north–west to south–east direction, ca. parallel to the direction of the Paraná River): the spatial arrangement of patches and corridors in a heterogeneous landscape is expected to affect plant diversity patterns (Malavasi et al. 2016). The spatial structure of Simpson's diversity can be related to the mass effect postulated by Shmida and Wilson (1985): high biodiversity may not be explained by the environmental conditions of the site itself, but by the high biodiversity of nearby plant assemblages.

Spatial structure was also observed for the functional divergence in trait values, possibly expressing that close plant assemblages share their resilience ability or their level of complementarity in resource use (Díaz and Cabido 2001; Petchey and Gaston 2006). An autocorrelation pattern in diversity indices can be observed because environmental gradients are themselves spatially structured and/or due to dispersal (Jones et al. 2008; Meynard et al. 2011; Arnan et al. 2015). Besides, the east–west spatial trend of the species richness may denote that part of the variability was not explained by the variables included in this study. Some of the variables not evaluated that can influence diversity patterns are sedimentation rate (Bornette et al. 2008) and anthropic impacts, mainly due to cattle grazing and its associated effects (herbivory, trampling causing soil compaction and pocking, cattle excretes) (Baigún et al. 2008). In the particular case of species richness, the closer to the Paraná River was the given sampling site (with cattle pressure being more intense, authors' pers. obs.), the higher tended to be the residual of the fitted model.

In this floodplain, functional α -diversity captured different information than phylogenetic or taxonomic diversity (cf. Pavoine et al. 2013; Malavasi et al. 2016). The fact that the patterns of phylogenetic diversity did not follow those of functional diversity suggests that the set of traits used in this study were not strongly phylogenetically conserved (Kraft et al. 2007), which is expectable for traits such as tolerance to anoxia or salinity that can be convergent in different lineages. Prediction 1b was partially supported by our data: a soil variable (mean pH) was better predictor than topographic positions for the number of PFTs. Morandeira and Kandus (2016) have shown that the presence–absence and the cover–abundance of eight PFTs could be explained by both soil and hydrogeomorphic features, with up to 84% of the variance explained by a single model. Thus, the identity and cover–abundance of the PFTs (and not the number of PFTs) seem to be the most relevant variables to understand plant functional responses to the environment. The other functional diversity indices did not show a response to environmental features, contradicting Prediction 1b.

Our approach addressing β -diversity patterns imply the study of lateral variations within the floodplain (*sensu* Amoros and Bornette 2002), at a section of the river of ca. 100 km length. Longitudinal variations of aquatic plant assemblages and their diversity patterns along the Paraná River have been addressed by Neiff et al. (2014). Involving

a longer time period than the assessed herein would allow including several flood pulses and cycles of vegetation community development, so that a temporal β -diversity component could be incorporated in the analysis. Also, some increase in α -diversity may be observed due to the input plant species from more than one flood. According to our results, differences in species composition do not necessarily led to differences in functional or phylogenetic composition (higher taxonomic than phylogenetic or functional β -diversity), suggesting that some redundancy is present in the pools species of the studied floodplain. Although two assemblages may differ little in their taxonomic and phylogenetic diversity, high functional β -diversity highlights that the assemblages differ in their ability to respond to disturbance or to environmental changes (Díaz and Cabido 2001). For example, one of the sites of pair p3 (Figure 6) was dominated by only one PFT with a limited ability to survive flood, whereas the second site of pair p3 presented five PFTs, and those with very low abundance-cover had history traits conferring anoxia tolerance and probably success in flooded environments (Morandeira and Kandus 2016).

In relation to the factors conditioning β -diversity patterns in the floodplain, our results suggest that environmental variability (rather than geographic distances) led to differences in the phylogenetic richness (partially supporting Prediction 2a) and to replacements in the functional strategies and life stories between sites. The fitted models had a relatively low explanatory power (<10%), being the best models those fitted for the functional β -diversity (consistently with Prediction 2b). Due to the low explanatory power of the models, we postulate that other factors may be related to β -diversity – including stochastic variability, interspecific competition and additional sources of environmental dissimilarities such as sedimentation rates or cattle pressure. The functional pattern dominated by β_{repl} in response to environmental features is consistent with habitats that require different traits (Cardoso et al. 2014), that is, environmental filtering selects individuals of species with a given set of trait values, but not necessarily affects plant species richness.

Conclusion

The diversity patterns addressed in a large floodplain wetland highlight the importance of environmental heterogeneity, especially in what refers to hydrogeomorphic patterns driving a local control effect of the flood pulse. Thus, conserving moisture and flooding gradients and a diversity of patches and landscape elements favour macrophyte biodiversity at the scale of the floodplain. Owing to the complex nature of large floodplain wetlands, biological indicators of environmental features may combine dominant species, plant functional types and a multifaceted approach of α - and β -diversity. Also, temporal β -diversity patterns within the floodplain can be incorporated in order to address vegetation changes due to phenology, flood pulses, different sedimentation or erosion rates and the impact of anthropic disturbances.

Acknowledgements

Most of the field work was conducted at farms owned by J. Nazar and A. Matera. L. Bello and his family were very helpful and kind. M. Borro, F. Schivo, C. Hernando, F. Baronetti, S. Varela and M. Schoo helped with the field work. This work was supported by Agencia Nacional de Promoción Científica y Tecnológica (Argentina) [PICT 1849/06, PICTO-CIN-2010 022, PICT Bicentenario 2227] and by Neotropical Grassland Conservancy [Memorial Grant ‘Derald G. Langham’ to N. S. M.].

Funding

This work was supported by Agencia Nacional de Promoción Científica y Tecnológica (Argentina) [PICT 1849/06, PICTO-CIN-2010 022, PICT Bicentenario 2227] and by Neotropical Grassland Conservancy [Memorial Grant ‘Derald G. Langham’ to N. S. M.].

Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental data for this article can be accessed [here](#).

ORCID

Natalia Soledad Morandeira  <http://orcid.org/0000-0003-3674-2981>

Patricia Kandus  <http://orcid.org/0000-0001-6660-2977>

Notes on contributors

Natalia S. Morandeira is an ecologist with an interest in wetland ecosystems, plant ecology, landscape ecology and remote sensing and geographic information system applications.

Patricia Kandus is a professor whose work is focused on wetland inventory, plant ecology and remote sensing applications.

References

- Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* 47:761–776.
- Arnan X, Arnan X, Cerdá X, Cerdá X, Retana J. 2015. Partitioning the impact of environment and spatial structure on alpha and beta components of taxonomic, functional, and phylogenetic diversity in European ants. *PeerJ* 3:e1241.
- Arnan X, Cerdá X, Retana J. 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. *Ecography* 40:448–457.
- Baigún CRMM, Puig A, Minotti PG, Kandus P, Quintana RD, Vicari RL, Bó RF, Oldani NO, Nestler JA. 2008. Resource use in the Parana River Delta (Argentina): moving away from an ecohydrological approach? *Ecology & Hydrobiology* 8:245–262.
- Bates D, Maechler M, Bolker BM, Walker S. 2014. Fitting linear mixed-effects models using lme4 [Internet]. [cited 2016 Sep 11] Available from: <http://arxiv.org/abs/1406.5823>
- Bornette G, Amoros C, Lamouroux N. 1998a. Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology* 39:267–283.

- Bornette G, Amoros C, Piegay H, Tachet J, Hein T. 1998b. Ecological complexity of wetlands within a river landscape. *Biological Conservation* 85:35–45.
- Bornette G, Tabacchi E, Hupp C, Puijalón S, Rostan JC. 2008. A model of plant strategies in fluvial hydrosystems. *Freshwater Biology* 53:1692–1705.
- Borro MM, Morandeira NS, Kandus P, Salvia MM, Minotti PG, Perna P. 2014. Mapping shallow lakes in a large South American floodplain: a frequency approach on multitemporal Landsat TM/ETM data. *Journal of Hydrology* 512:39–52.
- Botta-Dukát Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16:533–540.
- Cardoso P, Rigal F, Carvalho JC. 2015. BAT – biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution* 6:232–236.
- Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PAV, Podani J, Schmera D. 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography* 41:749–761.
- Carignan R, Neiff JJ. 1992. Nutrient dynamics in the floodplain ponds of the Paraná River dominated by the water hyacinth *Eichhornia crassipes*. *Biogeochemistry* 17:85–121.
- Carvalho P, Thomaz SM, Kobayashi JT, Bini LM. 2013. Species richness increases the resilience of wetland plant communities in a tropical floodplain. *Austral Ecology* 38:592–598.
- Cressie NAC. 1993. *Statistics for spatial data*. New York (NY): Wiley.
- DeLong Jr DC. 1996. Defining biodiversity. *Wildlife Society Bulletin* 24:738–749.
- Diaz S, Cabido M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16:646–655.
- Dos Santos AM, Thomaz SM. 2007. Aquatic macrophytes diversity in lagoons of a tropical floodplain: the role of connectivity and water level. *Austral Ecology* 32:177–190.
- Dray S, Dufour A-B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22:1–20.
- Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61:1–10.
- Franceschi EA, Prado DE. 1989. Distribution of herbaceous communities of the river Paraná valley along an elevation gradient after a catastrophic flood. *Coenoses* 4:47–53.
- Fu H, Zhong J, Yuan G, Guo C, Ding H, Feng Q, Fu Q. 2015. A functional-trait approach reveals community diversity and assembly processes responses to flood disturbance in a subtropical wetland. *Ecological Research* 30:57–66.
- Goslee SC, Urban DL. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22:1–19.
- Graham CH, Fine PVA. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters* 11:1265–1277.
- Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:902–910.
- Hamilton AJ. 2005. Species diversity or biodiversity? *Journal of Environmental Management* 75:89–92.
- Hubbell SP. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton, New Jersey: Princeton University Press.
- Iriondo MH. 2004. The littoral complex at the Paraná mouth. *Quaternary International* 114:143–154.
- Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB, Olivas PC. 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. *Oecologia* 155:593–604.
- Junk WJ, An S, Finlayson CM, Gopal B, Květ J, Mitchell SA, Mitsch WJ, Robarts RD. 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquatic Sciences* 75:151–167.
- Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. Dodge DP, editor. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106:110–127.
- Junk WJ, Piedade MTF. 1997. Plant life in the floodplain with special reference to herbaceous plants. In: Junk WJ, editor. *The central Amazon floodplain: ecology of a pulsing system*. New York (NY): Springer-Verlag Berlin Heidelberg; p. 147–185.
- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3:157–164.
- Keddy PA. 2010. *Wetland ecology: principles and conservation*. 2nd ed. Cambridge (UK): Cambridge University Press.
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kraft NJB, Cornwell WK, Webb CO, Ackerly DD. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist* 170:271–283.
- Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.
- Latrubesse EM, Stevaux JC, Sinha R. 2005. Tropical rivers. *Geomorphology* 70:187–206.
- 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.
- Lichstein JW. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology* 188:117–131.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- Malavasi M, Conti L, Carboni M, Cutini M, Acosta ATR. 2016. Multifaceted analysis of patch-level plant diversity in response to landscape spatial pattern and history on Mediterranean dunes. *Ecosystems* 19:850–864.
- Malvarez AI. 1997. *Las comunidades vegetales del Delta del Río Paraná. Su relación con factores ambientales y patrones de paisaje*. Ph.D Thesis in Biological Sciences. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.
- Marchetti ZY, Aceñolaza PG. 2012. Pulse regime and vegetation communities in fluvial systems: the case of the Parana River floodplain, Argentina. *Flora – Morphology, Distribution, Functional Ecology of Plants* 207:795–804.
- Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112–118.
- Meynard CN, Devictor V, Mouillot D, Thuiller W, Jiguet F, Mouquet N. 2011. Beyond taxonomic diversity patterns: how do α , β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecology and Biogeography* 20:893–903.
- Morandeira NS, Kandus P. 2015. Multi-scale analysis of environmental constraints on macrophyte distribution, floristic groups and plant diversity in the Lower Paraná River floodplain. *Aquatic Botany* 123:13–25.
- Morandeira NS, Kandus P. 2016. Plant functional types and trait values in the Paraná River floodplain: modelling their association with environmental features. *Flora – Morphology, Distribution, Functional Ecology of Plants* 220:63–73.

- Neiff JJ, Casco SL, Mari EKA, Di Rienzo JA, Poi ASG. 2014. Do aquatic plant assemblages in the Paraná River change along the river's length? *Aquatic Botany* 114:50–57.
- Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pavoine S, Bonsall MB. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* 86:792–812.
- Pavoine S, Gasc A, Bonsall MB, Mason NWH. 2013. Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetation Science* 24:781–793.
- Pavoine S, Vallet J, Dufour A-B, Gachet S, Daniel H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118:391–402.
- Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61:167–234.
- Petchey OL. 2004. On the statistical significance of functional diversity effects. *Functional Ecology* 18:297–303.
- Petchey OL, Gaston KJ. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741–758.
- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [Internet]. [cited 2016 Sep 11] Available from: <http://www.r-project.org/>
- Rao CR. 1982. Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* 21:24–43.
- Revell LJ. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3:217–223.
- Shmida A, Wilson M. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1–20.
- Steiger J, Gurnell AM. 2003. Spatial hydrogeomorphological influences on sediment and nutrient deposition in riparian zones: observations from the Garonne River, France. *Geomorphology* 49:1–23.
- Stevens PF. 2012. Angiosperm phylogeny website. Version 13 [Internet]. [cited 2016 Sep 11] Available from: <http://www.mobot.org/MOBOT/research/APweb/>
- Talbert M, Richards J, Mielke P, Cade B. 2016. Blossom: statistical comparisons with distance-function based permutation tests. R package version 1.4 [Internet]. [cited 2016 Sep 11] Available from: <http://cran.r-project.org/package=Blossom>
- Umaña MN, Norden N, Cano Á, Stevenson PR. 2012. Determinants of plant community assembly in a mosaic of landscape units in Central Amazonia: ecological and phylogenetic perspectives. *PLoS One* 7:1–9.
- Villéger S, Mason N, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.
- Ward JV. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83:269–278.
- Webb CO, Ackerly DD, Kembel SW. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24:2098–2100.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.
- Webb CO, Donoghue MJ. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Resources* 5:181–183.
- Wikström N, Savolainen V, Chase MW. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences* 268:2211–2220.
- Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlenn DJ, O'Meara BC, Moles AT, Reich PB, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506:89–92.
- Zelnik I, Čarni A. 2008. Distribution of plant communities, ecological strategy types and diversity along a moisture gradient. *Community Ecology* 9:1–9.
- Zoffoli M, 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 Parana Delta Region. *Landscape Ecology* 23:833–848.
- Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York (NY): Springer.