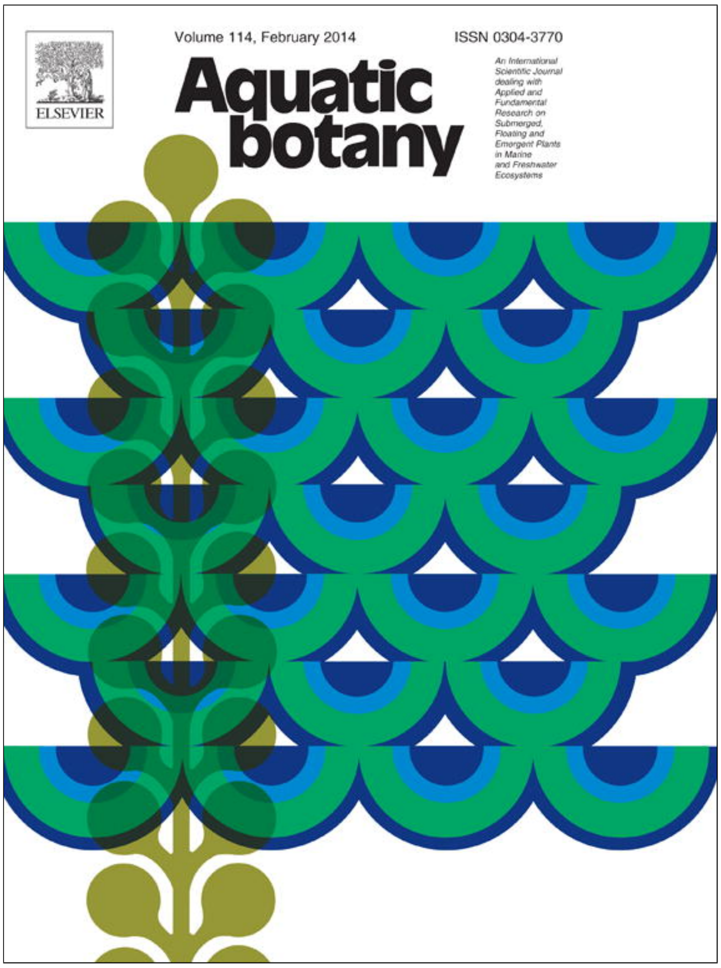
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Do aquatic plant assemblages in the Paraná River change along the river's length?

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ABSTRACT

We studied the distribution pattern of aquatic plants along the Paraná River from its confluence with the Iguazú River to the Delta (2366 km). At three representative locations, Upper Paraná, Lower Paraná, with Paraná-Paraguay confluence and Paraná-Santa Fe section and, Delta, data were collected during extreme low waters (limnophase) and high waters (potamophase). Species richness and abundance at 325 sites were analyzed for both periods using β diversity and the Indicator Species Analysis (ISA). To evaluate the importance of species-hydrological-phase combinations, linear discriminant analysis was applied. We compared hydrological time series at the same sites using PULSE software. Although there are differences in species richness along the river, we found no clear longitudinal pattern in the distribution and diversity of vegetation along the course of the river. From a total of 62 species for the entire study area, the ISA separated 17 indicator species. There are indicator species in each section and hydrological phase, although 29% of the total was recorded in all river sections. Estimates of β diversity (spatial turnover of species) among the river sections was higher during low water ($\beta = 16\%$) than during high water ($\beta = 11\%$) and varied between 12 and 58% among plots depending on the hydrological phase. Results of this study will contribute to incorporate spatial variation into pulse regime theories of large floodplain rivers.

1. Introduction

The distribution, diversity and abundance of plant assemblages in large rivers generally undergo changes from the headwaters to the mouth. These changes may be gradual or abrupt depending on the nature of the changes to the river environment: geology/geomorphology, hydrology, water quality, land use change and engineering interventions (Khedr and El-Dermash, 1997).

Using published data for Paraná River it is appears to that aquatic macrophyte (gamma) diversity in the upper section (62 species, Thomaz et al., 2004) is lower than that observed for the lower section (114 species, Neiff, 1986). These results could be an indication that a downstream longitudinal diversity gradient exits in the Paraná. Depending on author, site and sampling intensity, the species richness of herbaceous vascular aquatic plants can range from 30 to 74 species (Morello, 1949; Burkart, 1957; Souza et al., 1997; Malvárez, 1997; Bini et al., 2001; Casco, 2003; Campos, 2004; Varandas Martins et al., 2013).

However, at each river section pulse regime encompass a wide hydrological variability from short to long duration floods (Neiff, 1990a,b, 2001). The hydrological dynamic and the different degree of connectivity drive the productivity of organisms both on the floodplain and the river channel.

The objective of this study was to identify changes in the spatial (longitudinal-lateral) and seasonal (low water and high water, called limnophase and potamophase, respectively) variability in aquatic plant assemblages along the Argentine section the Paraná River.

We tested the hypotheses that (1) the aquatic macrophyte diversity increased along the river from the upper section to the low section, (2) the turnover rate of species richness in low waters is higher than in high waters, and (3) there are indicator species in each section and hydrological phase.

Results of this study will contribute to incorporate of spatial variation into pulse regime theories of large floodplain rivers.

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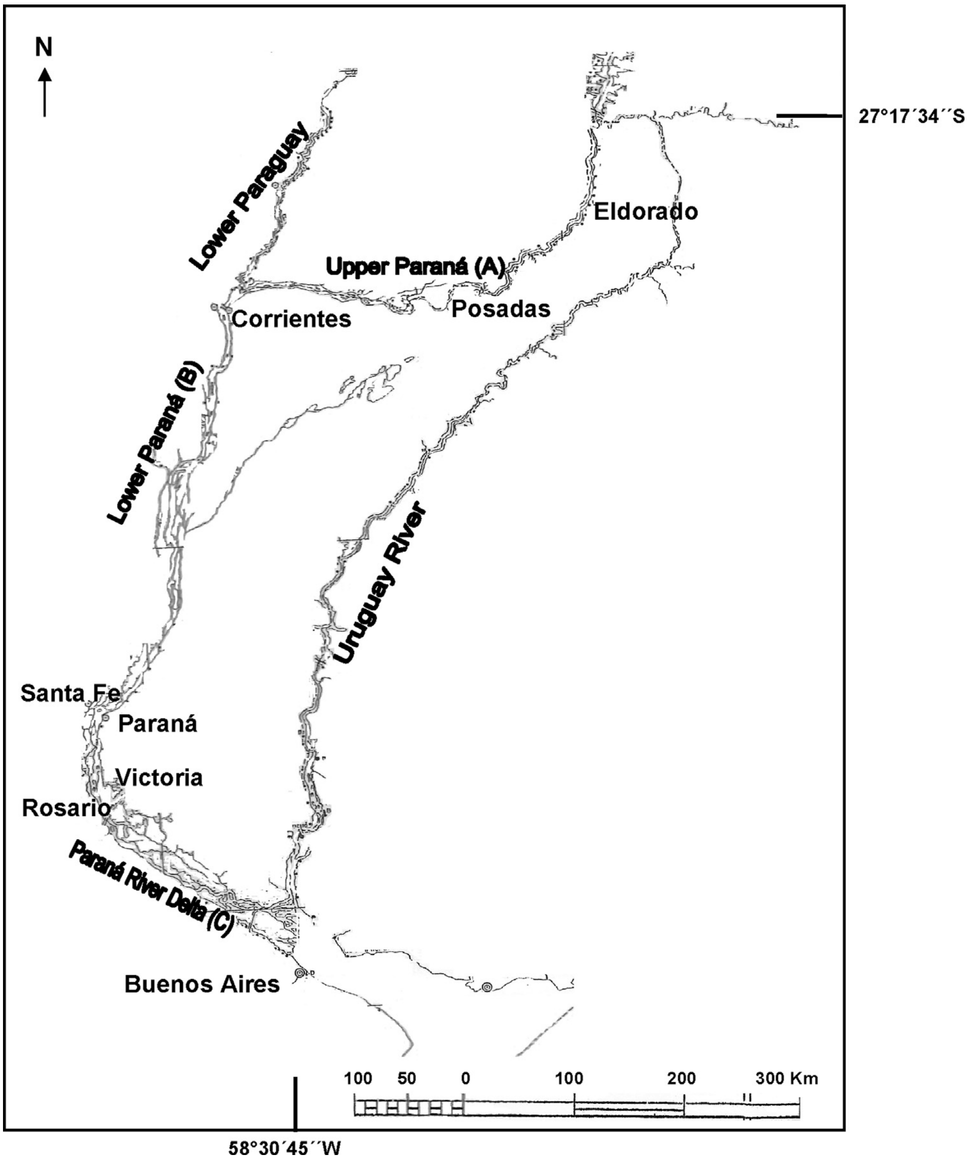

Fig. 1. Map of the study area with the stretches of Paraná River (Upper, Lower and Delta Paraná River).

2. Methods

2.1. Study area

The Paraná River is the second longest river in South America (3900 km long), and the largest river of the Río de la Plata basin with 3.1×10^6 km^2. The study area covers the Argentine stretch of the Paraná River from its confluence with the Iguazú River (25°35′31″S; 54°35′32″W) to the Río de la Plata (34°17′37″S; 58°19′34″W), a distance of 2366 km (Fig. 1, Table A.1). The geology, geomorphology, hydrology, water quality, sediment, regional vegetation and other features of the basin are described in previous contributions (Bonetto, 1985; Bonetto and Orfeo, 1984; Neiff, 1986; Bonetto et al., 1989; Stevaux et al., 2012). Based on these environmental features, two stretches have been delimited in the Argentine section of the Paraná River: the Upper and Lower Paraná (Neiff, 1990a; Orfeo and Stevaux, 2002; Fig. 1).

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In the Upper Paraná, from Iguazú (Misiones, km 1583) to Itá Ibaté (Corrientes, km 1244), the river has a very narrow floodplain, and the wet cross-section of the stream has a "V" profile. Aquatic vegetation, when present, covers small areas, especially downstream of Candelaria (km 1600). This section is characterized by large braided reaches (8–30 km long) separated by shorter nodal reaches (single-channel reaches) of 1–3 km (Orfeo and Stevaux, 2002).

The Lower Paraná extends from the confluence of the Paraguay and Paraná Rivers (Km 1244) to the Río de la Plata (Km 0). The mean channel width of this stretch ranges from 1.9 to 4.7 km (minimum: 1.0 km, maximum: 7.4 km). The channel has a slope of about 0.085 m km^{-1} and comprises 20% of the total alluvial valley surface. In this section the Paraná River drains a plain without terraces. Third part of the river valley is occupied by aggradation and relict bars, flooded every year – emerging bars – or remaining emergent during ordinary floods – islands – (Orfeo and Stevaux, 2002). Water level fluctuation is much higher in the Upper Paraná than in the Lower Paraná.

The Delta of the Paraná River is an atypical delta, in form, triangular, occupying 3500 km^2. The main course is split into two

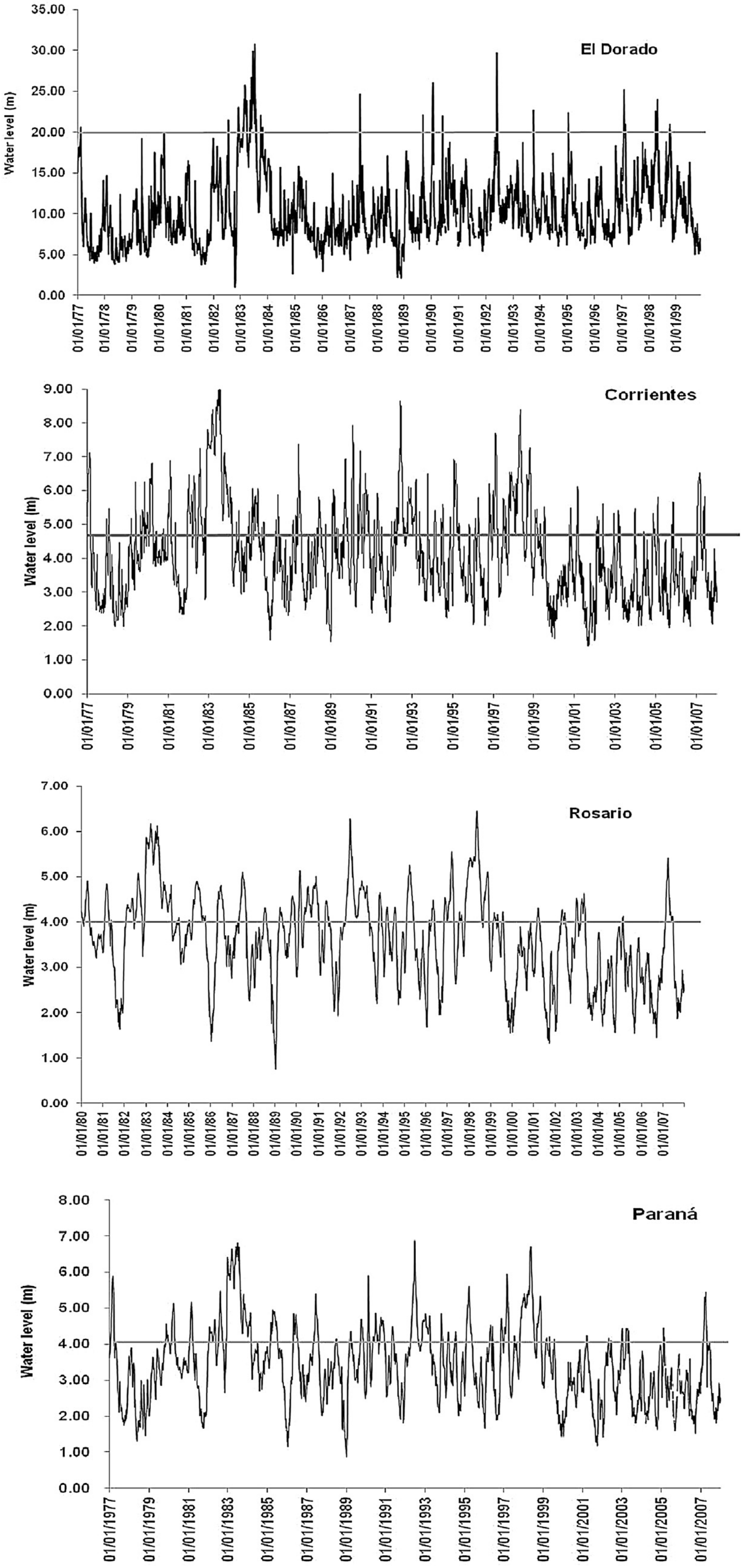

Fig. 2. Water level fluctuations (m) of the Paraná River in gauges at El Dorado, Corrientes, Paraná and Rosario cities. Horizontal lines indicate approximate bankfull where floodplain inundates.

channels: Paraná Guazú and Paraná de las Palmas. The islands are slightly concave with marginal dikes 1–2 km tall. The fringe floodplain occupies 54 km width (Iriondo, 2005).

2.2. Data set

This study is focused on aquatic and wetland herbaceous plants that inhabit lentic or lotic habitats of the river course and its floodplain. We included emergent macrophytes (plants that are rooted in submersed soils or in soils that are periodically inundated), floating-leaved macrophytes, submersed macrophytes, free-floating macrophytes and those growing on the peatland soils surrounding the lakes of the oldest islands of the Upper Paraná.

Upstream of the Iguazú confluence, the Paraná flows through Brazil; we therefore make some comparisons with information on the Brazilian portion of the Paraná provided by Thomaz et al. (2004), Campos (2004), Dos Santos and Thomaz (2007), Stevaux et al. (2012), Varandas Martins et al. (2013), and data from a field trip (J.J. Neiff, *unpublished*).

Only for operational purposes, one analysis of the Upper and Lower Paraná was subdivided into subsections as follows:

SECTION A: Upper Paraná

A_0: From the headwaters to the Paraná/Iguazú confluence (Brazil) - km 1928.

A_1: From the Paraná/Iguazú confluence to the city of Candelaria -Misiones -km 1600.

A_2: From Candelaria to the city of Ita Ibaté -Corrientes-km 1380.

A_3: From Ita Ibaté to the Paraná/Paraguay confluence -Paso de la Patria, Corrientes-km 1242.

SECTION B: Lower Paraná

B_1: Below the confluence of the Paraná and Paraguay rivers. This area is strongly influenced by sediments and nutrients provided by the Paraguay River (Carignan and Neiff, 1992; Carignan et al., 1994).

B_2: Paraná-Santa Fe cross-section. The waters of the Paraná and Paraguay rivers are already fully mixed, without differentiation in the suspended load and chemical properties between the river's margins (Orfeo and Stevaux, 2002).

SECTION C: Paraná River Delta

C_1: Paraná River Delta: Rosario–Victoria cross-section. The hydrological regime is more complex and less predictable than upstream (Neiff, 1986).

2.3. Sampling procedure

A total of 325 sampling units were examined during a period of prolonged drought from March 10th, 2007 to February 15th, 2008, and an equal number of units were analyzed in the same places during the floods of 2009–2010. The sampling unit was a set of 5 plots of 20 m^2 each. Four were arranged around a central one. In each plot, we recorded species coverage (C). According to coverage each species was scored as 0, 1 or 2 in each plot depending on whether the species was not present, having a coverage of less than 20% or greater of 20% respectively. Then, an importance value (Iv) for each species was calculated as sum of the scores in each plot. The Iv ranged from 0 (absent) to 10 (very important).

The sampling plot size of 20 m^2 was established using of the species/area curve methodology (Braun-Blanquet, 1979). Because further problems in the comparison of species richness among sites arise when the number of samples taken has been inadequate to represent the assemblage (Gotelli and Colwell, 2001), species richness counts were compared among sections following the species-accumulation curves. In each hydrological condition, logarithmic species-area curves were generally significant (R^2 between 0.7863 and 0.8435). The variable intersection with a linear fit led us to set sample area up to 39 (Upper Paraná), 127 (Lower Paraná at Corrientes), 29 (Lower Paraná at Santa Fe) and, 22 (Delta).

2.4. Data analysis

The spatial changes in biodiversity were studied using β diversity (turnover rate of species) between the sections of the river and within each section and hydrological phase. We use Whittaker's expression with the modification proposed by Harrison et al. (1992) as presented by Magurran (2004):

$$\beta\mathrm{w} = \left[\frac{\left[(S/\bar{\alpha}) - 1 \right]}{N - 1} \right] \times 100$$

where S is the total number of species registered in the study area, α is the mean species richness in each section or in each hydrological phase, and N is the number of sites. βw ranges between 0 (no difference between samples) and 100 (each sample has a unique assemblage of species).

Species turnover was quantified at the river level, considering all sample units ($n = 650$), and within four sections (Upper Paraná: $n = 114$; Lower Paraná at Corrientes: $n = 382$; Lower Paraná at Santa Fe: $n = 88$; and at Delta: $n = 66$).

To determine which species are representative or "characteristic" of each section of the river and in each hydrological phase, we used the Indicator Species Analysis (ISA) proposed by McCune and Grace (2002) using PC-Ord, including only those species with a $p \leq 0.05$ in each stretch, during high and low water as the two extreme conditions of the river system.

In an attempt to measure potential differences among sections of the river taking into account the hydrological phase, we used linear discriminant analysis to investigate whether it is possible to discriminate among sections according to vegetation assemblages. To accomplish this analysis, the Iv of each species in both hydrological phase of the river were used as discriminant variables. So the data matrix was 325 rows (sample units) by 125 columns: a class variable indicating the river section plus 62 species evaluated in two hydrological phases. The absolute value of the weights (AVW) used to calculate the scores of the first axes of discriminant space was used as an index of the relative importance of the species-hydrological-phase combination on the separation of the river sections. A multivariate procedure for pair-wise comparison of mean vectors (generalized DCC, Di Rienzo et al., 2002, 2011, 2013) was applied as a confirmatory analysis of separability of the river sections. Because of statistical assumptions of this method, it was applied to the first 30 principal components (90% of information on the original data) of the same data set used in the discriminant analysis.

As in other large rivers, hydrological variability is a synthetic indicator of the regional climate influences on aquatic vegetation. In a time-series, fluctuations appear as a sinusoidal pattern of water level. The hydrometric level at first flooding occurred at a particular point of the river plain was considered as zero value. The time when water level was above this value is seen as the period of inundation or *potamophase*, and the values found below correspond to a condition of isolation of the floodplain from the main course, also called dry phase or *limnophase*. The temporal sequence of these curves has been called *pulse regime* and depends mainly on and geomorphology (Neiff, 2001).

Using Google Earth images we selected the sampling areas and we determined the topographic position for the water table during the maximum flood period for each landscape and macrophyte types in the floodplain. The hydrologic connectivity was defined by determining the date of initial connection to the river in relation to the water level of the Paraná River in the gauges located near the study sites (Neiff and Poi de Neiff, 2003).

Table 1
Eco-hydrologic attributes of the Paraná River in each stretch. Overflow level indicate the beginning of potamophase. Frequency of pulses is the number of complete pulses (potamophase and limnophase). Intensity of potamophase is absolute value registered in the hydrological series.

	El Dorado	Corrientes	Paraná	Rosario
Hydrological series (days)	8366	11,322	12,053	10,227
Years	1977–1999	1977–2009	1977–2007	1980–2007
Overflow level (m)	20	4.80	4.20	4.00
(m a.s.l.)	215	42.39	10.154	3.594
Frequency of pulses	21	110	43	50
Intensity of potamophase (m)	30.74	9.02	6.89	6.44
Amplitude of potamophase (days)	279	3085	2514	3783
Time of year flooded (%)	3.34	27.24	20.86	36.99
Quotient annual pulse frequency	0.95	3.67	1.43	1.85

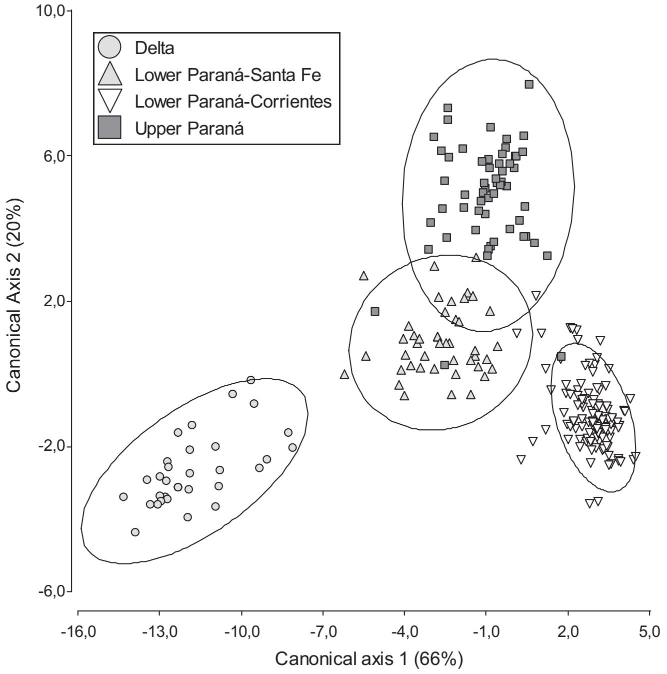

Fig. 3. Sampling sites in the discriminant space generated by the first two canonical axes. The sites for the four sections of the river are identified with different symbols. The contours around the points corresponding to each stretch of the river represent approximate 95% prediction ellipsoids, with 0.001 significance level.

The daily water levels of the river at the cities of El Dorado (Upper Paraná), Corrientes (downstream of the Paraná-Paraguay confluence), Paraná (Lower Paraná River) and Rosario (Delta) were supplied by the National Division of Navigable Ways and Ports in Argentina. Pulse attributes were analyzed using PULSO 1.05 software (Neiff and Neiff, 2004). According to Neiff (1996, 2001) and Neiff and Poi de Neiff (2003), we calculated several attributes of the pulses based on the overflow as follows (Frequency of pulses, Intensity of the potamophase and limnophase, Amplitude of potamophase). The quotient annual pulse frequency was calculated as the total number of complete pulses in a time series/number of years in a time series.

3. Results

3.1. Hydrology

In each section and each site of the floodplain, there were differences in the periods over which the soil remained flooded or dry in the same time series. This is due to geomorphological differences in the floodplain, the bed slope and changes in flow that occurs in alternating stages of flooding and dry soil.

Table 2
Percentage distribution of discriminant variables observed in limnophase according to the classification of the AVW into 2, 3, 4 or 5 approximately equal-size classes.

	Interval	Low water %	*P*-value
Two classes	[Min-P50]	36	
	[P50-Max]	63	0.0023
Three classes	[Min-P33]	25	
	[P33-P66]	60	
	[P75-Max]	64	0.0006
Four classes	[Min-P25]	14	
	[P25-P50]	56	
	[P50-P75]	67	
	[P75-Max]	60	0.0001
Five classes	[Min-P20]	14	
	[P20-P40]	52	
	[P40-P60]	59	
	[P60-P80]	65	
	[P80-Max]	67	0.0003

Pxx, percentile xx of the AWV distribution; Min, minimum AWV; Max, maximum AWV; P-value, the *p*-value of the Chi-square test for equality of percentages.

The water level fluctuations in the main cities of Upper and Lower Paraná are presented in Fig. 2. Unfortunately, the dates do not coincide due to a lack of records for certain periods. However, it is possible to see some trends: the proportion of days in flooded

Table 3
List of 20% combinations "Species/Hydrological phase" most important for their contribution to the first discriminant axis. The combinations are arranged in decreasing order of absolute value of the discriminant coefficients by which each combination of species-hydrological phase contribute to the construction of the first discriminant axis.

Hydrological condition	Species	Coefficient
Low water	*Scirpus californicus*	−1.62
Low water	*Sagittaria montevidensis*	−1.18
Low water	*Cleome trachycarpa*	−0.99
Low water	*Myriophyllum quitense*	−0.98
Low water	*Ludwigia peploides*	−0.93
Low water	*Hydrocleis nymphoides*	−0.91
Low water	*Echinochloa polystachya* var. *polystachya*	−0.76
Low water	*Cyperus entrerianus* var. *entrerianus*	−0.72
Low water	*Bacopa monnieri*	0.59
Low water	*Nymphoides indica*	−0.58
Low water	*Pontederia rotundifolia*	−0.56
Low water	*Azolla filiculoides*	−0.53
Low water	*Panicum grumosum*	−0.50
Low water	*Echinodorus grandiflorus* ssp. *grandiflorus*	−0.47
Low water	*Hydrocotile bonariensis*	−0.47
Low water	*Luziola peruviana*	−0.43
High water	*Myriophyllum quitense*	−0.93
High water	*Ceratophyllum demersum*	0.86
High water	*Utricularia foliosa*	−0.78
High water	*Polygonum ferrugineum*	−0.75
High water	*Cabomba caroliniana* var. *caroliniana*	0.56
High water	*Echinodorus longiscapus*	−0.46
High water	*Oplismenopsis najada*	−0.41
High water	*Panicum elephantipes*	−0.40

Table 4
List of 20% combinations of "Species/Hydrological phase" most important for their contribution to the second discriminant axis. The combinations are arranged in decreasing order of absolute value of the discriminant coefficients by which each combination of species-hydrological phase contribute to the construction of the second discriminant axis.

Hydrological condition	Species	Coefficient
Low water	*Polygonum ferrugineum*	0.95
Low water	*Panicum grumosum*	0.82
Low water	*Echinodorus grandiflorus* ssp. *grandiflorus*	−0.63
Low water	*Cleome trachycarpa*	−0.52
Low water	*Schoenoplectus californicus*	−0.50
Low water	*Eichhornia azurea*	0.48
Low water	*Nymphoides indica*	0.46
Low water	*Myriophyllum aquaticum*	0.45
Low water	*Panicum elephantipes*	0.42
Low water	*Zizaniopsis bonariensis*	0.40
Low water	*Sagittaria montevidensis* ssp. *montevidensis*	−0.30
Low water	*Pontederia rotundifolia*	−0.27
Low water	*Rhynchospora corymbosa* var. *corymbosa*	0.27
Low water	*Najas marina*	0.26
Low water	*Ceratophyllum demersum*	−0.24
Low water	*Thalia geniculata*	0.23
High water	*Panicum grumosum*	0.91
High water	*Eichhornia azurea*	0.38
High water	*Cabomba caroliniana* var. *caroliniana*	0.35
High water	*Echinodorus longiscapus*	0.31
High water	*Pontederia rotundifolia*	0.26
High water	*Ricciocarpus natans*	0.25
High water	*Hydrocotile ranunculoides*	0.24
High water	*Alternanthera philoxeroides*	0.23

soil and dry soil, pulse frequency, duration and seasonality are different in each hydrograph. A comparison of some pulse attributes is presented in Table 1.

In the Upper Paraná, the river runs in a narrow channel, and therefore, there are few pulses, and the riverbanks are flooded for short periods. Downstream, the floodplain is wider, the number of flooding days is also higher and the pulses have longer durations. The increase in the fluvial connectivity from the Upper Paraná to the Delta shows that the landscape and vegetation are more connected with the waters of the river further downstream. In the Paraná River Delta, the intensity of the pulses decreases further because the flow expands to a sheet 50 km wide during floods. Consequently, the floodplain remains flooded longer than the other sections (37% of the study period, Table 1).

The number of flood pulses is two to three times higher in Corrientes (Quotient annual pulse frequency 3.67) than in the other sections of the river.

In the delta, the mean number of pulses/year was 1.85. The high number of pulses (Table 1) is due to the influences of various factors: the effect of local rainfall on flat relief (Iriondo, 2005), and marine floods produced by SE winds (Neiff, 1990a).

3.2. Differences among sections

Fig. 3 displays the ordination of the 325 sampling sites in the first two dimensions of the discriminant space. Multivariate pair-wise comparison, using a 0.001 significance level, confirmed the separability of the sections. The maximum separation among river sections is shown along the first discriminant axis. This axis captures approximately 66% of the information. Maximum separation in the discriminant space is between Upper Paraná and Delta and Lower Paraná sections are more alike to Upper Paraná than to Delta.

The AVW of each discriminant variable (Iv of each species evaluated during the two hydrological phase) used to calculate the scores of the first axis of the discriminant space is an index of the relevance of each species-hydrological-phase combination to separate river sections. A preliminary inspection of AVW suggested that low-water phase is the hydrological phase in which differences among river sections are more relevant. To confirm this idea, AVW were grouped into 2, 3, 4 or 5 classes of approximately equal-size. A comparison of the percentage of the low-water phase among classes was performed. A significant difference was found (Chi-square test; $p < 0.001$) independently of the number of classes used (Table 2).

In order to choose the most relevant combinations of species-river-phase, we selected those combinations having AVW equal or greater than the 80th percentile of the empirical distribution of AVW (top 20% selected). In this category 67% of species belong to the low-water phase (Table 3).

The same procedure was used to obtain the coefficients of the second discriminant axis. The top 20% of AVWs are listed in Table 4. Species-river-phase combinations including the low water phase were the most prevalent (70%) within these weights.

3.3. Spatial changes of species (β diversity)

Sixty-two species of aquatic vascular plants were recorded for the entire study area in both hydrological phases. The species richness in each section varied between 38 and 51 in low water, being this value registered in the Low Paraná at Santa Fe. At high water the species richness varied between 23 and 29 (Table 5). β diversity among the river sections was higher during low water ($\beta = 16\%$) than during high water ($\beta = 11\%$).

At both hydrological phases, the Whittaker index indicated a high turnover of species among plots in the Delta (Table 5), whereas in the Lower Paraná at Corrientes β diversity among plots was lowest.

3.4. Indicator species in each stretch

Seventeen species were selected as indicators in all sections in the limnophase and potamophase. In the Upper Paraná River, the following indicator species were as identifies: *Panicum grumosum* Nees (indicative values: 42% in the potamophase and 46% in the limnophase) and M. Gómez (15% at high water and 20% at low water). They are constantly present and could be called *persistent*.

At Lower Paraná at Corrientes, *Azolla cristata* Kaulf. (21%) was the most frequent species in the potamophase, whereas *Eichhornia crassipes* (Mart.) Solms was more frequent (24%) in the limnophase.

The primary species at Santa Fe city was *Panicum elephantipes* Nees ex Trin (30%) during both the potamophase and the limnophase. *Salvinia biloba* Raddi (47%) and *Hydrocotyle ranunculoides* L.f. (15%) were also selected as indicator species at high and low waters, respectively.

Table 5
Species richness (*S*) and β diversity (*β*) among the plots in both hydrological phases.

	Upper Paraná		Lower Paraná Corrientes		Lower Paraná Santa Fe		Delta	
	High waters	Low waters	High Waters	Low Waters	High waters	Low waters	High waters	Low Waters
S	28	38	24	40	29	51	23	43
β	37%	41%	16%	12%	32%	42%	58%	42%

In the Delta, *Ludwigia peploides* (Kunth) P.H. Raven was the indicator species selected for the potamophase with a value of 31% and for the limnophase with 42%. *Schoenoplectus californicus* (C.A. Mey) Soják was also selected as an indicator with values of 12% (high water) and 24% (low water). Other species that were frequent in both phases were *Polygonum punctatum* Buch. Ham. Ex D. Don (16%) and *Sagittaria montevidensis* Cham. & Schltdl (22%).

4. Discussion

Our first hypothesis, that plant assemblage's change predictably along the Paraná River course from Upper to Delta was partially supported by our results. Although the Upper Paraná and Delta have the maximum separation in the discriminant space, the richness increases in Lower Paraná at Corrientes, and decrease in the Delta. The turbid waters of the Lower Paraná below the confluence of the Paraguay River is strongly influenced by sediments and nutrients provided by this river (Carignan and Neiff, 1992; Carignan et al., 1994). The effect of suspended load can reach to 400 km below the confluence (Orfeo and Stevaux, 2002). The low transparency prevents the development of submerged plants, which were frequently registered in the Delta.

We found no clear longitudinal pattern in the distribution and diversity of vegetation along the course of the river. At high water, the species richness is similar among sections. Thus, the floods seem to have a homogenization effect on the aquatic environments as Thomaz et al. (2009) reported for the Upper Paraná in Brazil. Diversity increased at low water by increasing spatial heterogeneity in the floodplain. Stevaux et al. (2012) indicated that during low water the geomorphology of the floodplain results in patches of habitat with different water storage capacities and depths in the Upper Paraná. Our results suggest that in low water there was high β diversity, therefore we accept the hypothesis two.

The species selected by ISA with indicative values up to 15% belong in two life forms: free floating plants and rooted emerged plants. *E. crassipes*, *A. cristata* and *S. biloba* are adapted to changes in the water level, especially during the potamofase. *E. crassipes* grows limited by nitrogen during low water (Carignan and Neiff, 1992) whereas during the prolonged floods the leaf size and biomass values increases and nutrient content in the green leaves is highest (Neiff et al., 2001). *P. grumosum*, *P. elephantipes* and *L. peploides* have a broad niche (amphitolerants) and develop ecophenos adapted to each hydrological phase (Neiff, 1990a).

The hypothesis that there are indicator species in each section and hydrological phase is accepted. However 29% of the species recorded for the entire study area in both hydrological phases can live along the Paraná River in different hydrological conditions, indicating that most of them have broad niches.

Author contributions

J.J.N. conceived the project, conducted the research, carried out the field work, and led the writing; S.L.C. and E.K.A.M. carried out the field work and suggest contributions to the manuscript. J.A.DiR. collaborated with the statistical processing. A.S.G.P. contributes with unpublished previous information and improved the final version of the manuscript.

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References

Bini, L.M., Thomaz, S.M., Souza, D.C., 2001. Species richness and beta diversity of aquatic macrophytes in the upper Paraná river floodplain. Arch. Hydrobiol. 151, 511–525.

Bonetto, A.A., 1985. The Paraná river system. In: Davies, B.R., Walker, K.F. (Eds.), The Ecology of River Systems. Dr. Junk Publishers, Dordrecht, pp. 541–555.

Bonetto, A.A., Orfeo, O., 1984. Caracteres sedimentológicos de la carga en suspensión del río Paraná entre Confluencia y Esquina (Prov. de Corrientes). Rev. Asoc. Arg. Min. Petr. Sed. 15, 51–61.

Bonetto, A.A., Wais, I.R., Castello, H.P., 1989. The increasing damming of the Paraná Basin and its effects on the lower reaches. Regul. River 4, 333–346.

Braun-Blanquet, J., 1979. Fitosociología. Base para el estudio de las comunidades vegetales. Blume, Madrid.

Burkart, A., 1957. Ojeada sinóptica sobre la vegetación del Delta del Río Paraná. Darwiniana 11, 457–561.

Campos, J.B., 2004. Spatial characterization of the vegetation. In: Thomaz, S.M., Agostinho, A.A., Hahn, N.S. (Eds.), The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation. Backhuys Publishers, The Netherlands, pp. 369–380.

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

Carignan, R., Neiff, J.J., Planas, D., 1994. Limitation of water hyacinth by nitrogen in subtropical lakes of the Paraná floodplain (Argentina). Limnol. Oceanogr. 39, 439–443.

Casco, S.L., 2003. Poblaciones vegetales centrales y su variabilidad espacio-temporal en una sección del Bajo Paraná influenciada por el régimen de pulsos. Tesis Doctoral. Universidad Nacional del Nordeste, Corrientes, Argentina.

Di Rienzo, J.A., Guzmán, A., Casanoves, F., 2002. A multiple-comparisons method based on the distribution of the root node distance of a binary tree. J. Agric. Biol. Environ. Stat. 7, 129–142.

Di Rienzo, J.A., Valdano, S.G., Fernández, P., 2011. How to group genes according to expression profiles? Int. J. Plant Gen., 261975, http://dx.doi.org/10.1155/2011/261975.

Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., Robledo, C.W., 2013. InfoStat versión 2013. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina http://www.infostat.com.ar

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

Gotelli, N., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.

Harrison, S., Ross, S.J., Lawton, J.H., 1992. Beta diversity on geographic gradients in Britain. J. Anim. Ecol. 61, 151–158.

Iriondo, M.H., 2005. El complejo litoral en la desembocadura del río Paraná. In: Barrio, R.E., de Etcheverry, R.O., Caballé, M.F., Llambias, E. (Eds.), Geología y Recursos Minerales de la Provincia de Buenos Aires. XVI. Congreso Geológico Argentino, La Plata, pp. 255–264.

Khedr, A.H., El-Dermash, M.A., 1997. Distribution of aquatic plants in relation to environmental factors in the Nile delta. Aquat. Bot. 56, 75–86, http://dx.doi.org/10.1016/S0304-3770(96)01090-X.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell, Oxford.

Malvárez, A.I., 1997. Las comunidades vegetales del delta del río Paraná. Su relación con factores ambientales y patrones de paisaje. Tesis Doctoral. Universidad de Buenos Aires, Buenos Aires, Argentina.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, Oregon.

Morello, J.H., 1949. Las comunidades de las islas cercanas al Puerto de Rosario. Tesis Doctoral. Museo de La Plata, Buenos Aires, Argentina.

Neiff, J.J., 1986. Aquatic plants of the Paraná system. In: Davies, B.R., Walker, K.F. (Eds.), The Ecology of River Systems. Dr. Junk Publishers, Dordretch, pp. 557–571.

Neiff, J.J., 1990a. Aspects of primary productivity in the Lower Paraná and Paraguay riverine system. Acta Limnol. Bras. 3, 77–113.

Neiff, J.J., 1990b. Ideas para la interpretación ecológica del Paraná. Interciencia 15, 424–441.

Neiff, J.J., 1996. Large rivers of South America: toward the new approach. Verh. Internat. Verein. Limnol. 26, 167–180.

Neiff, J.J., 2001. Diversity in some tropical wetland systems of South America. In: Gopal, B., Junk, W., Davis, J. (Eds.), Biodiversity in Wetlands: Assessment, Function and Conservation. Backhuys Publishers, Holanda, pp. 157–186.

Neiff, J.J., Poi de Neiff, A., Casco, S.L., 2001. The effect of prolonged floods on *Eichhornia crassipes* growth in Paraná river floodplain lakes. Acta Limnol. Bras. 13, 51L 60.

Neiff, J.J., Neiff, M., 2004. PULSO. Software diseñado para estudiar fenómenos recurrentes en el tiempo. www.neiff.com.ar

Neiff, J.J., Poi de Neiff, A., 2003. Connectivity processes as a basis for management of aquatic plants. In: Bini, L.M., Thomaz, S.M. (Eds.), Ecología e Manejo de Macrófitas Aquáticas. Eduem, Maringá, pp. 39–58.

Orfeo, O., Stevaux, J., 2002. Hydraulic and morphologic characteristics of middle and upper reaches of the Paraná River (Argentina and Brazil). Geomorphology 44, 309–322.

Souza, M.C., Cislinski, J., Romagnolo, M.B., 1997. Levantamento florístico. In: Vazzoler, A.E.A.M., Agostinho, A.A., Hahn, N.S. (Eds.), A Planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. Eduem, Maringá, pp. 345–370.

Stevaux, J.C., Corradini, F.A., Aquino, S., 2012. Connectivity processes and riparian vegetation of the upper Paraná River, Brazil. J. South Am. Earth Sci., http://dx.doi.org/10.1016/j.jsames.2011.12.007 (in press).

Thomaz, S.M., Carvalho, P., Padial, A.A., Kobayashi, J.T., 2009. Temporal and spatial patterns of aquatic macrophytes diversity in the Upper Paraná river floodplain. Braz. J. Biol. 69, 617–625.

Thomaz, S.M., Bini, L.M., Pagioro, T.A., Murphy, K.J., Dos Santos, A.M., de Souza, D.C., 2004. Aquatic macrophytes: diversity, biomass and decomposition. In: Thomaz, S.M., Agostinho, A.A., Hahn, N.S. (Eds.), The Upper Paraná River and its Floodplain. Backhuys Publishers, Leiden, pp. 331–352.

Varandas Martins, S., Milne, J., Thomaz, S.M., McWaters, S., Mormul, R.P., Murphy, K., 2013. Anthropogenic and natural drivers of changing macrophyte community dynamics over twelve years in a subtropical riverine floodplain system. Aquat. Conserv.: Mar. Freshw. Ecosyst. 23, 678–697.