Vegetation communities and their relationship with the pulse regime on islands of the Middle Paraná River, Argentina

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ABSTRACT - Vegetation associated to the Paraná River is subject to conditions imposed by the pulse regime. This study aimed to evaluate the pulse regime influence on the vegetation of the Paraná River islands. Using multivariate techniques for classification and ordination, six communities were identified and described: willow forests of marginal levees, riverine forest of internal levees, floating meadows, floating rooted plants, a tall grass herbaceous community and a marshy community. The forests were the most diverse and the richest communities while the floating meadows and the marshy community were less rich and diverse. Our results indicate that duration and recurrence of floods are important variables in determining the characteristics of the vegetation. However, forests with a similar flood recurrence and duration showed important differences in physiognomy, structure and floristic composition. The differences between the forests could be explained by the connectivity degree, geomorphological dynamics and succession time.

Key words: vegetation assemblages, diversity, hydrological dynamics, water energy

RESUMO – **Comunidades vegetais e sua relação com o regime de pulso em ilhas do Paraná, Argentina**. A vegetação associada ao rio Paraná está sujeita ao regime do pulso. O objetivo deste estudo é avaliar como o pulso influencia a vegetação em ilhas do rio Paraná. Após aplicação de técnicas multivariadas, seis comunidades foram identificadas e descritas: mata de salgueiro de diques marginais, mata ciliar de diques internos, vegetação aquática flutuante, comunidade aquática arraigada, comunidade herbáceas de grama alta e comunidade pantanosa. As matas foram os mais diversos e o mais rico entre as comunidades. Entretanto, as vegetações flutuantes e pantanosas foram menos ricas e diversas. Nossos resultados indicam que o tempo e periodicidade das inundações é uma variável importante para determinar as características da vegetação. No entanto, a mata, com semelhantes periodicidade e duração de inundações mostrou diferenças na fisionomia, estrutura e composição florística.

Palavras chave: comunidades vegetais, gradiente de inundação, diversidade e riqueza, energia da água

INTRODUCTION

The growing and diverse literature on wetland environments, communities and ecological processes has turned this issue into one of the most documented topics in recent years (Bournette *et al*., 1998; Ward *et al*., 1999; Van Coller *et al*., 2000; Panitsa & Tzanoudakis, 2001; Decocq, 2002; Campos & Souza, 2002; Finlayson, 2005; Stoll et. al., 2006; Budke & Jarenkow, 2007; Sarr & Hibbs, 2007; Martins *et al*., 2008). Wetlands are increasingly considered as macrosystems that provide several environmental services: sources of clear water, wildlife habitat, organic material production, fertilizer decomposition and river shore stabilization are just a few examples of them (Neiff, 1997; Carvalho *et al*., 2005).

The Paraná River is the second most important river in South America (Franceschi *et al*., 2000) and it has been identified as a fluvial system of remarkable characteristics at a global level (Neiff, 1996, 1999) because it originates in a humid tropical climate and ends in a humid temperate region (Aceñolaza *et al*., 2004; Oakley *et al*., 2005). In Argentina, an important quantity of simple and composed islands is distributed along the main channel of the Paraná River and they are among the most representative geomorphological elements/units (according to its development degree) of the Paraná River. The floodplain of the Paraná River, where the islands are an important geomorphological element, covers 7,200 km2 only in the Middle Paraná (Drago, 1981). Both the floodplain and the islands of the main channel are subject to the influence of hydro-sedimentological pulses of the river (Neiff 1990, 1996, 1999). In the spring-summer period a high water phase or an ordinary flood phase occurs once a year. During this high water phase the river has a flow of up to 25,000 m3 s-1 and it is followed by a low water phase from the end of winter to the beginning of spring. In unusual floods, the river may reach a flow of 60,000 m^3 s-1 (Neiff, 1979), triggering substantial changes in vegetation (Franceschi *et al*., 2000) as well as important economic losses.

This variability in the hydrological dynamics determines the structure and evolution of the floodplain and of the islands in the main channel of the Paraná River (Lewis & Franceschi, 1979; Neiff, 1996; Ramonell *et al*., 2000). Moreover, this variability produces a significant heterogeneity, which is characterized by high species richness and diversity (Aceñolaza *et al*., 2004, 2005, 2008) and complex ecological processes. The role of vegetation was studied in the low Paraguay River (the major tributary of the Paraná River) by Neiff *et al*. (2006), who found that the vegetation in the floodplain produced a reduction of runoff up to 25 % during the extraordinary flood of 1982. However, it should be pointed out that the "buffer" function of the vegetation depends on its structure, diversity, biomass and distribution. In this regard, the study of such characteristics in different vegetation types constitutes a key step in environments characterized by a high hydrological variability. Only from this point the relationship between the vegetation and the pulse regime can be understood and the associated environmental functions of the vegetation can be valued.

Several studies have been conducted on the vegetation of environments associated to the Paraná River (Neiff, 1979, 1986; Kandus *et al*., 2003; Aceñolaza *et al*., 2004; Marchetti & Aceñolaza, 2005; Casco et. al., 2005; Aceñolaza *et al*., 2008; Sione *et al*., 2009); nevertheless, phytosociological analyses of the vegetation, the relative importance of species in different vegetation units and their relationship with the pulse regime are scarce in the middle section of the Parana River (Franceschi & Lewis, 1979; Franceschi et. al., 1985; Aceñolaza & Muñoz, 2003). Moreover, the topographic level as a key factor in relation to the pulse regime and the colonization range of vegetation units on islands of the main channel are unknown. This work had two aims: 1- to define vegetation communities on islands of the main channel and 2- to assess the effect of the pulse regime on their structure and specific composition according to their location along the topographic gradient.

METHODS

Study Area

The study was carried out on the Chapeton Islands in the main channel of the Paraná River in Entre Ríos Province, Argentina (31° 33´49´´ S, 60° 18´21´´ W). The study zone covers 1,500 hectares (Fig.1) and it was chosen because it combines vegetation units and geomorphological elements, which are representative of the main environments associated to the Middle Paraná River. Alluvial soils (Entisols) have textures ranging from silty, clayey to sandy or any combination thereof, usually without an evolved profile. The climate is humid, temperate/warm, with a mean annual temperature of 19 ºC and an annual rainfall of 900 mm, with most rains (73 %) from October to April (Rojas & Saluso, 1987). The extensive livestock is widely developed in the study zone and it involves fire as the main management practice at the end of winter (Sione *et al*., 2009). The pulse regime, represented by high and low, ordinary and extraordinary water phases, characterizes the superficial hydrology in the study zone.

Vegetation analysis

Homogeneous vegetation units were identified using Landsat TM 7 satellite images (2006) of the

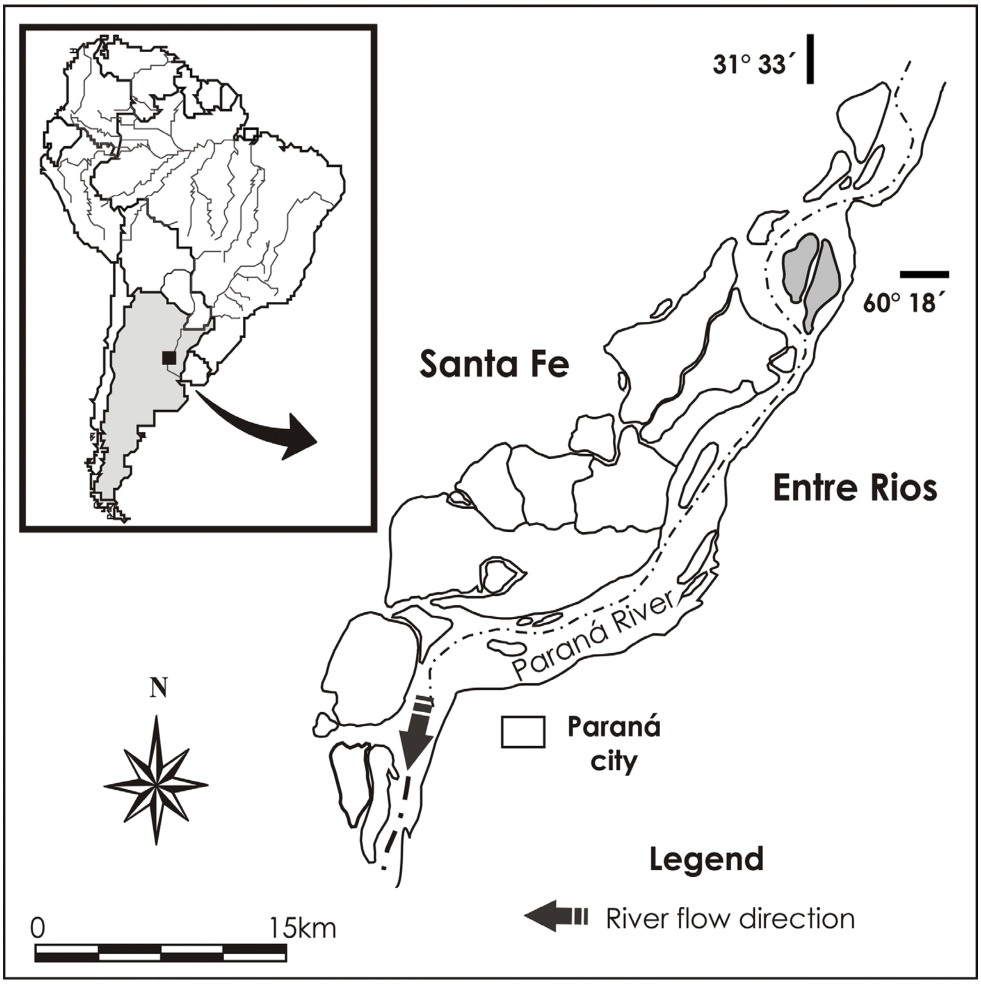

Fig. 1. Location of the study zone. Chapetón Islands (grey), in the course of the Paraná River.

study zone provided by CONAE (Comisión Nacional de Actividades Espaciales). The surface surveyed was according to the physiognomy, and the stabilization of the species/area curve was used according to the proposal by Chytrý & Otýpková (2003). Sampling units of 400 m^2 for woody vegetation and of 25 m^2 for herbaceous vegetation were defined from the stabilization of the species/area curve. The number of sampling units was variable according to the surface of each vegetation type. Twenty-seven censuses of woody vegetation and 22 of herbaceous vegetation were carried out in each physiognomic type, totaling an area of 10,800 m^2 and 550 m^2 for woody and herbaceous vegetation respectively. Vascular plants not identified at the species level were collected for later taxonomic identification. The botanic nomenclature followed Zuloaga *et al*. (1994), Zuloaga & Morrone (1996, 1999). The vegetation surveys were conducted during the summer, applying the abundance-coverage scale of Muller-Dombois & Ellenberg (1974). The structure of each sampling unit was described according to number, height and cover of each strata and its most important species were identified from their abundance-coverage percentage. The differentiation between young and developed forests was made from the dbh (diameter at breast height > 10 cm) recorded in 20 randomly chosen trees in each forest. Finally, the topographic level of vegetation units was performed using a Leica topographic level. For marshy vegetation, the topographic level was the ground level, because all the fieldwork was performed during a low water phase (1.83 meters at the nearest hydrometric gauge in Paraná city, Entre Ríos). The topographic level assigned to aquatic communities was the water body level during the fieldwork. This water level was referred to the hydrometric level of the Paraná River, recorded in the mentioned gauge on the specific day on which the fieldwork was performed. In each homogeneous vegetation unit, 20 readings were recorded in order to obtain minimum, medium and maximum values of the topographic levels. All the topographic levels were referred to the hydrometric 0 (zero) of the mentioned nearest gauge. Based on these data, the mean topographic level of each community was related to the hydrological regime of the Paraná River in a 10-year series (1997-2007), from which the flooding recurrence for each community was established. Every time in the 10-year series that the hydrometric level was higher than the mean topographic level of each community, a flooding was counted in this community. The hydrometric levels were provided by Prefectura Naval Argentina. They were recorded in the mentioned gauge and converted to meters a.s.l.

Data analysis

Vegetation data were analyzed by multivariate techniques currently used to define vegetation communities (Heung-Lak & Hong, 2006; Cheng & Nakamura, 2006; Isermann, 2008). The signals "r" and "+" in the abundance-coverage scale were transformed to 0.2 and 0.5 respectively, in order to be analyzed with numerical methods. Similarities among the vegetation sampling units were calculated via cluster analysis, using Euclidean Distance and Farthest Neighbor as a linking criterion (McCune & Mefford, 1999). In order to identify the environmental gradients an ordination analysis using DCA (Detrended Correspondence Analysis) was performed. It was also considered that the sampling units are discrete but were taken in a perpendicular transect from the river, covering in this way the flooding gradient. This technique was broadly used in different contributions (Koutecky & Prach, 2005; Härdtle *et al*., 2006; Chang-Seok *et al*., 2009) to study environmental gradients. DCA was based on a primary matrix of abundance-coverage species and a secondary matrix with the number of communities as a classifying variable. The number of each community was defined from the cluster analysis. PC-ORD 4.1 software was used for data analyses. Finally, the presence and abundance of species in each community is shown in a phytosociological table where the specific composition of each community and the importance of each species can be appreciated. The richness of species and the Shannon-Wiener diversity were obtained for each community.

Mean topographic distribution of each vegetation unit was related to the hydrological level dynamics in a 10- year time series.

RESULTS

Floristic composition

One hundred species of vascular plants belonging to 43 families and 79 genera were recorded. *Asteraceae*, *Poaceae*, *Fabaceae*, *Solanaceae*, *Cyperaceae*, *Polygonaceae* and *Euphorbiaceae* were the most represented families, with 4 to 12 species each. Considering the percentage composition, only the first three families had 34 % of the total species richness, while 38 families represented 48 %. With regard to life forms, 65 % of the species are herbs, 13 % are climbing species, 12 % are shrubs and 10 % are trees.

Classification of vegetation units and characterization of plant communities

The classification of sampling units differentiated 6 principal communities (Fig. 2). Species composition and abundance-coverage of each species are shown in Table 1.

Community 1: Willow forest of marginal levees. These forests correspond to a mature woody community defined by the constant presence of *Salix humboldtiana* Willd. var. *humboldtiana*. They are distributed on the marginal levees of the river and on the main tributary streams. Since they are located on the most elevated areas of the island (16.3 m a.s.l., see Tab. 1), this vegetation unit is only affected by extraordinary floods. Structurally, this community presents three vegetation strata: two woody strata (trees and shrubs) and one herbaceous stratum of 12, 1.5 and 0.30 meters height, respectively. Among all the strata, the soil coverage varies between 80 and 100 %. From their abundance-coverage values the most important accompanying species are: *Tessaria integrifolia* Ruiz et. Pav. var. *integrifolia*, *Croton urucurana* Baill., *Hyptis mutabilis* (Rich.) Brinq., *Paspalum conjugatum* Bergius, *Mikania cordifolia* (L.f.) Willd. and *Coniza sumatrensis* (Retz.) E. Walter var. *sumatrensis*.

Community 2: Riverine forest on internal levees. This unit is characterized by the presence of *Nectandra angustifolia* (Schrad.) Nees *et* Mart. ex Nees, *Albizia inundata* (Mart.) Barneby *et* J.W. Grimes and *Inga affinis DC*. in the upper layer of trees and, *Smilax campestris* Griseb., *Panicum sabulorum*

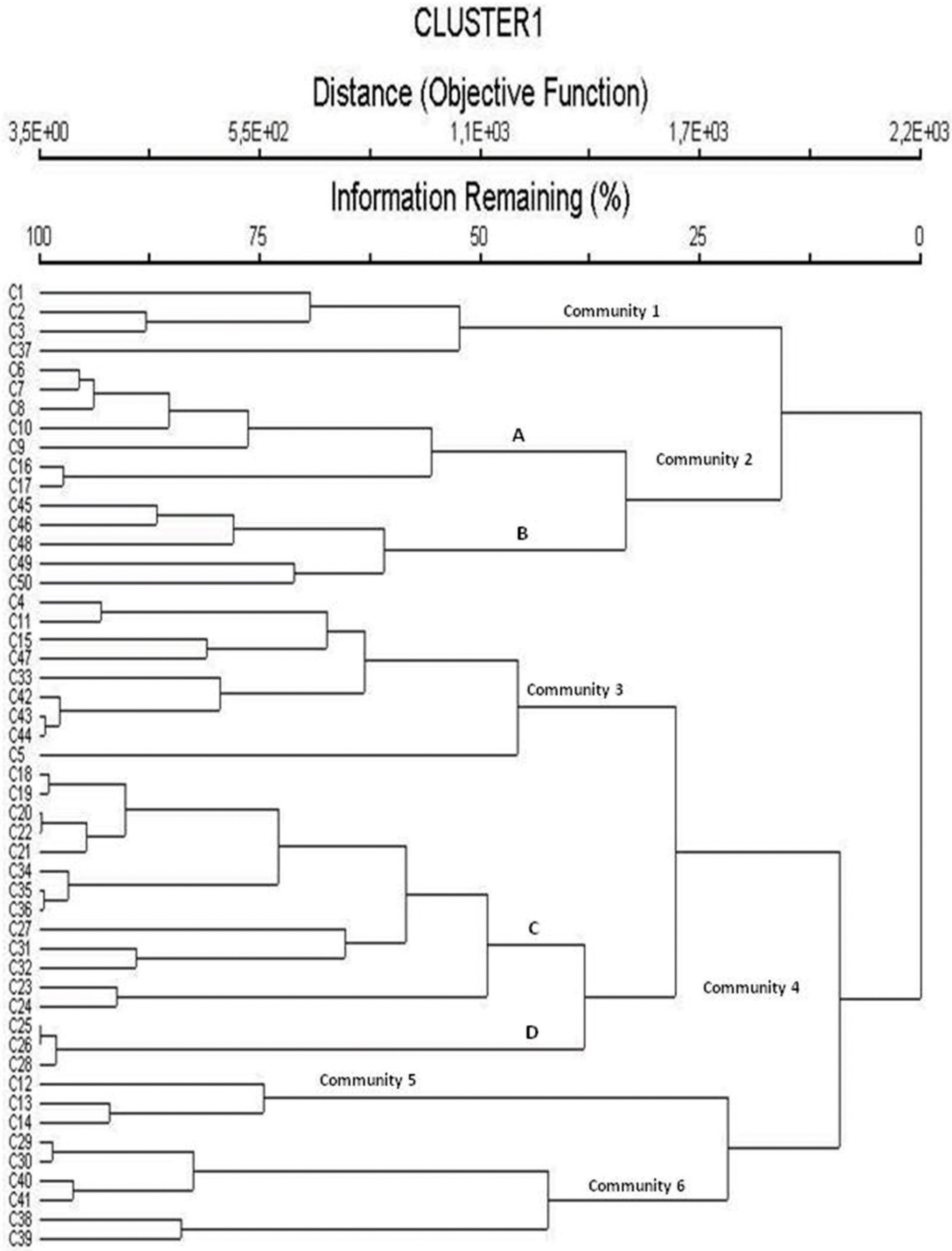

Fig. 2. Sampling units classification (Euclidean distance, farthest neighbor). Communities: Willow forests of marginal levees; Riverine forests of internal levees; Floating meadows; Floating rooted plants; Tall grass herbaceous community; Marshy community.

Lam. var. *sabulorum*, *Iresine diffusa* Humb. *et* Bompl. ex Willd. var. *diffusa* and others in the inferior strata. This forest has a high and closed canopy and it is placed on the internal levees of the islands, located on average at 15.5 m a.s.l. This community has several vegetation strata, covering 40 to 95 % of the soil.

There are two trees strata, the highest up to 15 m tall (where *A. inundata*, *I. affinis* and *N. angustifolia* are the most frequent species) and the lowest stratum of 6 m height (dominated by *C. urucurana*). The shrubs reach 1.5 m height, while the herbaceous stratum reaches 0.50 m. Some of the accompanying species are: *Solanum reflexum* Schrank, *Vigna adenantha* (G. Mey.) Marechal, Mascherpa *et* Stainer, *M. cordifolia*, *Aspilia silphioides* (Hook. *et* Arn.) Benth., *Sicyos polyachanthus* Cog. and *Urera aurantiaca* Wedd. Based on Figure 2, it is possible to distinguish two sub-communities: *Nectandra angustifolia* riverine forests (Fig. 2 A) and *Albizia inundata* and *Croton urucurana* riverine forests (Fig. 2 B).

Community 3: Floating meadows. These communities colonize ponds and old watercourses (meander scrolls, oxbow ponds) and are disconnected from the main channel. The water level was 12.8 m a.s.l during the field work (1.83 m in the Paraná River). For this hydrometric level, these old watercourses are lentic or semilentic environments; the latter may become lotic during the floods, which change the water level and the specific composition. Although this unit has a low number of species, a gradient in its specific composition can be observed from the shoreline to the open water zone. Up to 0.30 m in depth, the more frequent species are *Myriophyllum aquaticum* (Vell.) Verdc., *Hydrocotyle bonariensis* Lam., *Polygonum punctatum* Elliott, and *Salvinia biloba* Raddi, among others. Floating species, such as *Eichhornia crassipes* (Mart.) Solms and *Eichhornia azurea* (Sw.) Kunth become dominant as depth increases. V*ictoria cruziana* Orb., *Limnobium laevigatum* (Humb. *et* Bonpl. ex Willd.) Heine, *E. crassipes*, *E. azurea* and *Azolla filiculoides* Lam. are frequent in the deepest zone of the ponds. Because of the high growth rate of some aquatic species, monospecific stands can establish covering up to a 100 % of the water surface.

Community 4: Floating rooted plants. This vegetation unit includes a set of species distributed at an average elevation of 14.5 m a.s.l. in direct contact with the main water channel (river or stream). This unit is characterized by two subgroups, woody and herbaceous respectively. The first one includes small forests of *T. integrifolia* and *S. humboldtiana* (Fig. 2 C), which are represented by trees with small diameters and high density. In general, these pioneer forests are monospecific, with one species as dominant and the others accompanying. They are structurally homogeneous, presenting a layer of trees of up to 10 m tall, which covers more than 80 %. The herbaceous vegetation is very scarce in these forests. Only isolated plants of *P. punctatum*, *L. elegans* and *E. crassipes* can be found after a flood. *Mikania periplocifolia* and *V. adenantha* are the most common accompanying species. In the herbaceous subgroup (Fig. 2 D), its most important species form a sequence of a contiguous belt of vegetation: the first belt is represented by *Panicum elephantipes* Nees ex Trin, it is in direct contact with the river and it reaches from 0.40 to 0.60 m tall and covers 100 % of the soil/water surface; the second belt is represented by *Echinochloa polystachya* (H.B.K.) Hitchc. var. *polystachya*, it reaches 2 m tall and covers 100 % of the soil/water surface; the third belt, of more than 2 m tall, is represented by *Polygonum ferrugineum* Wedd., *E. polystachya* and *Echinochloa crus-pavonis* (Kunth) Schult. with similar coverage values. The accompanying species are *Commelina diffusa* Burm. f., *Ludwigia elegans* (Cambess.) H. Hara and *Mikania periplicofolia* Hook. *et* Arn., among others.

Community 5: Tall grass. Dominated by *Panicum prionitis* Nees and located approximately at 15.3 m a.s.l. This community is found between levees and ponds, being one of the most representative herbaceous communities in the floodplain of the Parana River. Structurally, it presents two vegetation strata: the one on the top, of up to 3 m tall, composed by *P. prionitis* and, to a lesser extent, by shrubs such as *Sesbania virgata* (Cav.) Pers and *Mimosa pigra L.*, and the bottom stratum, of about 0.50 m tall, composed by accompanying species found at equivalent frequencies in other communities: *Cynodon dactylon* (L.) Pers. var. dactylon, *Setaria parviflora* (Poir.) *Kerguélen* var. *parviflora*, *C. sumatrensis*, etc. *Leptochla fusca* (L.) Kunth ssp. *uninervia*, *Mitracarpus megapotamicus* (Spreng.) Kuntze, *Paspalum denticulatum* Trin., *Paspalum notatum* Flüggé var. *notatum* are exclusive and very frequent species in this community. There are also climbing species such as *Muehlenbeckia sagittifolia* (Ortega) Meisn, *Solanum angustifidum* Bitter. This is the richest herbaceous community of the islands.

Community 6: Marshy community. This vegetation unit is found between the tall grasslands (Community 5) and the littoral zone of the ponds, in an average topographic position of 14.3 m a.s.l. Depending on the water level, it may include completely flooded areas with aquatic vegetation or unflooded ones during the low water phase. In any case, the vegetation is mostly

Table 1. Specific composition and abundance-coverage (Muller-Dombois & Ellenberg, 1974) of each ones, in every defined vegetation community. Mean topographic level as m a.l.s, SD (standard deviation). Physiognomy: W (woody); HH (high herbaceous); LH (low herbaceous). Dotted lines indicate transition species groups and full lines show characteristic species groups in each unit. Communities: 1. Willow forests of marginal levees; 2. Riverine forests of internal levees; 3. Floating meadows; 4. Floating rooted plants; 5. Tall grass herbaceous community; 6. Marshy community.

N° Community	1				2											3									4																5			6					
Richness	32				52											23									28																24			23					
Diversity	1.44				1.68											1.21									1.31																1.34			1.31					
Mean topographic level (SD)	16.28 (0.13)				15.47 (0.96)											12.81 (0.74)									14.50 (0.5)																15.3 (0.13)			14.28 (0.44)					
Physiognomy	W				W											LW									W/LH																HH			LH					
Species / Sampling units	1	2	3	37	6	7	8	9	10	16	17	45	46	48	49	5	33	42	43	44	4	11	15	47	18	19	35	36	31	32	34	20	21	22	23	24	25	26	28	27	12	13	14	38	39	29	30	40	41
Eichhornia azurea (Sw.) Kunth	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	2	2	3	5	5	3	3	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eichhornia crassipes (Mart.) Solms	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	2	2	.	4	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Azolla filiculoides Lam.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	2	5	3	4	4	.	.	.	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hydrocleis nymphoides (Willd.) Buchenau	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	1	.	1	2	2	.	.	.	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hydrocotyle bonariensis Lam.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	1	1	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Myriophyllum aquaticum (Vell.) Verdc.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nymphoides indica (L.) Kuntze	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salvinia biloba Raddi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	5	3	2	3	1	1	4	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Victoria cruziana Orb.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	5	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Enhydra anagallis Gardn	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	1	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	2	2	2
Mimosa pigra L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2	2	2	.	1
Solanum glaucophyllum Desf.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	1	1	4	4
Funastrum clausum (Jacq.) Schltr.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.	.	.	.
Symphyotrichum squamatum (Spreng.) G.L. Nesom	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.
Echinochloa crus-pavonis (Kunth) Schult.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	1
Solanum amygdalifolium Steud	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.
Cirsium vulgare (Savi) Ten.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum punctatum Elliott	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3	3	1	2	.	4	2	4	1	3	3	3	.	.	.	.	.	.	.	.	1	2	2	1	.
Tessaria integrifolia Ruiz & Pav. var. *integrifolia*	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	5	5	1	2	5	4	5	4	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.

Continue

Table 1. Continuation

N° Community	1				2											3									4																5			6					
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Physiognomy	W				W											LW									W/LH																HH			LH					
Species / Sampling units	1	2	3	37	6	7	8	9	10	16	17	45	46	48	49	5	33	42	43	44	4	11	15	47	18	19	35	36	31	32	34	20	21	22	23	24	25	26	28	27	12	13	14	38	39	29	30	40	41
Salix humboldtiana Wild. var. *humboldtiana*	3	4	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	5	1	1	1	.	.	4	3	3	*	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Lippia alba (Mill.) N.E. Br	.	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	4	.	.	3	1	.	1
Muehlenbeckia sagittifolia (Ortega) Meisn.	1	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	4	1	1	.	.	.	.
Sesbania virgata (Cav.) Pers	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	.	2	1	1	1	1
Panicum prionitis Nees	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	4	4	3	.	.	.	.
Eupatorium hecatanthum (DC.) Baker	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.
Leptochla fusca (L.) Kunth ssp. *uninervia*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	.	.	.	.	.	.
Mitracarpus megapotamicus (Spreng.) Kuntze	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Paspalum denticulatum Trin	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.
Paspalum notatum Flüggé var. *notatum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.
Paspalum conjugatum Bergius.	4	4	2	4	.	1	1	1	.	.	.	1	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Sida rhombifolia L.	.	.	1	1	2	2	1	2	2	2	2	1	2	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Mikania cordifolia (L.f.) Willd.	4	3	3	2	2	3	2	3	2	.	.	2	2	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*	.	.	.	.	.	.
Croton urucurana Baill.	1	3	1	2	.	*	.	2	.	2	1	4	4	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cyperus entrerianus Boeck. var. *entrerianus*	1	.	1	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hyptis mutabilis (Rich.) Brinq.	4	4	4	2	3	3	3	4	3	2	3	1	1	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ipomoea cairica (L.) Sweet	1	1	1	3	1	.	*	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Steinchisma hians (Elliott) Nash	1	1	1	5	2	3	3	3	3	1	2	3	4	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urera aurantiaca Wedd	.	1	1	.	2	2	3	2	2	1	1	2	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aspilia silphioides (Hook. & Arn.) Benth	.	.	.	1	1	2	.	1	*	1	.	*	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Continue

Table 1. Continuation

N° Community	1				2											3									4																5			6					
Richness	32				52											23									28																24			23					
Diversity	1.44				1.68											1.21									1.31																1.34			1.31					
Mean topographic level (SD)	16.28 (0.13)				15.47 (0.96)											12.81 (0.74)									14.50 (0.5)																15.3 (0.13)			14.28 (0.44)					
Physiognomy	W				W											LW									W/LH																HH			LH					
Species / Sampling units	1	2	3	37	6	7	8	9	10	16	17	45	46	48	49	5	33	42	43	44	4	11	15	47	18	19	35	36	31	32	34	20	21	22	23	24	25	26	28	27	12	13	14	38	39	29	30	40	41
Solanum reflexum Schrank	.	.	.	1	*	*	2	1	.	1	1	1	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Albizia inundata (Mart.) Barneby & J.W. Grimes	.	.	.	1	2	2	2	2	.	.	.	5	4	3	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chenopodium ambrosioides L.	.	.	1	.	1	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erythrina crista-galli L.	.	1	.	.	2	2	2	4	2	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Teucrium vesicarium Mill.	.	.	.	3	3	3	2	1	2	3	3	4	4	3	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Telypteris sp.	.	.	.	.	2	1	1	1	3	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cestrum guaraniticum Chodat & Hassl.	.	.	.	.	1	1	1	1	1	.	1	1	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nectandra angustifolia (Schrad.) Nees & Mart. ex Nees	.	.	.	.	4	4	4	2	4	4	4	2	3	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Iresine diffusa Humb. & Bompl. ex Willd. var. *diffusa*	.	.	.	.	1	1	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Panicum sabulorum Lam. var. *sabulorum*	.	.	.	.	.	.	.	.	2	.	.	2	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Commelina diffusa Burm. f.	.	.	1	1	*	*	1	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Solanum pilcomayense Morong var. *pilcomayense*	1	1	.	.	.	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Byttneria filipes Mart. ex K. Schum.	.	.	1	1	.	.	.	.	.	.	.	.	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Morus sp.	.	.	.	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Smilax campestris Griseb.	.	.	.	.	*	*	.	.	.	1	1	*	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pfaffia glomerata (Spreng.) Pedersen	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicliptera squarrosa Nees	.	.	.	.	*	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Serjania meridionalis Cambess.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vigna adenantha (G. Mey.) Marechal, Mascherpa & Stainier	.	.	.	1	.	.	.	.	.	.	.	2	1	2	2	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Sicyos polyachanthus Cog.	.	.	.	.	.	1	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2	2	4	2	3	1	1	.	.	.	.	.	.	.	.	.	.	.
Sagittaria montevidensis Cham. & Schltdl. ssp. montevidensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	*	.	1	.	1	3	.	4	5	5	.	.	.	.	.	.	.	.	.	.

Continue

Table 1. Continuation

N° Community	1				2											3									4																5			6					
Richness	32				52											23									28																24			23					
Diversity	1.44				1.68											1.21									1.31																1.34			1.31					
Mean topographic level (SD)	16.28 (0.13)				15.47 (0.96)											12.81 (0.74)									14.50 (0.5)																15.3 (0.13)			14.28 (0.44)					
Physiognomy	W				W											LW									W/LH																HH			LH					
Species / Sampling units	1	2	3	37	6	7	8	9	10	16	17	45	46	48	49	5	33	42	43	44	4	11	15	47	18	19	35	36	31	32	34	20	21	22	23	24	25	26	28	27	12	13	14	38	39	29	30	40	41
Echinochloa polystachya (H.B.K.) Hitchc. var. *polystachya*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	2	2	3	.	.	.	.	.	.	.	.	.	.
Polygonum ferrugineum Wedd.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	3	3	3	.	.	.	.	.	.	.	.	.	.
Hymenachne pernambucense (Spreng.) Zuloaga	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	.	.	.	.	.	.	.	.	.	.
Ludwigia elegans (Cambess.) H. Hara	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	*	1	3	.	1	.	.	.	.	.	.	.	.	.	.	.
Cyperus giganteus Vahl	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	.	.	.	.	.	.	.	.	.
Inga affinis DC.	.	.	.	.	.	.	.	.	.	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Other species																																																	
Solanum angustifidum Bitter	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Alternanthera pungens Kunth	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Deyeuxia viridiflavescens var. *viridiflavescens*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex bonariensis Desf. ex Poir. var. *bonariensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryopteris concolor (Langsd. & Fisch.) Kuhn	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eclipta prostrata (L.) L	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*	.	.	.	.	.	.	.	.	.	.
Eriochloa punctata (L.) Desv. ex Hamilton f. *punctata*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Baccharis salicifolia (Ruiz & Pav.) Pers.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	*	1	.	.	.	1
Oplismenopsis najada (Hack. & Arechav.) Parodi	.	.	.	1	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Setaria parviflora (Poir.) Kerguélen var. *parviflora*	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	1	1	1	1	1	1	1	1	2	.	3	1	.	.	.	.	.	.	.	1	1	3	2	2	3	4	3

Continue

Table 1. Continuation

N° Community	1				2											3									4																5			6					
Richness	32				52											23									28																24			23					
Diversity	1.44				1.68											1.21									1.31																1.34			1.31					
Mean topographic level (SD)	16.28 (0.13)				15.47 (0.96)											12.81 (0.74)									14.50 (0.5)																15.3 (0.13)			14.28 (0.44)					
Physiognomy	W				W											LW									W/LH																HH			LH					
Species / Sampling units	1	2	3	37	6	7	8	9	10	16	17	45	46	48	49	5	33	42	43	44	4	11	15	47	18	19	35	36	31	32	34	20	21	22	23	24	25	26	28	27	12	13	14	38	39	29	30	40	41
Panicum dichotomiflorum Michx.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynodon dactylon (L.) Pers. var. *dactylon*	2	1	2	1	.	1	1	1	1	.	.	1	1	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	1	1	3	*	.	.	.
Panicum elephantipes Nees ex Trin.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyla reptans (Kunth) Greene	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Paspalum repens Bergius	.	1	1	.	.	.	.	.	.	.	.	1	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	1	.	.	.	.
Schoenoplectus californicus (C.A. Mey.) Soják var. *californicus*	1	.	.	1	.	1	1	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	*	.	.	.
Acmella decumbens (Sm.) R.K. Jansen var. *decumbens*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Coniza sumatrensis (Retz.) E. Walter var. *sumatrensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
Mikania periplocifolia Hook. & Arn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Xylosma venosa N. E. Br.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Jaborosa integrifolia Lam.	.	.	.	.	.	.	.	.	.	*	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cissus verticillata (L.) Nicolson & C.E. Jarvis ssp. *verticilliata*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cissus palmata Poir. var. *palmata*	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cuphea racemosa (L. f.) Spreng. var. *palustris* Lourteig	.	.	.	.	*	.	.	.	*	.	.	*	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salvia pallida Benth.	.	.	.	.	.	.	.	.	.	.	.	.	*	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sapium haematospermum Müll. Arg.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stigmaphyllon bonariense (Hook. & Arn.) C. E. Anderson	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senna pendula (Willd.) H.S. Irwin & Barneby var. *paludicola* H.S. Irwin & Barneby	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

herbaceous, occasionally including shrubby species such as *Solanum glaucophyllum* Desf., *S. virgata* or *M. pigra*, which are also present in other communities. Some other species are common in this unit: *Mitracarpus megapotamicus* (Spreng.) Kuntze, *Enydra anagallis* London J. Bot., *Echinochloa crus-pavonis* (Kunth) Schult and *Funastrum clausum* (Jacq.) Schltr. The shrubby layer reaches 2 m tall, while the herbaceous layer is 0.10 to 0.50 m tall, covering from 20 to 100 % of the soil surface respectively. *Cynodon dactylon* and *Baccharis salicifolia* (Ruiz et Pav.) Pers. are found in drier soils, while *P. punctatum* is located in wet areas, representing a transitional stage to Community 3.

Vegetation communities and flooding frequency

The schematic distribution of the vegetation units in the topographic level is shown in Fig. 3. Communities 1 and 2 are usually located at the highest elevations. The forests included in Community 4 are placed in middle positions of the topographic gradient together with some herbaceous communities. Among the latter, the aquatic vegetation of the lotic environments (Community 3) is placed in the lowest areas, while Community 5 occupies the middle-high portion of the topographic gradient. Finally, the unit described in Community 6 is located between Community 5 and the ponds.

The monthly variation in the hydrometric level of the Paraná River (for a 10-year series), such as the mean topographic distribution of all the sampling units corresponding to each community (Tab. 1), allows to estimate the pulse regime for each defined community (Fig. 4). It must be noted that, taking into account the average topographic level of each vegetation unit, Communities 1 and 2 were the least connected to the main water course (duration and intensity of floods were lower). While Community 1 was related to 5 floods, Community 2 was related to 8 floods during the considered period.

On the other hand, Community 5 had flooded 11 times, while Communities 4 and 6 had the highest flood frequency during the same period. Finally, Community 3 was flooded most of the time, except for September 2001.

Ordination

The spatial distribution of the sampling units in DCA (Fig. 5) indicates that the first ordination axis is directly associated with the recurrence and the duration of the floods. Communities 1 and 2 (the highest ones in the topographic level) are placed on the negative extreme on axis 1 of Figure 5. They represent the communities less exposed to the floods. On the other hand, Community 3 is found in the positive extreme on the first axis and it is distributed on the lowest topographic level, being consequently the most exposed to the floods. Those communities are usually found in intermediate topographic positions, which are adapted to intermediate flooding conditions (Communities 5, 6 and 4), appear in the middle position of the same axis.

On the second ordination axis, communities 4, 1 and 2 are associated to high-energy environments (running water, primary and secondary water courses) and they are mostly on the positive side. On the contrary, Communities 6 and 3, composed of transitional species and free life aquatic species respectively, are on the opposite extreme. This distribution in the vegetation communities suggests a water energy gradient.

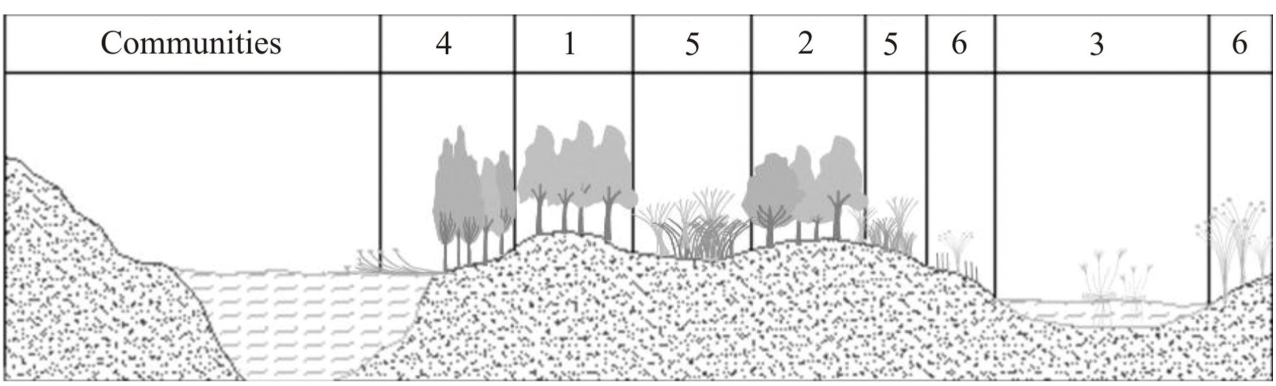

Fig. 3. Schematic representation of the spatial distribution of the studied communities. 1. Willow forests of marginal levees; 2. Riverine forests of internal levees; 3. Floating meadows; 4. Floating rooted plants; 5. Tall grass community; 6. Marshy community.

DISCUSSION AND CONCLUSION

Floristic composition

Floristic composition data revealed a large number of families represented by few species each, which indirectly reflects environmental heterogeneity of Parana River islands. Similar studies carried out by Faggi & Cagnoni (1989), Aceñolaza & Muñoz (2003), Aceñolaza *et al*. (2004, 2005 & 2008) have found a comparable composition for the first 7 families mentioned above. Hence, it can be stated that the families mentioned are among the richest in environments associated to the middle Paraná River even on the islands of the main course.

Table 1 allows identifying some interesting situations. For instance, Community 4 is composed of 2 variants: one dominated by young forests of

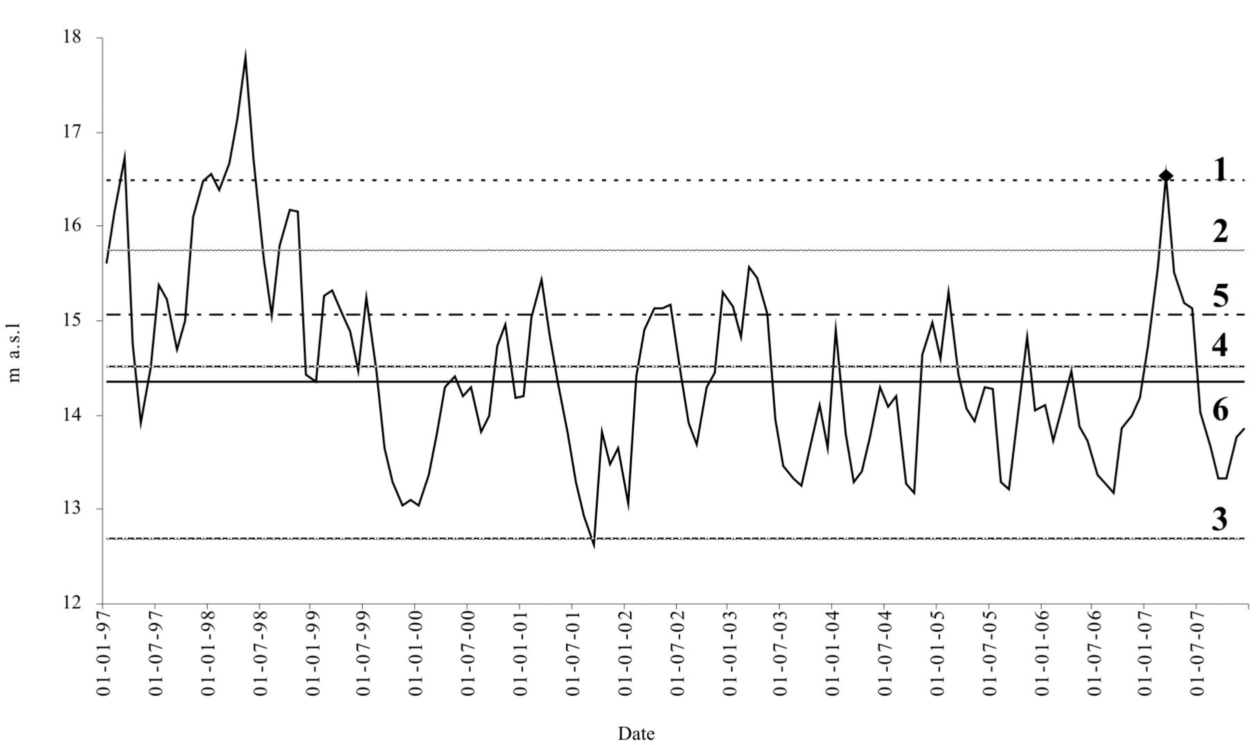

Fig. 4. Water level variations of the Paraná River at the Paraná city (1997-2007) and its relationship with vegetation communities. 1. Willow forests of marginal levees; 2. Riverine forests of internal levees; 3. Floating meadows; 4. Floating rooted plants; 5. Tall grass herbaceous community; 6. Marshy community.

S. humboldtiana and *T. integrifolia*, whereas the second corresponds to an herbaceous-sub-shrubby unit dominated by species of *Polygonum spp.* and *Echinochloa spp*. In spite of the fact that this community has a similar flood frequency to Community 3 (both communities are on the right extreme on axis 1 of Fig. 5), they are different in physiognomy and specific composition. While Community 3 only comprises the herbaceous species (aquatic rooted or free-living), Community 4 includes woody components. Despite the fact that the species in both communities are tolerant to high flood frequency, the difference may reside in the degree of connectivity to the main water channel and, through it, to the water energy. While Community 3 colonizes lentic environments, Community 4 is located along the main channel and it is associated to high-energy courses (lotic environments). In this way, system energy (either mostly lentic or lotic) would be a secondary factor that influences the floristic differentiation in communities with a high frequency of floods. In addition, Community 6, which colonizes the ponds, is close to Community 3. Both communities are related to floods of low energy, which originate when the secondary channels drive water into the ponds.

On the other hand, the woody component of Community 4 is similar to Community 1 in relation to the presence and permanence of *S. humboldtiana*. This species is pioneer colonizing bars in the main channel, which are the first geomorphological elements in the formation of the islands. From the successive phases of the hydro-sedimentological regime, *S.*

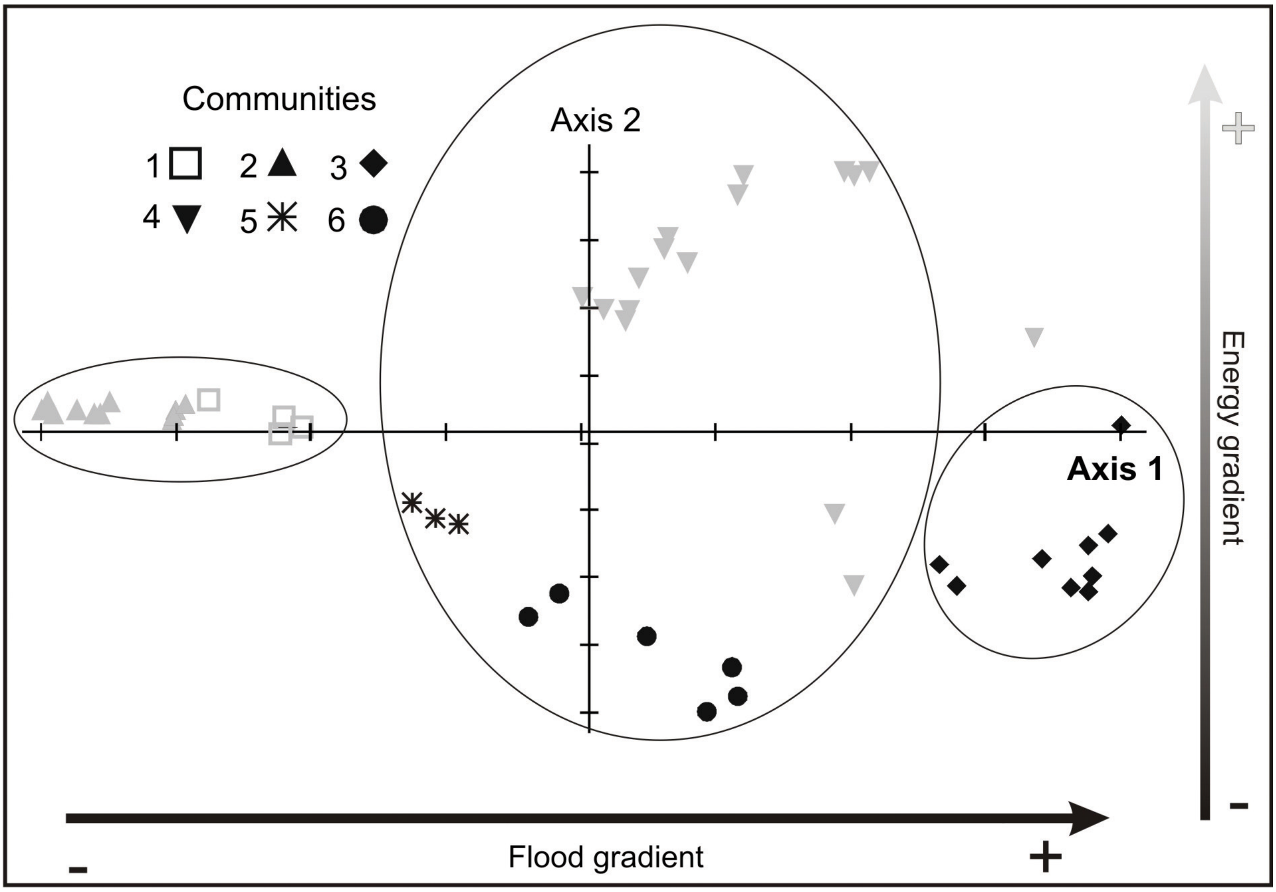

Fig. 5. Two-dimensional representation of DCA (Detrended Correspondence Analysis) based on species abundance-coverage data. Communities: 1. Willow forests of marginal levees; 2. Riverine forests of internal levees; 3. Floating meadows; 4. Floating rooted plants; 5. Tall grass herbaceous community; 6. Marshy community. Axis 1 represents a flood gradient; on the left are placed the communities with the highest topographic elevation; on the right are placed the lowest communities. On axis 2 (Energy gradient) the grey color shows communities associated to primary and secondary water courses with a high energy (lotic environment), in black color it appears communities associated to ponds or swamp with a low water energy (lentic environment).

humboldtiana is able to develop monospecific forests (Lewis & Franceschi, 1979). Because of that, it can be considered that the woody subgroup of Community 4 dominated by *S. humboldtiana* and *T. integrifolia* represents an earlier stage of more developed forests represented in Community 1. Neiff (2004) has documented the ecological plasticity of these species, which enables *S. humboldtiana* and *T. integrifolia* to occur in environments exposed to diverse flooding regimes, such as Communities 1 and 4 with different flooding frequencies.

Similar communities to those herein studied have been identified in neighboring areas (Franceschi & Lewis, 1979; Lewis & Franceschi, 1979; Franceschi *et al*., 1985). Franceschi *et al*. (1985) identified and described the vegetation units on a group of islands located 120 km to the south of our study zone. Forests studied in this work have similar physiognomic, structural and floristic characteristics to those described by Franceschi *et al*. (1985). Authors described the internal forests as insular forests dominated by *N. angustifolia* and in earlier stages dominated by *A. inundata*. In this regard, Figure 2 displays a clear differentiation among the censuses, which form Community 2. These data suggest the existence of a variant of fluvial forests represented by an association of *A. inundata* and *C. urucurana* that could correspond either to the earlier stages mentioned by Franceschi *et al*. (1985) or to a more developed subtype of Community 2.

Distribution of vegetation units

The pattern of spatial distribution of the plant communities herein studied is similar to those presented by Casco (2003) and Neiff (1986) for other latitudes of the Lower Parana floodplain, by Campos *et al*. (2000) for the Upper Parana and by Kalesnik & Aceñolaza *et al*. (2008) for the Parana Delta.

Soares & Perez Filho (1997) mentioned that environmental diversity of large rivers is related to the physical and chemical variation of the sediments. Apart from that, the interaction between the topography and the hydrological regime has an impact on diversity. Indirectly, the differences in the topographic position regulate the influence of pulse regime on plant communities; either enhancing or reducing the water energy caused by high or low river water levels.

Other studies carried out in southeastern Brazil in order to test the relationship between riparian forest diversity and channel width, have found that the main variation was caused by the river hydrological phases (Metzger *et al*., 1997). These authors point out that the vegetation units more affected by floods had the lowest diversity and evenness values. In this work, the mentioned situation corresponds to the forests of Community 4, which has low richness and diversity values. On the other hand, riverine forests of internal levees (Community 2) are less flooded and they constitute the most complex and diverse formation of the fluvial environments. Willow forests of marginal levees share the same topographic elevation as riverine forests of internal levees, but the first ones are simple in their structure, less diverse and with important differences in their specific composition. The mentioned differences between forests related to similar flood intensities (e.g. Communities 1 and 2) suggest that, apart from the flood frequency, other factors are regulating the characteristics of the vegetation communities. A possible hypothesis may be inferred from the analysis of the second axis in Figure 5, where communities with similar flood frequencies are opposites. Community 4 (on the positive side of the axis) colonizes lotic environments, while communities 3 and 6 (on the negative side) correspond to vegetation associated with lentic water bodies. It must be assumed that a second variable, presumably water energy, could cause these differences. In the internal and lowest topographic positions of the island, species respond to a different rate of water vertical movement, which is not necessarily related to the hydrometric height of the river. During the low water phase and due to the reduction of water bodies the vegetation associated with lentic water (Community 3) can survive only in the deepest ponds. During these periods with low water level, tall grasslands and herb species (Community 5) partially colonize these low sites, creating a particular specific composition (Community 6). During these fast colonization and regression processes, the communities become fragmented in patches, which will be in accordance with the micro topographic conditions.

It can be concluded that micro topographic differences (which establish the relationship between the vegetation and the pulse regime) and the water energy (determined by the connectivity degree with the main water channel) could be the most important factors in determining the composition and distribution of the vegetation in the environments of the middle Paraná. Nevertheless, the differences in richness and structure of the forests could not be explained from these factors. Despite the fact that they are distributed at the same topographic level they have strong differences in richness and structure. Other factors like the geomorphological dynamics, succession, the quality of sediments and groundwater should be taken into account to explain the characteristics and distribution of fluvial forests in the Paraná River floodplain.

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