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Pulse regime and vegetation communities in fluvial systems: The case of the Parana River floodplain, Argentina

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ABSTRACT

Aim of this study was to evaluate the influence of flood pulse regime attributes (pulse frequency, pulse average intensity and amplitude, and flooded days) on the floristic differentiation of the Argentinian Middle Parana river floodplain vegetation in a 39-year period. Besides on floristic composition richness, diversity, evenness, percentage of woody species and topographic position were assessed for 7 communities. Pulse regime attributes were evaluated for each community taking into account different topographic positions and hydrological levels of the Parana River. Our result showed that fluvial vegetation is not floristically differentiated according to its topographic position and there is a weak relation between pulse regime attributes and diversity of woody and herbaceous species. Because of the same topographic position has been colonized by different vegetation communities, floristically different communities share similar pulse frequency, pulse average intensity and amplitude, and flooded days. Pulse regime effects on fluvial vegetation are dependent on more than the topographic position; other aspects of the dynamics of fluvial systems such as the geomorphologic architecture, sediment load and channel dynamics should be included in order to explain the floristic differentiation of the Parana River floodplain vegetation.

Introduction

Like other lowland subtropical rivers, the Parana River, the second most important one in South America, is characterized in its hydrological regime by seasonal and successive phases of high and low water, also known as ‘flood pulse’ (Junk et al., 1989) or ‘pulse regime’ (Neiff, 1996). Unlike the well known flood pulse, ‘pulse regime’ considers both flood and drought phases, which are characterized by different and complementary ecological processes (Neiff, 1999). Water, sediments, nutrients and seeds are all distributed to different places of fluvial systems during high water phases, when local vegetation experiences dormancy periods (Worbes, 1985), leaves falling (Worbes, 1997) and plants fruiting (Colonello, 1991). On the contrary, germination, seedling growth and colonization of new sites, as well as growth of already settled vegetation, all this takes place during low water phases (Neiff, 2004).

Pulse regime dynamics have been acknowledged as a modelling agent of fluvial systems (Casco, 2004; Neiff, 1996) and as one of the main conditioning factors of the characteristics and spatial distribution of biological communities there (Junk et al., 1989). Among the ecosystem components, the vegetation of fluvial systems has key ecological functions [providing food and refuge to different species (Dibble and Pelicice, 2010); functioning as corridor for species dispersal (Naiman et al., 1993), and modifying sedimentation rates (Dezzeo et al., 2000)]; social functions [as food, medicine and as raw material in family productions (Carhuanca, 1995)], and economic functions as well [mitigating the flood wave during floods (Neiff et al., 2006)]. These functions depend on vegetation development and persistence, and so the study of processes that affect them is a necessary step in understanding not only the vegetation dynamic in fluvial systems but its associated ecological, social and economic functions too.

The relationship between vegetation and pulse regime (either as hydrological dynamic or flood pulse) has been studied in different fluvial systems, such as the Mississippi (Moore et al., 2011), Orinoco (Chacón-Moreno et al., 2004; Rosales, 1990), San Francisco (Carvalho et al., 2005), Amazon (Puhakka et al., 1993; Valle Ferreira and Stohlgren, 1999) as well as in other water courses of South America (Budke et al., 2008, 2010; Giehl and Jarenkow, 2008). These studies have considered different aspects of hydrological dynamics such as water quality, sediment concentration, sedimentation rates, floods, soil features and topography. In the Parana fluvial system, up till now the topographic position of plant species and

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vegetation communities has been almost the only aspect considered addressing the relationship between vegetation and pulse regime (Casco, 2003; Casco et al., 2010; Marchetti and Aceñolaza, 2011).

The above mentioned studies arrived at different results; while some of them emphasized pulse regime or its flood phase as the main determinant of the characteristics and distribution of fluvial vegetation, others pointed out that other variables are just as important or have even more influence than the interaction of topographic position and pulse regime affecting the floodplain plant cover. As a result, the effects of pulse regime on the vegetation characteristics of fluvial systems and the role of topographic position as a key variable to evaluate these effects in the Parana River system is still a confusing and poorly known subject.

The present study is aimed at evaluating vegetation characteristics (richness, diversity, evenness and woody species percentage) in relation to pulse regime attributes, such as pulse frequency, intensity and amplitude average pulse, and flooded days in the Middle Parana River floodplain. The aim is to answer the following questions: 1. Is the vegetation floristically differentiated according to its topographic position?, 2. Is there a relationship between pulse regime attributes and vegetation characteristics?, 3. Is it sufficient to consider topographic position in order to study the pulse regime effects on vegetation communities?

Materials and methods

Study area

The present work was carried out in a sector of the Middle Parana River floodplain where, besides the Parana, there is also the Colastine River, the region's second most important watercourse (Fig. 1). Both rivers belong to the La Plata River basin, the second most important drainage basin in South America and among the ten largest fluvial systems in the world (3,100,000 km^2). The Parana River is more than 2000 km long and has an annual mean flow of 17,000 m^3 s^{-1}. The main tributary of the Parana River in the study zone, the Colastine River, is 35 km long and has a mean flow of about 17,000 m^3 s^{-1}. The hydrological dynamics of the Parana River are characterized by high water phases with flows of up to 25,000 m^3 s^{-1} which take place from October to March, and by low water phases with flows of less than 16,000 m^3 s^{-1} which occur from April to September (Neiff, 1990a). These regular water phases take place every 2 or 3 years and produce water level variations of 2–3 m. The hydrological dynamics of the Parana River also experience, every 8–10 years, extreme events of 60,000 and 8000 m^3 s^{-1}, respectively (Ceirano et al., 2000), as extraordinarily high and low water phases (Fig. 2). The Colastine River is connected to the Parana River (both at its headwater and mouth), and because of this, it experiences the high and low water phases of the Parana.

In its middle section the Parana River created a floodplain of 600 km in length and 13–60 km in width with a surface of about 7200 km^2. The geomorphology of the floodplain is characterized by channels and flood deposits (Drago, 1971). The former are represented by geomorphological units such as sandbanks, meander plains and spills, while the latter are found in plains of hindered drainage (Iriondo and Drago, 1972). This geomorphological differentiation determines that, although the entire floodplain shares a common pulse regime (Neiff, 1990a), its effects are not equal across the whole floodplain.

The climate of the Parana River floodplain is humid subtropical with a mean annual temperature of 19 °C. Rainfall ranges from 900 to 1000 mm per year, with 73% of it occurring mainly from October to April (Rojas and Saluso, 1987).

Soils consist of successive layers of sediment carried and deposited by the river with each flood phase. As a result, the spatial distribution and thickness of sediment layers are heterogeneous. Fluvial soils correspond to Entisol group and Fluvent and Acuent subgroups (Orellana and Bertoldi De Pomar, 1969). Fluvents correspond generally to high places (levees), while Acuents correspond to soils of low places (marshes).

Data collection

Vegetation sampling

Seven sampling sites (A–G in Fig. 1) were selected in the study area, based on previous field research and on satellite images Landsat 5 TM Path 227/Row 082, showing high and low water phases. Between 2 and 4 different vegetation types were identified in each sampling site. A total of 65 vegetation samples were taken from the 7 sampling sites (A–G, Fig. 1). The coverage-abundance of each species included in the sample units (from herbaceous to woody species) was recorded according to the coverage-abundance scale of Müller-Dombois and Ellenberg (1974). It considers the following categories: r: just one individual is detected and it covers less than 5% of the sample surface, +: approximately among 2–20 individuals are detected and they cover less than 5% of the sample surface, 1 = more than 20 individuals covering less than 5% of the sample surface, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100% sample surface coverage. Minimal area of each sample unit was determined by constructing a species-area curve for each vegetation sample (Chytrý and Otýpková, 2003). The curve was calculated in the field within the surface occupied by each homogeneous vegetation unit. The species-area curve was achieved avoiding counts of species from another vegetation unit (Perelman et al., 2005). Thus, vegetation sampling was performed in an area of 400 m^2 (20 m × 20 m quadrants) and 25 m^2 (5 m × 5 m quadrants) for woody and herbaceous vegetation, respectively. Species that could not be identified in the field were collected for taxonomic determination. Botanical nomenclature of all species followed Zuloaga et al. (2008a,b,c).

Topographical position of vegetation

Ten records of topographic position were performed in the field (using a theodolite) for each of the 65 vegetation samples. The final value of each topographic position was calculated considering the following terms: (1) reading of the specific point (with reference to the water level in the river, which was also referenced to the zero hydrometric of the closest harbor), (2) topographic position of zero hydrometric of the closest harbor (Parana city, Entre Ríos province) and (3) level increase due to local hydraulic slope (0.45 cm/km). Daily topographic readings were referenced to Parana River's water level at the time.

Pulse regime of the Parana River

The pulse regime of the Parana River was assessed through a 39-year-hydrological series (1970–2009), which is shown in Fig. 2. This period was selected because it corresponds to a uniform period in the variability of the river flow for the last century (Amsler et al., 2005). Hydrometrical levels used to study river dynamics correspond to the daily records made by Prefectura Naval Argentina in the Parana city harbor, Entre Ríos. Monthly values were obtained from averaging daily records.

Data analysis

Vegetation communities

Vegetation samples were organized in a primary matrix made from abundance-cover data of each species. Symbols "r" and "+",

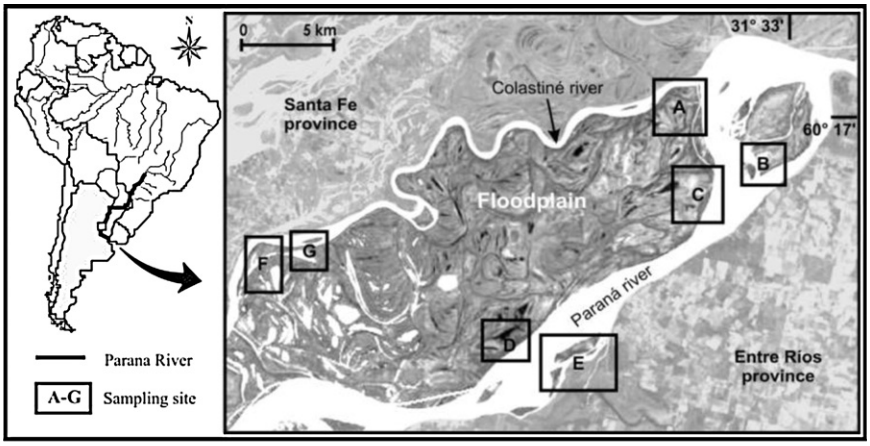

Fig. 1. Study area: a sector of the Parana River floodplain in its lower part, located between the Parana and Colastine Rivers.

included in the Müller-Dombois and Ellenberg abundance-cover scale, represent an abundance-cover value lower than 1, which is the following number in the scale. Symbols "r" and "+"were transformed to values "0.20" and "0.50", respectively, in order to include them together with the rest of the values (1–5) in the classification analyses.

The main matrix was classified using a cluster analysis, with Euclidean distance as dissimilarity measure and Ward method as linkage criterion.

A multi-response permutation procedure (MRPP, McCune and Grace, 2002) was performed to test the difference in floristic composition among the communities defined by the cluster analysis. MRPP is a nonparametric method for testing multivariate differences among predefined groups (Zimmerman et al., 1985).

Richness, Shannon-Wiener diversity index, evenness and percentage of woody species were obtained for each vegetation community. All floristic analysis was carried out with PC Ord 4.1 software (McCune and Mefford, 1999).

Topographic positions

Since data did not meet normality and homoscedasticity assumptions, statistical differences in topographic position among vegetation communities were assessed using a non parametric analysis of variance. A Kruskal–Wallis test was applied for a significance level of 0.05 (Zar, 1999).

Pulse regime

Different attributes of the pulse regime, such as frequency, intensity, average amplitude pulse and flooded days were assessed for the 39-year period in relation to each of the ten topographic position values for each vegetation community. Pulse regime attributes were computed using PULSO 1.1 software (Neiff and Neiff, 2003) in which "frequency" refers to the number of pulses (high water phase *plus* low water phase) recorded in a given period; "average intensity" refers to the magnitude achieved by the high or low water phase (recorded in meters in the hydrometrical scale); "average amplitude" considers the average days of pulse duration during the studied period and "flooded days", also call 'potamophase days', refers to the amount of flooded days throughout the entire period (Fig. 3). All mentioned attributes correspond to each topographic position of each point in the fluvial landscape.

Relationship among vegetation communities and pulse regime

Since data did not meet normality and homoscedasticity assumptions, differences among vegetation communities regarding pulse frequency, pulse average intensity and amplitude, and flooded days were evaluated using a Kruskal–Wallis non parametric analysis of variance.

A simple regression analysis was performed to evaluate the relation between pulse regime attributes (pulse frequency, pulse

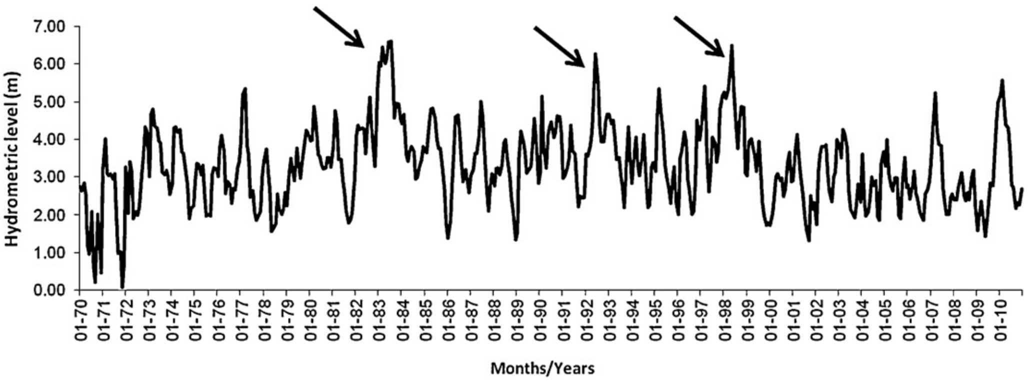

Fig. 2. Hydrometric levels of the Parana River recorded at Parana harbor from 1970 to 2009 by Prefectura Naval Argentina. The arrows show extraordinary floods.

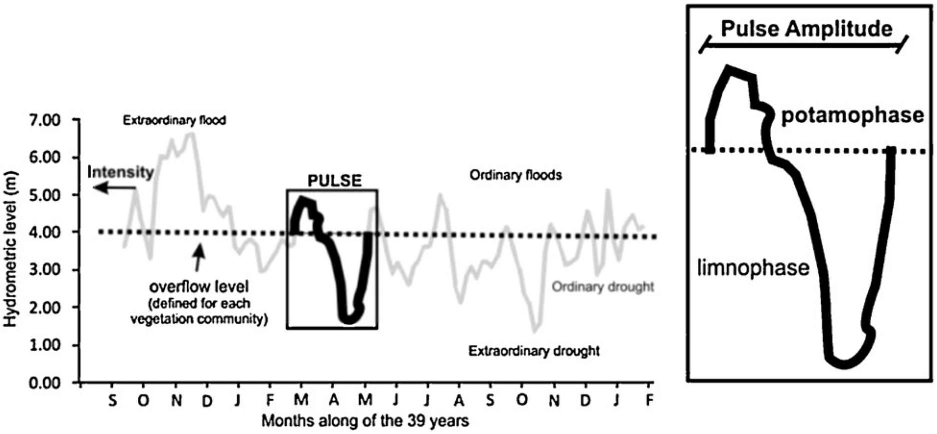

Fig. 3. Schematic representation of pulse regime attributes.

Source: Modified from Neiff (1996).

average intensity and amplitude, and flooded days) and total diversity as well as woody and herbaceous species diversity. In each case the statistical significance was evaluated. Statistical analyses were performed with STATISTICA 7.1 (StatSoft., 2005).

Results

Floristic differentiation of fluvial vegetation

One hundred and seventy-nine species were identified in 65 vegetation samples. The classification analysis allowed the identification of seven floristically and statically different communities (Fig. 4), according to the non-parametric analysis of multi-response permutation (MRPP).

Marshy-Terrestrial and Marshy communities are located inside the floodplain and are both associated with lentic water bodies. The first one is occasionally flooded and it is floristically and physiognomically dominated by *Polygonum punctatum*, a marshy species. The second one is frequently flooded and it is represented by a set of rooted or floating aquatic species.

The Alder forest is dominated by *Tessaria integrifolia* (Alder); it is one of the simplest vegetation communities in both structure and species composition. The Alder forest colonizes bars and islands of the main channel. The Tall grassland is an herbaceous community, but unlike the other herbaceous communities which range from 0.50 to 1 m in height, the Tall grassland is more than 2 m in height, includes shrubby species and colonizes more elevated topographic positions.

The Acacia forest (*Acacia caven*), not so frequent in fluvial landscapes, has a simple structure. The Pluri-specific canopy forest (forests in which the upper stratum is dominated by several species of trees) shows a more complex structure; it is located mainly on levees placed along secondary water courses and is among the richest and most diverse woody communities. The last identified community, the Willow forest (dominated by Willow, *Salix humboldtiana)*, is simple in its structure but floristically as rich and diverse as the Pluri-specific canopy forest. It is located on bars and levees in diverse degrees of development, placed along water courses of higher energy.

The most frequent species, richness, diversity, evenness and woody species abundance of each vegetation community are shown in Table 1. High richness values were found in the Tall grassland and the Alder forest; however, both diversity and evenness were higher in the Willow forest and the Pluri-specific canopy forest. The Marshy community and the Marshy-Terrestrial community presented the lowest richness values while, as expected, the woody species increased in woody communities.

Topographical position of different vegetation communities

Since topographic position has been proposed as essential to determine the pulse regime effects (Casco, 2004), we recorded at least 10 points of topographic position within each one of the 65 sample units. The topographic position was significantly different among vegetation communities, both between and within herbaceous and woody communities (Table 2).

Pulse regime for each vegetation community in a 39-year period

The seven vegetation communities showed two different kinds of behavior regarding their relationship with the pulse regime (Fig. 5). Herbaceous communities showed a behavior that was clearly different from woody communities (Table 3). Herbaceous communities experienced the highest pulse frequency (from 28 to 50 times during the 39-year period), also showing the highest values of flooded days (from 48.6% to 65% of the considered period). Their pulse average amplitude (from 290 to 518 days) and pulse average intensity (from 1.9 to 2.5) were the lowest. On the contrary, woody communities had the lowest pulse frequency (from 3 to 48 times) and the lowest number of flooded days (18.4 to 35.8% of considered period); pulse average amplitude (from 296 to 3451 days) and intensity (1.9 to 3.2) were higher than in herbaceous communities.

No significant differences among herbaceous communities were found for all pulse regime attributes. On the contrary, the Alder forest showed significant differences in frequency and pulse average amplitude compared with the Pluri-specific canopy and the Willow forests.

Finally, significant differences were found for different pulse attributes between herbaceous and woody communities (Fig. 5).

Pulse regime and diversity

Although the relationship between pulse attributes and diversity was significant in all cases, the pulse attributes had a low explanatory power for vegetation diversity. Fig. 6 considered diversity for all species together, Fig. 7 for woody species, and Fig. 8 for herbaceous species. All analysis showed the same pattern: The highest diversity values were recorded at the lowest pulse

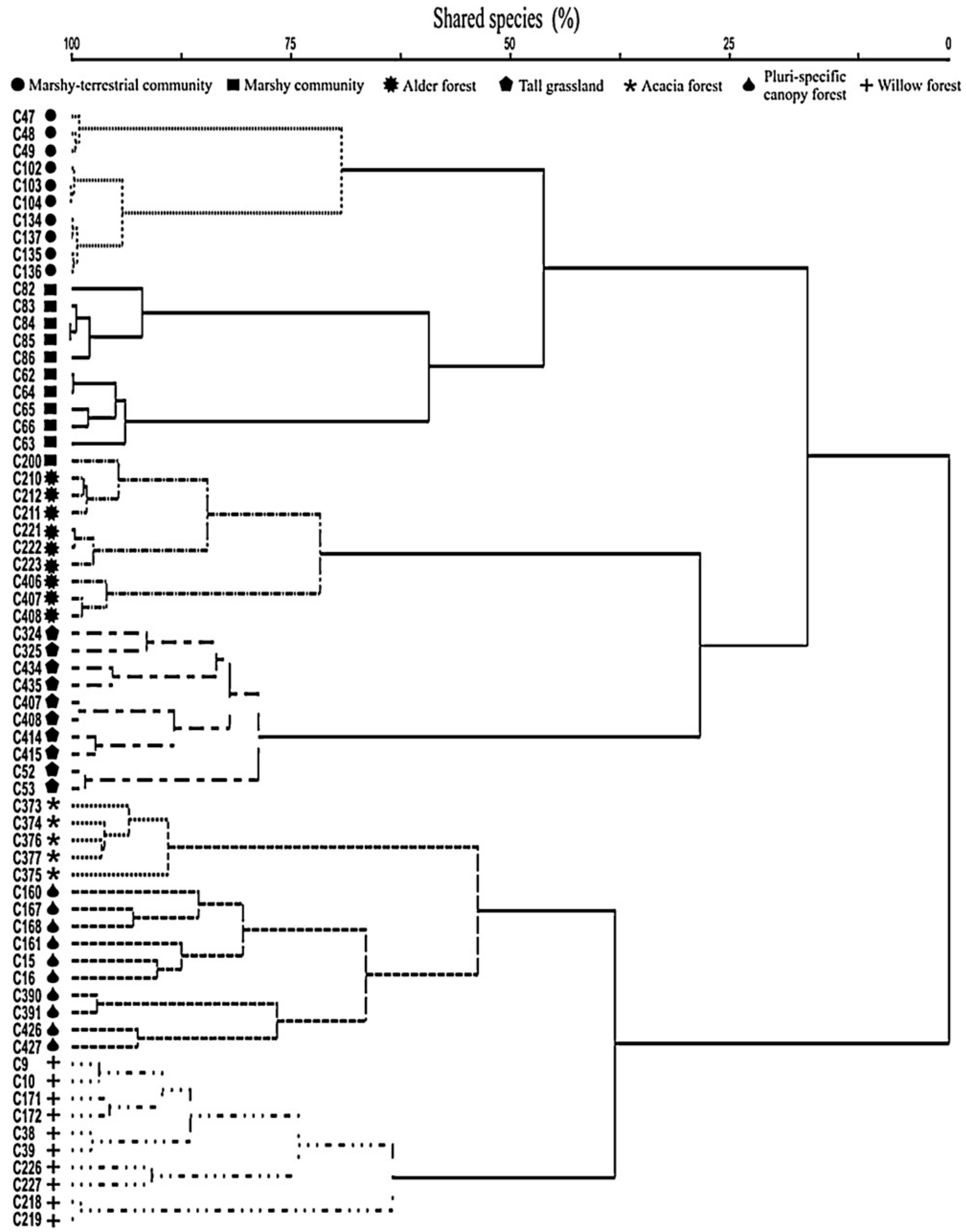

Fig. 4. Classification of 65 vegetation samples through Euclidean distance as dissimilarity measure and the Ward Method as linkage criterion. Seven vegetation communities can be identified.

frequency, at medium level of flood pulse amplitude and intensity, and at lowest values of flooded days (Figs. 6–8). Nevertheless, high diversity values were also found at different levels of all pulse attributes. The better fit ($R^2 = 0.32$) was found between woody species and pulse intensity and flooded days, but the data dispersion is considerably high.

Discussion

Pulse regime as determining factor of the floristic differentiation of fluvial vegetation

Different aspects related to the spatial-temporal hydrological dynamics of fluvial systems have been proposed as conditioning factors for the floristic differentiation, distribution and characteristics of the floodplain vegetation (Junk et al., 1989; Rosales, 1990; Puhakka and Kalliola, 1993; Puhakka et al., 1993; Salo et al., 1986; Malvárez, 1997; Casco et al., 2005a; Geissler and Gzik, 2010). Concerning the principal vegetation types, herbaceous vegetation usually prevails at low topographic positions (more floodable), woody vegetation is more restricted to the highest topographic positions (less floodable).

This pattern implies that the floristic differentiation should be related to the topography-pulse regime interactions shaping different communities. Our results confirm this pattern only partially, since all vegetation communities identified were significantly different in their floristic composition, but only some of them showed significant differences in their topographic position. The Marshy community colonized the lowest topographic position and was significantly different from all other vegetation communities. According to Franceschi et al. (2000), floristic differentiation and spatial distribution of herbaceous communities inhabiting fluvial systems are a consequence of moisture regime and topographic gradients. This could explain the floristic separation of the often waterlogged Marshy community from the two other herbaceous communities. Nevertheless, these other two herbaceous

Table 1
Summary of main species and vegetation features. S: richness, H: Shannon-Wiener diversity index, E: Pielou evenness. The last two attributes are expressed as a mean of all sample units which belong to the same vegetation community. In 'woody species': column 1 = category according to Müller-Dombois and Ellenberg (1974) which represents the coverage-abundance score of woody species in each vegetation community, 2 = percentage of woody species within the total number of species recorded in each vegetation community. HSC: herbaceous short-growing community, HTC: herbaceous tall-growing community, WTC: woody-tree community, WSC: woody-shrub community. Plant species names according to Zuloaga et al. (2008a,b,c).

Vegetation communities	Main species	S	H	E	Woody species	
					1	2
Marshy-terrestrial HSC	*Polygonum punctatum*, *Phalaris angusta*, *Plagiocheilus tanacetoides*, *Alternanthera philoxeroides* var. *philoxeroides*, *Eleocharis viridans*	36	2.04	0.84	+	2.8
Marshy HSC	*Panicum elephantipes*, *Ludwigia peploides* ssp. *peploides*, *Pistia stratiotes*, *Eichhornia crassipes*, *Azolla filiculoides*, *Myriophyllum aquaticum*, *Utricularia gibba*	16	1.72	0.83	0	0
Tall grassland HTC	*Panicum prionitis*, *Cynodon dactylon* var. *dactylon*, *Lippia alba*, *Setaria parviflora* var. *parviflora*, *Modiolastrum malvifolium*, *Acacia caven* var. *caven*, *Alternanthera philoxeroides* var. *philoxeroides*, *Sida rhombifolia*, *Salvia pallida*, *Sesbania virgata*	62	2.89	0.93	2	12.9
Acacia forest WTC	*Acacia caven* var. *caven*, *Sida rhombifolia*, *Lippia alba*, *Chenopodium ambrosioides*, *Modiolastrum malvifolium*, *Solanum pilcomayense* var. *Pilcomayense*	37	2.77	0.93		18.9
Alder forest WSC	*Tessaria integrifolia* var. *integrifolia*, *Salix humboldtiana* var. *humboldtiana*, *Mikania periplocifolia*, *Solanum pilcomayense* var. *Pilcomayense*	52	2.44	0.91	5	13.5
Pluri-specific canopy forests WTC	*Albizia inundata*, *Nectandra angustifolia*, *Erythrina crista-galli*, *Sida rhombifolia*, *Teucrium vesicarium*, *Conyza bonariensis* var. *bonariensis*, *Solanum reflexum*	54	2.97	0.95	5	31.5
Willow forest WTC	*Salix humboldtiana* var. *humboldtiana*, *Teucrium vesicarium*, *Commelina diffusa* var. *diffusa*, *Lippia alba*, *Mikania cordifolia*, *Croton urucurana*	59	2.93	0.94	4-5	27.1

Table 2
Differences in topographic position for the different vegetation communities. Contrasts were computed by Kruskall Wallis analysis.

	Marshy	Tall grassland	Acacia forest	Alder forest	Pluri-specific canopy forest	Willow forest
Marshy-Terrestrial	<0.01*	0.66	0.40	0.67	<0.01*	0.020*
Marshy		<0.01*	0.01*	0.01*	<0.01*	<0.01*
Tall grassland			0.23	0.99	<0.01*	<0.01*
Acacia forest				0.23	0.340	0.260
Alder forest					<0.01*	<0.01*
Pluri-specific canopy forest						0.850

* Differences for a significance level of $p < 0.05$.

communities, while being floristically different, did not show significant differences between them with respect to their topographic position.

Sediment layers have been identified as a possible factor of floristic differentiation in herbaceous vegetation (Chacón-Moreno et al., 2004). The Marshy-Terrestrial community of the Parana River floodplain colonizes silty layers to a depth of this substrate up to more than 1 m, while the Tall grassland colonizes superficially silty-clayed sediments below of which there are sandy layers (Marchetti, 2011). Chacón-Moreno et al. (2004) showed a significant relationship between the surface portion of clay and loam, and grassland distribution of flooding savannas of the Orinoco River. The amount of clay and loam modifies the capacity to accumulate water during flood events and determines evaporation rates. Dry soil shrinks and damages the roots of herbaceous plants. The Marshy-Terrestrial community has a superficial root system restricted to fine-grained, silty soil layers, while the Tall grassland root system is able to explore the deeper sandy layers. It is thus able to survive in drought stress conditions, when the Marshy-Terrestrial community disappears.

The topographic positions colonized by these herbaceous communities (Marshy-Terrestrial and Tall grassland) are also colonized by a woody community, the Alder forest. Although the three communities colonize similar topographic positions, they grow in different environments: While the herbaceous communities are associated to environments of low water flow energy inside the

Table 3
Mean (bold), followed by minimum and maximum values for each pulse regime attribute and each vegetation community in the 39-year series studied. **Pulse Frequency** is expressed in number of pulses (No) and involves high plus low water phases; **Pulse Average Amplitude** is the average number of days of pulse duration during the studied period (No days); **Pulse Average Intensity** expresses, how important the high water phase was; it is express in the hydrometric level reached; **Flooded days** expresses the number of days in this phase (No days) and the percentage that the flooded days represent in the 39-year series studied.

Vegetation communities	Sampling units	Average topographic positions	Pulse frequency	Pulse average amplitude	Pulse average intensity	Flooded days	
	No	Meters above sea level	No	No days	Hydrometric level	No days	%
Marshy-Terrestrial	**10**	**14.5**	**40** 28–47	**365** 308–518	**2.14** 1.96–2.45	**7589** 2362–11724	50.0
Marshy	**10**	**13.5**	**43** 39–50	**337** 290–370	**2.05** 2.01–2.15	**9342** 7219–10464	65.0
Tall grassland	**10**	**14.3**	**46** 43–49	**321** 296–337	**2.14** 2.05–2.21	**7090** 5795–9599	48.6
Acacia forest	**5**	**14.8**	**29** 23–37	**500** 369–633	**2.44** 2.33–2.54	**2719** 1711–4014	18.6
Alder forest	**10**	**14.3**	**37** 16–48	**453** 296–910	**2.30** 2.11–2.65	**5226** 1156–7548	35.8
Pluri-specific canopy forest	**10**	**15.4**	**24** 3–46	**1199** 315–3451	**2.61** 2.19–3.21	**2690** 370–6610	18.4
Willow forest	**10**	**15.6**	**16** 3–46	**1430** 315–3451	**2.70** 1.97–3.21	**2459** 368–11436	16.8

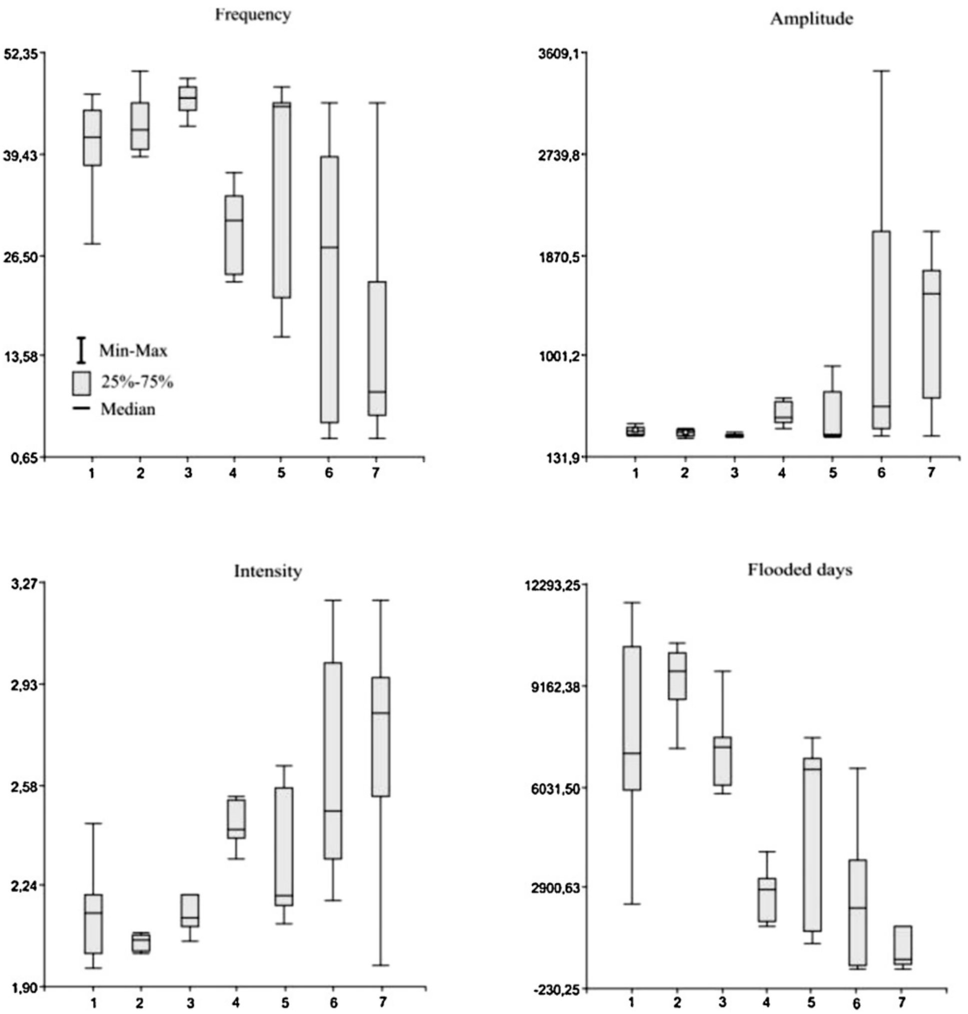

Fig. 5. Box-plot graph for each vegetation community and attribute considered. 1 – Marshy terrestrial, 2 – Marshy, 3 – Tall grassland, 4 – Acacia forest, 5 – Alder forest, 6 – Pluri-specific canopy forest and 7 – Willow forest. Frequency: number of events; Pulse amplitude: days; Pulse intensity: meter; flooded days: number within the considered time-span.

floodplain, the Alder forest is able to grow under influence also of high river streaming energy, e.g. on bars and islands of the main water course (Marchetti and Aceñolaza, 2011). Some woody species like Alder and Willow can develop adventitious roots and rearrange their foliage during floods (Neiff, 2004). This ecological plasticity has been formerly identified in riparian forests of the Pantanal and the Amazon near Manaus as another determining factor in vegetation differentiation (Damasceno-Junior et al., 2005; Valle Ferreira and Stohlgren, 1999). Such traits allow some woody species, in the Parana system, e.g., *Tessaria* and *Salix*, to establish their communities in environments and topographic positions which actually are frequently colonized by herbaceous communities, independently from the pulse regime.

Similarly, most of the woody communities did not differ with respect to their topographic position. This means that, in relation to their topographic position, woody communities have a similar pulse regime (similar pulse frequency, intensity, average amplitude and flooded days); nevertheless they are different in their floristic composition, physiognomy and structure. Among vegetation samples of the Pluri-specific canopy forest a clear floristic differentiation was found between samples belonging to sites A–C (Parana river) and those belonging to F–G (Colastine river). This floristic differentiation can be attributed to differences in channel dynamics, as was pointed out by Morais et al. (2008) for the alluvial plain of the Araguaia river, Brasil. The differences between Parana and Colastine rivers in length, width, depth, flow, channel pattern and sediments load may be reflected in the floristic differentiation of their vegetation communities.

In addition, geomorphological processes like erosion and sedimentation rates have been shown to be closely related to different vegetation patterns (Salo et al., 1986). This is reflected in the differentiation among the three main groups belonging to Alder forest (Fig. 4: C200–212, C221–223, C406–408), which seems to be associated to different landforms: bars, young islands and levees. Hence, even in the same water course erosion and sedimentation will have a different effect on different landforms and produce, as a result, different floristic groups.

The Pluri-specific canopy forest sites and some of the Willow forests included in our study (with comparable tree diameters as an indicator of forests age) were distributed on the highest topographic position in the study zone. They also appeared to be related to the same actual channel dynamics. Their differentiation in terms of floristic composition, structure and physiognomy may be explained primarily from two variables: the interaction among species or autogenic succession, which has been identified by Budke et al. (2008) as a determining variable in the floristic differentiation of scarcely flooded Brazilian wetland forests, and the geomorphological history and landform distribution, which has been pointed out by Dubs (1994) to explain the occurrence and physiognomic characteristics of some Pantanal forests. Both

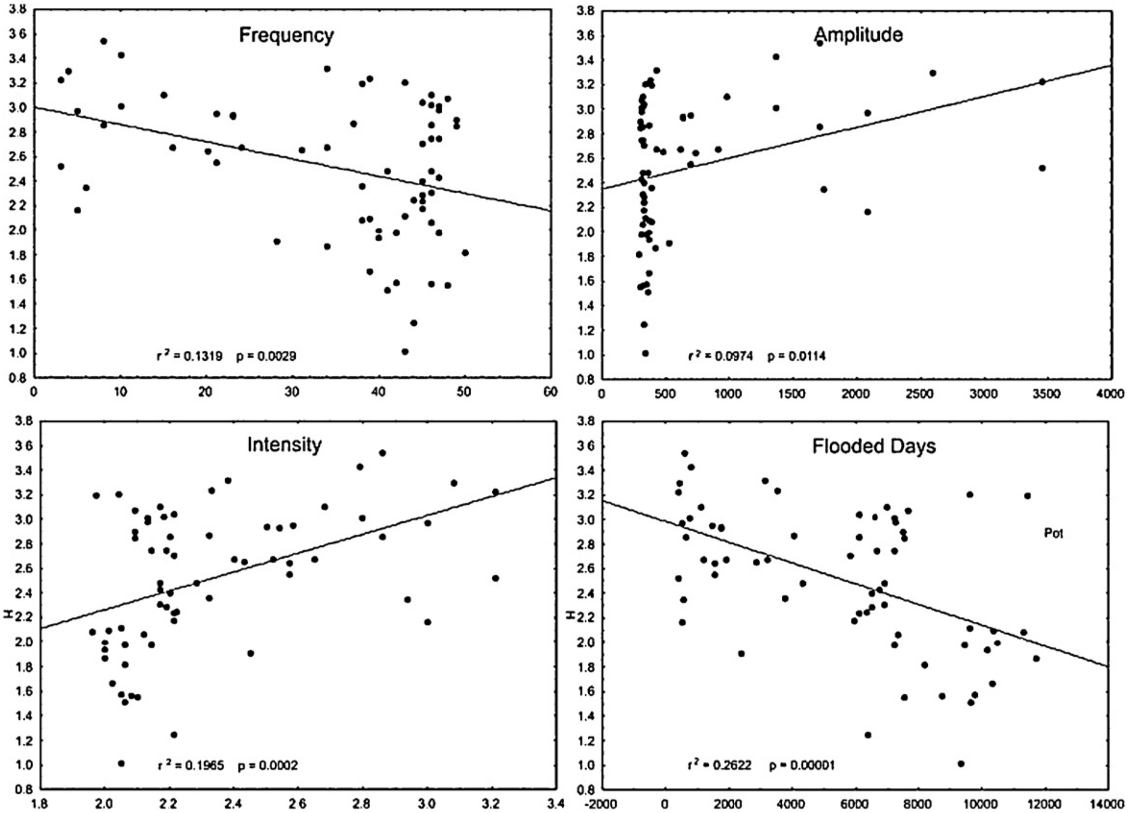

Fig. 6. Simple linear regression analyses of species diversity (woody + herbaceous) against pulse attributes (frequency, amplitude, intensity and flooded days). *Y*-axis: Shannon-Wiener diversity index; *x*-axes parameters as explained in legend of Fig. 5.

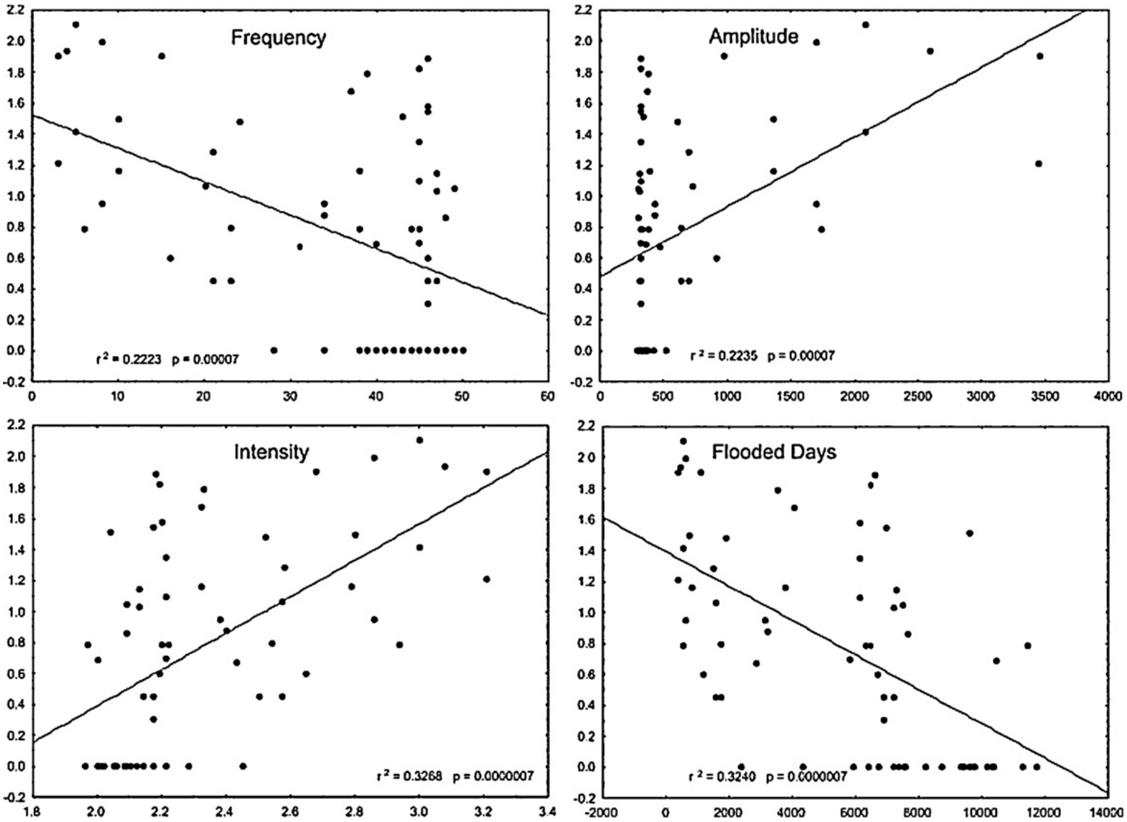

Fig. 7. Simple linear regression analyses of woody species diversity against different pulse attributes (frequency, amplitude, intensity and flooded days). *Y*-axis: Shannon-Wiener diversity index; *x*-axes parameters as explained in legend of Fig. 5.

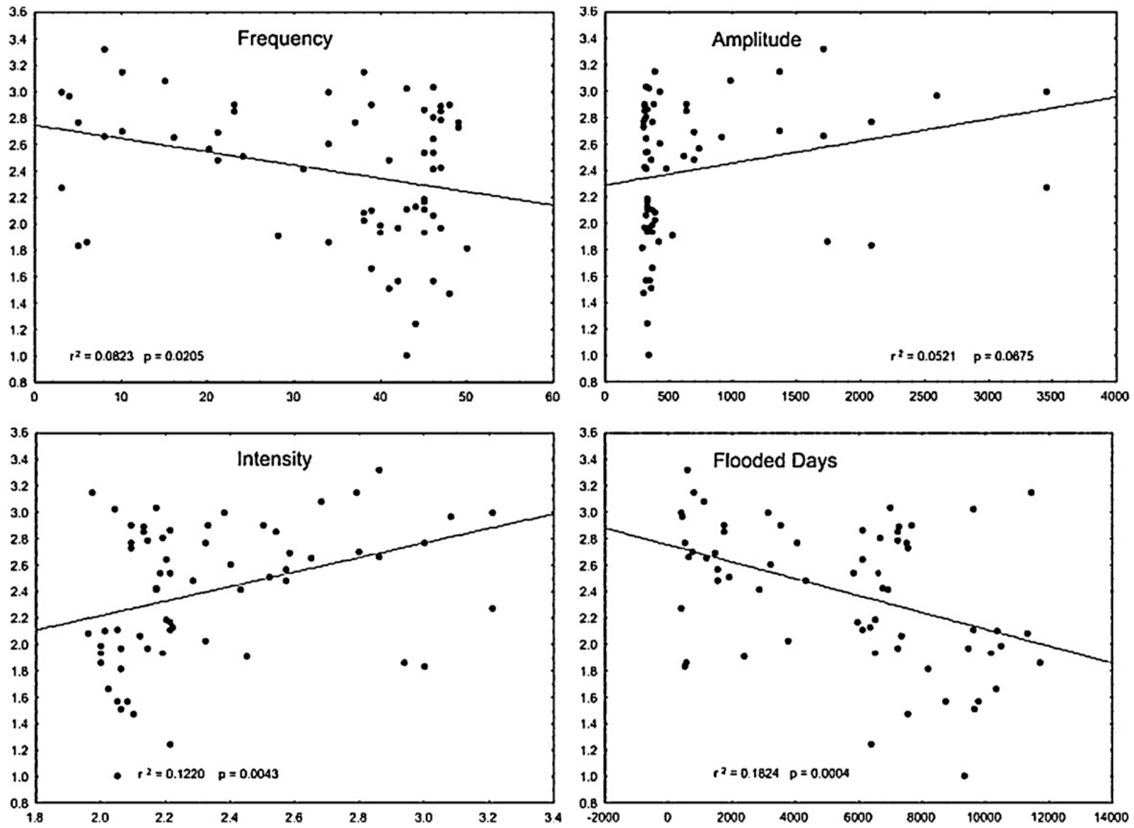

Fig. 8. Simple linear regression analyses of herbaceous species diversity against different pulse attributes (frequency, amplitude, intensity and flooded days). *Y*-axis: Shannon-Wiener diversity index; *x*-axes parameters as explained in legend of Fig. 5.

variables have been found by the mentioned authors to be more significant than floods shaping the respective vegetation structure. In our study zone, the Pluri-specific canopy forest appears to be associated to scroll bars and levees or either secondary channels or braided water courses which were losing their flow energy level. On the contrary, the Willow forest appears to be associated to levees of water courses with high streaming energy. It could be possible that, due to the high sedimentation rates associated locally to such water courses with high flow energy, Willow forest stand become increasingly separated from active water courses and, through autogenic succession, with time the willow forest undergoes a succession into a Pluri-specific canopy forest. However this is only a hypothetical assumption; studies about geomorphological dynamics should be done to reach a better understanding of floristic differentiation among the Parana River woody communities.

Relation between pulse regime and floristic characteristics of the vegetation

Although other studies have formerly related the fluvial vegetation features to frequency (Budke et al., 2010), duration (Valle Ferreira and Stohlgren, 1999; Damasceno-Junior et al., 2005) or intensity (Burke et al., 2003) of flood events, the present study found a low correlation between pulse attributes and vegetation diversity. Among them, just the pulse intensity and flooded days were more related ($r^2 = 0.32$) with the woody diversity. Similar results were reported by Budke et al. (2008) who found a weak relationship ($R^2 = 0.29$) between relative elevation and trees diversity. Similarly, Valle Ferreira and Stohlgren (1999) reported a correlation between flooded days and tree diversity in their investigated stands, although the coefficient was considerably higher ($r^2 = 0.78$). Eventually, this high correlation could be related to the methodological design: while in this study the sample sites were selected in a way to take into account the topographic variation, other studies have considered transects which not necessarily included the topographic variations of the communities.

Beside of differences in methodologies, the pulse regime scope for explaining vegetation features has been recognized by the mentioned authors and others as well. The "local control effect" (plot scale) of flood duration on richness and diversity of species of forests in Manaus has been emphasized by Valle Ferreira and Stohlgren (1999), and by Budke et al. (2008) for forests of Southern Brazil. In addition, Burke et al. (2003) recognized and acknowledged that floods affect the vegetation structure, but pointed to soils variables as other important conditioning factors. Similarly, Casco (2003) reported non-significant differences in richness of vegetation of the Parana floodplain among flooded sites at 9% and 50% of the studied period.

Final considerations

Our results allow us to answer the initial questions: (1) Vegetation is not floristically differentiated according to its topographic position. The same topographic position in the floodplain of the Parana river can be colonized by different vegetation communities. Similar frequency, intensity and average amplitude of the flood pulses, and similar amounts of flooded days were found for sites with floristically different communities, (2) There is a relationship between the pulse regime attributes and the vegetation features. Nevertheless, it is statistically only weakly backed and by itself does not explain the floristic differentiation among vegetation communities, (3) Paying attention to the topographic position of the vegetation types is not enough to study pulse regime effects on the plant communities. Other variables, such as the geomorphological architecture, different sediment loads and channel dynamics should be taken into account in order to interpret suitably the floristic differentiation of the floodplain vegetation.

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