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Plant species diversity in a Neotropical wetland: patterns of similarity, effects of distance, and altitude

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ABSTRACT

The Brazilian Pantanal is an extensive wetland with heterogeneous habitats, primarily due to the river-floodplain system and plants with differential adaptations and reproductive strategies. Factors such as altitude, distance among plant formations, and flood pulse must be considered to better understand its diversity. Aiming to assess the influence of biogeographic patterns in this system, we analyzed the floristic composition of six areas along the Paraguay River, including residual relieves, verifying the pattern of similarity, and effects of distance and altitude. We recorded 356 species in 87 families, mostly perennial (75%), and some annuals (15%) and pluriannuals (5%). Herbaceous plants were the most represented (48%), followed by arboreal (23%), shrubby (15%) and epiphytic (14%) habits, only 12% being endemic to Brazil. The studied areas showed low floristic similarity, but higher resemblance of species between neighboring areas, and no relation with altitude. The upper Paraguay River is diverse, with high spatial variability of species, predominantly perennial. The river-floodplain connectivity may be a determinant factor in species richness and occurrence of endemic species.

Key words: biogeography, floodplain, floristics, Pantanal, vegetation.

INTRODUCTION

Continental wetlands comprise a complex of ecosystems forming a mosaic with high species diversity (Nunes da Cunha and Junk 2001) that increases the spatial variability of their occurrence (Junk et al. 2006). Floods in wetlands may occur in a periodical and irregular hydrological cycle (Nunes da Cunha and Junk 2001), evidencing the traits of many terrestrial (Scarano 1998), amphibious, and

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aquatic plants (Scremin-Dias 2000, Scremin-Dias et al. 2011). These plants represent a diversified set of species with differential adaptations and ecological strategies for maintenance of diversity, allowing them to survive in waterlogged or flooded soils (Kozlowski et al. 1991, Cronk and Fennessy 2001, Cattanio et al. 2002). Different flood tolerances lead to changes in structure and species composition over a geographical gradient (Ferreira and Parolin 2007, Costa et al. 2009, Sanches et al. 2013). Several authors have reported altitude as one of the main factors to influence the pattern of species colonization (e.g., Lieberman et al. 1995, Pendry and Proctor 1996, Oliveira-Filho and Fontes 2000, Eisenlohr et al. 2013); but other combined factors must also be considered such as geographic distance between sites (Diniz-Filho et al. 2012), topography, flood duration (Damasceno-Júnior et al. 2005), and the transport of seeds (Harper 1988, Fenner and Thompson 2005). This set of factors directly influences characteristics of each species, such as propagation, reproduction, germination, and competition (Capon and Brock 2006), which may increase the species diversity over short distances (Brock 2011).

Tropical floodplain environments such as the Pantanal are the largest contributors to the global diversity (Myers et al. 2000), since the species abundance, population density, and their distribution usually act increasing and/or reducing the diversity of each environment (Scheiner and Rey-Benayas 1994). The Pantanal is considered one of the main tropical floodplains (Junk et al. 2014), including heterogeneous environments with different influences often from the river-floodplain interaction, but also from the distinct surrounding vegetation types, striking hydric seasonality, and edaphic variations (Alho 2008). Hence, studies on biogeographic patterns are indispensable for understanding the similarity among different plant communities (Pringle 2001) in the Pantanal floodplain and associated residual relieves.

In this context, considering that the upper Paraguay floodplain and residual relieves has been the less studied sub-region of the Pantanal wetland in terms of flora, but also for its importance, our aim was perform a floristic survey in this remote area to evaluate and compare both species composition and richness. We carried out this work in six vegetation formations along the Paraguay River, addressing the following questions: (i) Do areas connected during flood periods differ in floristic similarity? (ii) Is there a pattern of floristic composition associated with altitude? (iii) How floristic similarity can be explained by distance among areas?

MATERIALS AND METHODS

GENERAL CHARACTERIZATION OF THE STUDY AREAS

The six studied areas are located in the sub-region named Paraguay, along the Paraguay River in the Brazilian Pantanal (Silva and Abdon 1998). The whole area is located upstream from the town of Corumbá, State of Mato Grosso do Sul, near the border of the State of Mato Grosso, including part of the border stretch of Brazil and Bolivia (Fig. 1).

The climate of the region is classified as “Awa” type, tropical of altitude, megathermal, and with dry winter and rainy summer (Köppen 1948). Temperatures range from close to 0ºC between May and August and to 40ºC between November and March. The rainy season is between November and March, with mean annual rainfall of 1,070 mm and average annual relative air humidity of 76.8% (Soriano 1997). Moreover, the strong seasonality is characterized by well-defined periods of drought and flood (Carvalho 1986), with highest flood levels in June and July, and lowest levels in December and January (Figure S1 - Supplementary Material). Floods in this area depend on a three months of delayed flow from the headwaters and then cover large floodplain areas along the main riverbed

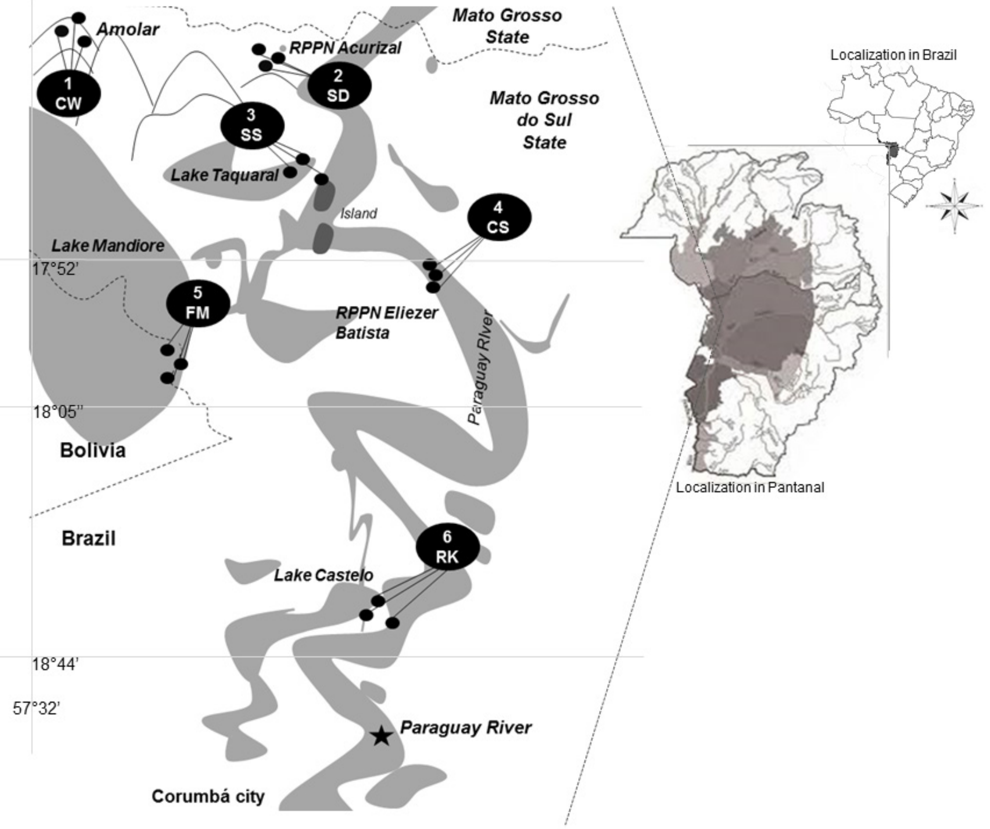

Figure 1 - Spatial distribution of the three collection sites in each studied area in the floodplain and residual relieves of the Upper Paraguay River, Pantanal wetland, Mato Grosso do Sul, Brazil, (map adapted from Silva and Abdon 1998). Area 1: CW (Cerrado woodland under impact of fire) - Serra do Amolar; Area 2: SD (seasonal semideciduous forest) - RPPN (private reserve) Acurizal; Area 3: SS (shrubby swamp with tree islets) - Lake Taquaral; Area 4: CS (Cerrado and semideciduous forest) - RPPN Eliezer Batista; Area 5: FM (floodable meadow) - Lake Mandioré; Area 6: RK (seasonal alluvial forest with rocky outcrop) - Lake Castelo.

(Hamilton et al. 1996). The Paraguay River level is highly variable among seasons, and oscillated between 1 and 4.20 meters in 2010 (Oliveira et al. 2014). Therefore, our collections were made in November 2010, when the river level was close to its minimum, allowing access, otherwise restricted due to flooding.

DATA SAMPLING

The study was carried out in six areas with different vegetation types, on the floodplain and residual relieves (Table I): Area 1: CW (Cerrado woodland under impact of fire) - Serra do Amolar; Area 2: SD (seasonal semideciduous forest)- RPPN (private reserve) Acurizal; Area 3: SS (shrubby swamp with tree islets) - Lake Taquaral; Area 4: CS (Cerrado and semideciduous forest) - RPPN Eliezer Batista; Area 5: FM (floodable meadow) - Lake Mandioré; Area 6: RK (seasonal alluvial forest with rocky outcrop) - Lake Castelo. To cover a wide range of species diversity, the survey was performed in three collection sites in each area (Fig. 1), considering the three sampled sites as a sampling unit. For correlation among areas they were separated considering the following variables: i. qualitative: vegetation and soil types; ii. quantitative: altitude (m) and geographic coordinates (the later for analysis of distance between areas) (Table I).

Time was utilized as a standard measure of sampling effort. A team comprising five people

TABLE I
Vegetation types, soil, altitude data and geographic coordinates of the six studied areas along the Paraguay River, Pantanal, Brazil. Area 1: CW - Serra do Amolar; Area 2: SD - RPPN Acurizal; Area 3: SS - Lake Taquaral; Area 4: CS - RPPN Eliezer Batista; Area 5: FM - Lake Mandioré; Area 6: RK - Lake Castelo.

Areas	Vegetation type	Altitude (m)	Soil type	Geographic coordinates (lat, long)
CW	Cerrado woodland with impact of fire	645	sandy-litolic	18º02’18,60”S, 57º30’55,00”W
SD	semideciduous forest	186	sandy-litolic	17º44’18,10”S, 57º41’27,80”W
SS	Shrubby swamp with islets	97	clay-sandy	18º02’32,40”S, 57º29’27,40”W
CS	Cerrado and semideciduous forest	95	sandy	18º05’40,20”S, 57º29’15,30”W
FM	Floodable meadow	90	clay-sandy	18º55’40,00”S, 57º30’10,50”W
RK	Seasonal alluvial forest with rocky outcrops	88	sandy	18º35’26,00”S, 57º32’44,70”W

spent an average of five hours per point until we observed a stabilization of additional number of species. Species were classified with regard to: i. habit [herbaceous, arboreal, shrubby, liana (climber) or epiphitic]; ii. vegetation type; iii. life cycle (perennial, annual or pluriannual); and iv. origin and endemism (native or exotic, and endemic or non-endemic to Brazil) (following Forzza et al. 2010). Since there is a low number of endemic species in the Pantanal because of its recent geological history (Ab’Saber 1939), and the flora originates itself from surrounding vegetation types (Pott et al. 2011), the information regarding endemisms were considered for Brazil (Pott and Pott 1999, Pott et al. 2011). We determined floristic differences between the studied areas with a dendrogram (Unweighted Pair Group Method – UPGMA), using the Jaccard index of community dissimilarity-because the matrix is binary.

Species identification was achieved by comparison with specimens of the Herbarium CGMS of the Universidade Federal de Mato Grosso do Sul (UFMS), plant guides (Pott and Pott 1994, 2000, Lorenzi 2008, Souza and Lorenzi 2008), and assistance from experts. For both fertile and sterile materials, we applied the usual herbarium techniques (Bridson and Forman 1992). Classification for Angisosperm families followed APG IV (2016), Shaw et al. (2011) for Bryophytes, and Kramer and Green (1990) and Smith et al. (2006) for Lycophytes. All collected fertile material was included in Herbarium CGMS (Table SI - Supplementary Material).

DATA ANALYSIS

To test the hypothesis that altitude drives patterns of the floristic variation, we summarized a matrix of presence/absence data using Principal Coordinates Analysis (PCoA), with Sørensen’s distance, which is equivalent to the Bray-Curtis measure in a binary form (presence/absence). The first three axes resulting from ordination were used as dependent variables in a model of Multivariate Analysis of Variance (MANOVA), and the p-value was estimated by Pillai-Trace statistics. In this model, we predicted that variations in species composition are explained by altitude as a quantitative parameter that represents vegetation type characterististics of sampling areas. The composition data were divided by four habits (herbaceous, arboreal, shrubby, and liana (climber or epiphytic)). Plant distribution patterns may be explained by altitude, which can lead to many changes in structure and species composition. Hence, we are predicting that the altitude is influencing variations in the vegetation composition. For species richness, we built a two-way ANOVA model, to seek the average difference of richness in altitude between the six sampling areas. In case of significant ANOVA results, we used Tukey's HSD (honest significant difference) test to stablish multiple comparisions.

To test the hypothesis that the floristic patterns are distance-dependent, we set a Generalized Linear Model (GLM) assuming both a Poisson error distribution and a log function. In this model we investigate whether the number of species shared between the sampled areas is explained by the linear distance between them. In order to build the independent variables in this model, we calculated the species richness shared between the studied areas and the linear distance in kilometers. Additionally, we used Mantel test to determine whether the community structure is correlated with distance between the sampled areas (controlling spatial autocorrelation). The Mantel coefficient was calculated by Pearson's product-moment correlation, in which we used 1.000 permutations and 500 interations for the bootstrapped confidence limits. Moreover, we constructed a similarity matrix of geographical coordinates using the Euclidian distance.

All analyses were performed in R environment (R core team 2015) using the vegan (Oksanen et al. 2015) and ecodist (Goslee and Urban 2007) packages.

RESULTS

FLORISTIC PATTERNS

The floristic survey showed 356 species in 268 genera and 87 families. Angiosperms are the group with the highest number of species, mainly represented by Fabaceae (40 species), followed by Poaceae (26), Cyperaceae and Euphorbiaceae (22 each), Rubiaceae (20), Malvaceae (14), Apocynaceae, Asteraceae and Melastomataceae (ten each), Myrtaceae (eight), Onagraceae (seven), Sapotaceae (six) and Annonaceae, Combretaceae, Crysobalanaceae and Passifloraceae (five species each) (Table SI). These families together represent almost 50% of the sampled specimens. *Cyperus* (Cyperaceae) and *Ludwigia* (Onagraceae) were recorded in all the sampled areas. Lycophytes represent thirteen recorded species and nine families: Pteridaceae (four species), Marsileaceae (two), plus seven other families with a single species each. Bryophytes are represented by a single family, Ricciaceae (Hepatophyta).

Regarding the life cycle, about 75% are perennial, 15% annual, and 5% pluriannual. The herbaceous habit was the most represented (150 species in total), followed by arboreal (83), shrubby (74), and lianas (48). Poaceae, Cyperaceae, Euphorbiaceae, and Asteraceae have the highest representativity within the herbaceous stratum, in which *Steinchisma laxum* was the most frequent species among different sampled areas. For the arboreal stratum, Fabaceae, Rubiaceae, and Myrtaceae comprise 70% of richness, with *Inga vera* recorded in about 50% of sampled areas.

Only 12% of sampled species are considered endemic to Brazil. The alluvial forest of Lake Castelo "RK" and the Cerrado "CW" on top of Serra do Amolar had the highest occurrence of endemic species (both with com 28%), followed by semideciduous forest and Cerrado "CS" of RPPN Eliezer Batista (17%), and shrubby swamp "SS" of Lake Taquaral (13%). The seasonal semideciduous forest "SD" (8%) and the floodable meadow "FM" (6%), near to the Bolivian border, showed lower percentage of endemic species (Table SI).

FLORISTIC SIMILARITY IN AREAS CONNECTED BY FLOOD

The six studied areas showed variation in species richness (Table II) and a great number of herbaceous plants (Table II). The richness data showed a significant mean difference for plant habit (Two-way ANOVA: $F_{3,15} = 7.71$, $p = 0.002$, Fig. 2a). Regarding the richness data per habit, lianas and herbs (Tukey's HSD: $p = 0.004$) and shrubs and herbs (Tukey's HSD: $p = 0.005$) were responsible for the significance in the ANOVA model. For herbs and trees, we observed a marginally significant mean difference (Tukey's HSD: $p = 0.09$).

We found the highest species richness in "SD", with recorded occurrence for all listed habits including 80% of families and genera with a single species each (Table II). In this area, we also found a single specimen of Orchidaceae, *Vanilla palmarum*, and 60% of the recorded Lycophytes (e.g., *Adiantum deflectens*, *Phlebodium decumanum*, *Selaginella sellowii* and *Thelypteris serrata*).

The areas "SS" and "RK" (with 79 and 74 species, respectively) exhibited mainly herbaceous species, mostly Fabaceae and Euphorbiaceae (Table II). The "SS" area also exhibited the highest occurrence of aquatic plants (macrophytes), such as *Ludwigia* (three species), *Cyperus* (four), *Eleocharis* (two), and *Victoria amazonica*. In contrast, in "RK" we found the only two recorded species of Cactaceae, *Pereskia sacharosa* and *Praecereus euchlorus*.

The areas with lowest species richness were "CW" (14%), followed by "FM" (10%), and "CS" (8%). The Cerrado area under influence of fire ("CW") exhibited a low number of herbaceous species, whereas it showed great richness of trees, shrubs and lianas. The "FM" area exhibited predominance of Cyperaceae, mainly species of *Cyperus*. Although "CS" showed the lowest species richness, there we recorded the only species of Bromeliaceae, the small epiphyte *Tillandsia loliacea*.

In general, a low species similarity occurred among the sampled areas, even with the connection of areas by the Paraguay River (Fig. 3). However, we were able to observe three groups: i. "SS" + "SD" - with highest species similarity (17 species); ii. "CS" + "CW" (seven); and iii. "FM" + "RK" (five), which in turn showed the lowest relation between areas.

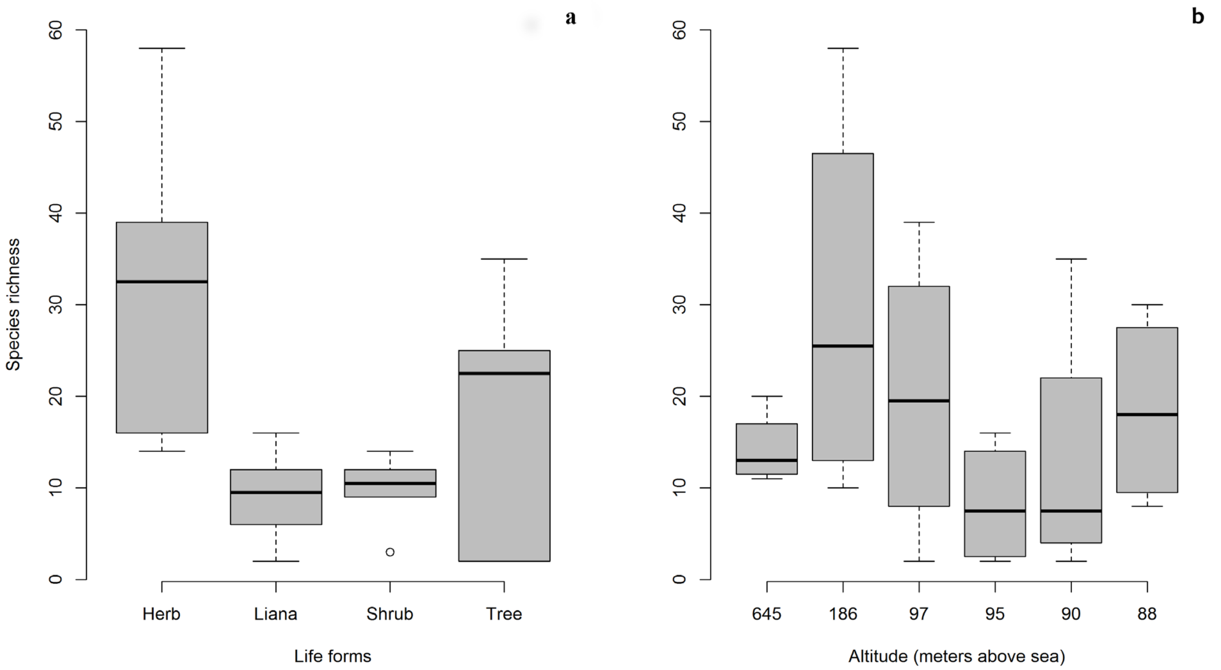

Figure 2 - Comparison of species richness in the sampled areas along the Paraguay River, Pantanal, Brazil. **a** - species richness per growth habit; **b** - species richness for each sampled environment (number of areas is available in Table I).

TABLE II

Richness of species, families and genera, and number of species per habit in the six studied areas along the Paraguay River, Pantanal, Brazil.

Area	Species richness	Family richness	Genus richness	Number of herbs	Number of trees	Number of shrubs	Number of epiphytes, lianas (climber or epiphytic)
CW	49	29	58	10	14	18	11
SD	100	37	100	46	25	21	10
SS	70	26	64	34	20	11	5
CS	29	14	43	11	2	6	10
FM	47	21	52	33	2	6	6
RK	60	21	64	22	20	12	6

The “SS” + “SD” areas showed a higher similarity due to the short distance between them. The increased similarity between these areas was higher because of the herbs, mostly *Eleocharis minima* and *Steinchisma laxum*. However, for the cluster “CS” + “CW” the similarity was maintained by the high number of trees and lianas, mainly Fabaceae.

Vegetation characteristics common to “FM” + “RK” did not contribute to increase their similarity, since the distance between them reduced it. In this cluster only *Eichhornia crassipes* exhibited high occurrence, but the richness of both Cyperaceae and Poaceae in “FM” area contributed to decrease the similarity.

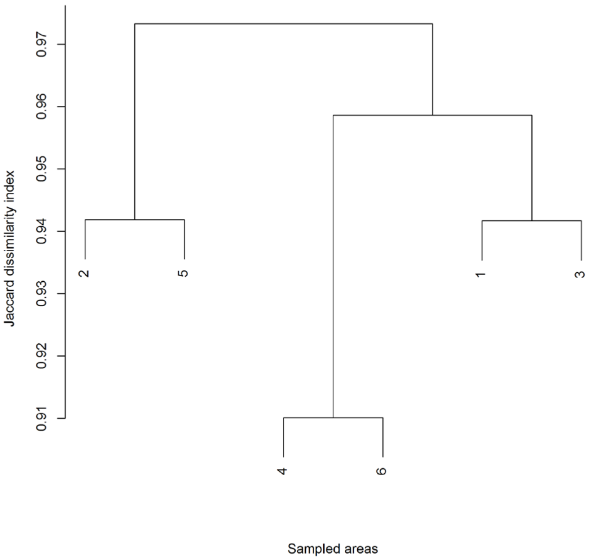

Figure 3 - Cluster (UPGMA) of species by similarity (Jaccard index) among the six sampled areas along the Paraguay River, Pantanal wetland, Brazil (number of areas are available in Table I).

ALTITUDE PATTERNS OF FLORISTIC VARIATION

The first three axes from the PCoA ordination generated 23% of the original variation, and we also observed that variation in species composition (MANOVA: Pillai-Trace = 0.69, p = 0.42) was not explained by altitude, but had marginally significant mean difference for richness (Two-way ANOVA: $F_{5,15} = 2.49$, p = 0.08, Fig. 2b).

DISTANCE EFFECTS OF FLORISTIC VARIATION

Mantel values showed that the community did not exhibit a significative spatial dependence (Mantel: $r_m = 0.12$, p = 0.31). Therefore, we were able to infer that no spatial auto-correlation exists between the sampled areas. Finally, the variation in number of shared species was not explained by linear distance between the studied areas (Poisson GLM: $\chi^2 = 27.41$, p = 0.95).

DISCUSSION

FLORISTIC PATTERNS

In this work, we observed the floristic diversity and the differences in vegetation composition between the sampled areas, which contributes to the heterogeneity found in the Brazilian Pantanal previously reported by other authors (e.g., Alho 2008). All Angiosperms herein recorded are included in the Pantanal plant list (Pott and Pott 1999), and also all Angiosperms, Bryophytes, and Lycophytes in the Brazilian Flora List (Forzza et al. 2010).

Our inventory reveals some endemic species to Brazil that compose the flora of the Pantanal, such as *Eragrostis hypnoides* (Poaceae). Other phytogeographic influences, such as Amazonia from the North and Cerrado from the East (Adámoli 1982), contribute to the low number of endemic species in the Pantanal. Furthermore, the interaction river-floodplain during the floods (Bornette et al. 1998) plus the recent geological history of the region (Ab'Saber 1939, Pott et al. 2011) are determinant factors that also contribute reducing the richness and occurrence of endemic species (Bornette et al. 1998).

Many of the largest Angiosperm families in Brazil (Fabaceae, Asteraceae, Euphorbiaceae, and Myrtaceae) have a strong endemism (Giulietti et al. 2005), but in the Pantanal they are just widespread among the vegetation types. In this case, the river-floodplain interaction may increase the species richness (Bornette et al. 1998). Our inventory also reported a high diversity of native plants, mainly within Fabaceae and Cyperaceae. The genus *Cyperus* is the most representative within Cyperaceae, with some species widely spread in the Pantanal (e.g., *Cyperus haspan, C. odoratus*, and *C. surinamensis*) (Pott and Pott 2000). The great number of native species of Fabaceae and Cyperaceae in the Pantanal was also reported in other studies (Pott et al. 2011, Amador et al. 2012, Catian et al. 2012, Rocha et al. 2015).

With regard to the both permanent and seasonal flooded environments, the presence of Alismataceae, Marsileaceae, Pontederiaceae, Ricciaceae, and Salviniaceae increased the diversity of aquatic macrophytes. The high diversity of aquatic plants is a consequence of their different life forms (Irgang et al. 1996), which allow them to grow in different habitats and hydric conditions (Scremin-Dias 2000), as observed in *Ludwigia.*

ALTITUDE, SPECIES RICHNESS AND PLANT ADAPTATIONS

The floristic composition among the sampled areas did not follow the altitudinal gradient, as species richness would be expected to decrease with increased altitude (Von Humboldt and Bonpland 1807, Brown and Gibson 1983, Givnish 1999). This suggests that the main shaping source of this community is the seasonal flood promoting some homogenization of different areas. The Pantanal wetlands comprise a high variation in species composition due to the different regimes of flood pulse by function of the altitudinal gradient (Junk et al. 1989), and both drought and flood periods may stimulate or inhibit seed germination (Casanova and Brock 2000) and seedling establishment (Simpson et al. 1989). The variation in flood pulse over the years may spread many seeds, thus increasing the chances of species establishment. Furthermore, periodical flood events promote an increase in the dispersal process, influencing the species distribution along a gradient. Hence, species richness varies over different gradient levels in response to the flood pulse within a spatial-temporal scale.

The variation in species richness between the sampled areas indicates that the particular adaptation traits are fundamental factors in the colonization of each environment. The Pantanal contains a high floristic diversity (Nunes da Cunha and Junk 2001), and the vegetation types are characterized by many plants assumed as indicators species; for the plants herein recorded, we can mention: *Qualea grandiflora*, widely distributed in the Cerrado (Ratter et al. 1996); *Curatella americana,* indicator of savanna; and *Xylopia aromatica,* indicator of semideciduous forest (Felfili et al. 2002), which supports the influence of the surrounding vegetation types on the floristic composition of the Pantanal (Adámoli 1982).

Ricciocarpos natans populations (Bryophyte) are common in flooded habitats in the Pantanal, mostly due to morphological and functional adaptations to survive under hydric stress. In contrast, the Lycophytes herein recorded are typical of seasonal forests (Smith et al. 1999), but non-endemic, although Brazil is considered one of the main centers of endemism and speciation of this group (Tryon 1986).

The low species diversity and the lower herbaceous ground cover observed in "CW" (Cerrado woodland under impact of fire) may be result of wildfire on top of the hill. This disturbance reduces the ground cover of herbaceous species and stimulates the production of buds and regrowth of shrubby species (Fidelis et al. 2014). On the other hand, the great ground cover of trees found in "CW" is probably due to their strategies against fire, such as growth in height and bark thickness (Dantas and Pausas 2013)–typical features of Cerrado woody species. Furthermore, altitude in this area may select species that are not flood-dispersed or areas that receive less incoming seeds during flood (Baldwin et al. 2010). Hence, the main dispersal vectors plus the flood events provide a further gain in species diversity in this region.

In general, some responses to the environmental factors were observed among the recorded species, such as: i. morphological structures and functional adaptations that provide the colonization by aquatic plants (Casanova and Brock 2000); ii. propagation strategies, such as bank of buds arising from the aerial and underground organs (Fidelis et al. 2014); and iii. reproductive strategies, such as dispersal and the soil seed bank by function of an altitudinal gradient (Baldwin et al. 2010). Seed dispersal, as well as germination and colonization of these species by function of a flood regime may evidence particular both morphological and physiological traits in response to environmental conditions. Considering the great number of floodable areas in the Pantanal (Pott and Pott 1999), we support that the predominance of herbaceous species in this region is due to their capability to establish under conditions of water stress (e.g., Scremin-Dias 2000, Leandro et al. 2016).

SIMILARITY AND DISTANCE EFFECTS

The most similar areas were grouped according to the characteristics of each vegetation type, which may be explained by their proximity. In these types of areas, diversity is usually higher and species composition may vary in short distances (Scheiner and Rey-Benayas 1994, Rodrigues-Iturbe et al. 2009), whereas large distances may decrease similarity for several reasons, such as variations in the gradient and differences in niche occupation and dispersal limitation (Necola and White 1999, Boedeltje et al. 2003, Nilsson et al. 2010). These variations may influence the pattern of species colonization, mainly due to dispersal strategies such as hydrochory (Barrat-Segretain 1996, Wittmann and Junk 2003, Riis and Sand-Jensen 2006, Hopfensperger and Baldwin 2009). Although the sampled areas are connected by the Paraguay River, the distance between them acts as a determinant factor, which increases and/or decreases the similarity between different formations (Gurnell et al. 2006, Thomaz et al. 2009).

In the Pantanal, seed transportation may be restricted to short distances due to natural barriers caused by the geomorphological complexity (Fantin-Cruz et al. 2011, Pagotto et al. 2011). Species richness and abundance increase due to different capabilities of seed retention (Bao et al. 2014), and also by the physiological limitation of seeds by function of the submersal period (Brock 2011). Therefore, the difference in species composition of these environments may be explained by the Paraguay River flood pulse, which directly influences the seed bank build-up (Baker 1989, Damasceno-Júnior et al. 2005). The river-plain interaction in flooding periods has been considered important to explain the similarities of differentes groups of aquatic organisms (Ward and Tockner 2001). Understanding these similarities may explain the patterns of species richness and rarity in wetlands, which allows to predict the community dynamics and to develop guidelines for biodiversity conservation (Bornette et al. 1998).

Since germination usually is influenced by factors such as dormancy, viability, physiology, temperature, light, and nutrients (Baker 1989, Dupin et al. 2009, Baskin and Baskin 2014), occasionally, seed arrival does not assure the species establishment. The variation in species richness within a community comprising species with diverse strategies of regeneration and maintenance can be influenced by a high percentage of perennial species (Callaway 1995). In this case, the community includes mainly grasses with stoloniferous rhizomes (Bonnis et al. 1995), along with some species with low propagation rates and restricted to a single area (Brock 2011). Equally, some environmental conditions shall be taken into account for reducing species similarity between environments–evidencing the high differential index in the floristic composition between distant areas.

Herein we report that there is no evidence of floristic variation influenced by altitude, however, the flood pulse and spatial proximity in the Pantanal is crucial to the structure of plant community. Our results suggest that the upper Paraguay floodplain includes a wide range of diversity along the river. Since the high richness herein highlighted indicates that these remote areas should be better studied to strengthen efforts concerning the biological heritage and definition of priority areas for biodiversity conservation, it is important to further investigate the processes that generate and maintain species composition and diversity.

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SUPPLEMENTARY MATERIAL

Figure S1 - Maximum and minimum water levels of the Paraguay River in centimeters (cm) at Ladário, Pantanal wetland, from 2000 to 2015. Data provided by the National Institute of Meteorology (INMET-BDMEP). The dashed line shows the level of the Paraguay River in 2010 indicating a low-level inundation when the collections were carried out.