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ORIGINAL PAPER

Geobotany in a fault in the world's largest continuous wetland in central South America

Teodoro Isnard Ribeiro de Almeida · **Cibele Hummel do Amaral** · **Moreno Botelho** · **Eduardo Francisco Ribeiro** · **Natasha Costa Penatti**

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Abstract The Pantanal is located in the center of South America in a tectonically active sedimentary basin of Quaternary age. Even though the relief is flat and the diversity of the sediments is low, its vegetation cover has high variability resulting from seasonal fluctuations in water levels and the presence of four surrounding biomes. Changes in elevation of less than 1 m influence the length and intensity of floods, powerfully affecting the vegetation. Faults with small vertical displacement can generate abrupt vegetation changes and, consequently, expressive vegetation lineaments. This study characterizes a lineament in the northern Pantanal, considering Land Surface Phenology, estimates of precipitation, and floristic survey. The phenological metrics, obtained from a 15-year time series from the Moderate Resolution Imaging Spectroradiometer processed by TIMESAT software, discriminate evergreen forests in the NW of this lineament from savanna-like physiognomies in the SE region. Plant taxonomic identification shows two distinct regional strata with a clear separation between species adapted to prolonged floods in the NW and typical species of the Cerrado biome, mostly xeromorphic, in the SE. Data from the Tropical Rainfall Measuring Mission complemented the analysis, showing different dependence on local rains on different sides of the lineament. The entire dataset defines this geological structure as a driver of the Pantanal's plant communities, being a boundary for the extensive establishment of propagules of the Amazon biome. This research, in addition to advancing knowledge of this singular region, which is essential for management studies, can be a stimulus to biological and forest investigations.

Keywords Pantanal · Vegetation lineament · Geobotany · Multitemporal remote sensing · Neotectonics

Introduction

The Pantanal, the world's largest continuous wetland, lies in the center of South America between 16–20°S

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T. I. R. de Almeida (✉) · E. F. Ribeiro · N. C. Penatti
Instituto de Geociências, Universidade de São Paulo, Rua do Lago 562, São Paulo, SP 05508-080, Brazil
e-mail: talmeida@usp.br

C. H. do Amaral
Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Avenida Purdue s/n, Viçosa, MG 36570-900, Brazil

M. Botelho
MB Soluções Florestais, Rua Vereador Gilberto Valério Pinheiro 134/102 - Santo Antonio, Viçosa, MG 36570-000, Brazil

and 55–58°W, comprising an exceptionally flat area of around 160,000 km^2. It is an active sedimentary basin, where the reactivation of Proterozoic age faults results in frequent earthquakes (Dias et al. 2016). These faults, reactivated with a vertical component displacement, may influence drainage and limit current depositional lobes (Assine et al. 2015). This study addresses a subregion of the northern Pantanal, encompassing a 100-km-long, little-studied vegetation discontinuity that separates the northern portion from the rest of the central Pantanal. Almeida et al. (2015) presented this linear feature as a boundary between regions with vegetation cover with later or discrete senescence at the NW and with early senescence at the SE. Xiao et al. (2006), discussing the leaf phenology of seasonally moist tropical forests in South America, defined the NW area as an isolated evergreen tropical forest with a linear southern boundary. This linear feature–considered here as a vegetation lineament—is the continuity to SW of a fault with some vertical displacement described out of Pantanal basin by Curto et al. (2014).

Remote sensing has been the most useful tool to acquire spatial and temporal information about wetlands, since they are often difficult to access on the ground and on-site mapping at the landscape scale is usually cost-prohibitive (Lang et al. 2009; Guo et al. 2017). Since most of the Pantanal is pathless and uninhabited, remote sensing is a valuable tool for studies of the region. Studies of the variability of the local vegetation and the processes involved in the lineaments of neighboring areas require floristic and phenological information. Floristic data depend exclusively on fieldwork, but phenological information may come from multitemporal optical images. The use of time series of vegetation spectral indices to obtain regional phenological information dates from the 1980s, when Townshend et al. (1985) used annual series of AVHRR sensor images. Later, Beurs and Henebry (2004) proposed the term Land Surface Phenology (LSP) for this type of study. While phenology refers to life-cycle events from in situ observations of individual plants or species, LSP, observed from time series of remote sensing images, collects information such as seasonal variability in greenness at the spatial–temporal resolution of satellite sensors (Tan et al. 2011). The availability of Moderate Resolution Imaging Spectroradiometer (MODIS) images since the end of the year 2000 represents an advance in studies of regional phenology, with substantially improved geometric and radiometric properties (Huete et al. 2002). Tan et al. (2011) used TIMESAT (Jönsson and Eklund 2004) for retrieving vegetation phenology metrics from MODIS vegetation indices. These metrics are descriptive parameters of the vegetation-growing season that are used to estimate the various phases of the annual cycle of vegetation development. Primarily based on time series of vegetation indices, they aim to describe the phenology of vegetation growth as observed by satellite imagery recovering the onset of greening and senescence, timing of the maximum of the growing season, and length of the growing season, among other information (Reed et al. 2006). Lumbierres et al. (2017), using algorithms based on LSP models, arrived at accurate estimations of plant biomass in seasonal wetlands with variable flood regimes and its spatiotemporal dynamics, which is essential information for resources management. The relationship between floristic and LSP data is very relevant but still rarely present in the literature. Wessels et al. (2011) concluded that the LSP metrics could capture sufficient functional diversity to classify and map vegetation patterns and function at biome level, proposing a method based on LSP to split the African biomes. Viña et al. (2012) presented data concerning the strong relationship between LSP and floristic similarity in a mountainous region of China, concluding that these metrics are a valuable tool for mapping and remotely monitoring floristic diversity patterns. Another possible source of remote sensing data, digital surface models, is potentially useful to study faults with vertical displacement. Their use, however, is problematic in flat areas with irregular distribution of arboreal vegetation, such as the Pantanal. Ribeiro (2016) used Shuttle Radar Topography Mission data (SRTM) in the studied lineament, including the method of O'Loughlin et al. (2016), to correct the vegetation effects, without success.

For centuries, wetlands were considered unproductive lands with little or no value that were necessarily drained for farming. This misconception led to the destruction of about 50% of wetland areas during the twentieth century (Fraser and Keddy 2005). However, nowadays they are recognized as biodiversity hotspots (Mitsch and Gosselink 2007), and scientists consider it essential to preserve these environments as habitats for species, flood control, aquifer recharge, water purification, and amenities and recreational opportunities (Woodward and Wui 2001; Alho 2008). In addition, there is a widespread scientific consensus about the existence of global warming, and the importance of wetlands is highlighted, as they are significant carbon sinks (Mitsch et al. 2013). It is not easy to express the monetary value of wetlands, but according to Barbier (1994), large inland wetlands provide several ecological services of high value to humanity, and tropical wetlands play an especially crucial role in economic development. Turner et al. (2000) warned about the high ecological, social, and economic losses from destruction of wetlands, proposing a minimum safe standard for their preservation.

The primary objective of the present study is to verify and understand the LSP and floristic variation on both sides of a particular 100-km-long vegetation lineament in the northern Pantanal in central South America. This lineament is a geobotanical boundary originating from a geological structure that is responsible for the subsidence of the NW block in relation to the SE block. The second objective is to verify the variability of the availability of water to the vegetation during the year, simultaneously considering precipitation and vegetation greenness. The third objective is to analyze the annual availability of water on both sides of the lineament, as the origin of the environmental diversity. In performing this research, we have adopted two working hypotheses. The first hypothesis considers this fault as a geobotanical boundary between two very different vegetation covers and habitats. The second hypothesis proposes that the origin of this environmental contrast is the differential availability of water to the vegetation, particularly during the months of drought. Multitemporal remote sensing data and the floristic survey of plots located on both sides of the lineament permitted the development of these working hypotheses. Although the focus of the research is on basic science, the response to the working hypotheses has two immediate applications. The first is to provide data for the management of the region, which is partially protected by the state; the second is to guide farming activities in the area with regard to the variability of the spatial–temporal availability of water in the region.

Methodology

Study area

The Pantanal Basin, a sedimentary basin developed in the Upper Pliocene/Lower Pleistocene (Ussami et al. 1999), has a relatively complex infilling history, considering that it is a Quaternary basin far away from active edges of the South American plate (Assine and Soares 2004; Assine et al. 2015). The infilling has been done by several megafans, which are sedimentary environments characterized by extensive distributary systems with areas of 10^3–10^5 km^2 and low slope gradients (0.1°–0.01°) (Leier et al. 2005). The region has a flat relief with an altitudinal variation of less than 100 m over the whole basin (Pott and Silva 2015). The lack of altitudinal variation might incorrectly suggest a lack of environmental variability. However, the high environmental heterogeneity has allowed authors to divide the Pantanal into several distinct macroenvironments based especially on geology and hydrology (Hamilton et al. 1996; Silva and Abdon 1998; Padovani 2010; Penatti and Almeida 2013). The humid to semiarid climate, with very marked seasons, results in the alternation of prolonged droughts and extensive floods.

The presence of neighbor biomes (Cerrado, Dry Seasonal Forest, Chaco, Amazon, and Atlantic Forest) influences biodiversity (Pott et al. 2011) by providing a vast genetic stock. Because of the flatness of the Pantanal, major rivers overflow their banks, and small variations in relief are responsible for the local presence, intensity, and duration of seasonal floods, the most critical ecological phenomenon in the Pantanal (Alho 2008). The flood dynamic promotes intense and rapid changes in vegetation cover, resulting in a great diversity of pioneer types, varying from herbaceous to woody formations (Pott et al. 2011). The vegetation may profoundly differ within the same soil type according to small variations in relief, with spatial patterns of “self-organized chaos,” with forest vegetation in the lands most preserved by the floods, grassland savannas in seasonally flooded areas, and aquatic vegetation in water bodies (Pott and Silva 2015). The maze of varying water levels forms a dynamic ecosystem, with a complex mosaic of habitats and diverse and abundant wildlife (Alho 2011), including about 1863 species of phanerogam plants, 263 species of fish, 41 species of amphibians, 113 species of reptiles (177 for the basin), 463 species of birds, and 132 species of mammals in the floodplain (Alho 2008).

The Pantanal relief is a function of sedimentation and erosion processes as well as the reactivation of basement faults with a vertical component. Assine et al. (2015) demonstrated the presence of several active fault systems cutting the basin, of which faults in the NE–SW direction are particularly significant. This fault system is believed to be associated with the Transbrasilian Lineament (LTB), a continental-scale geotectonic suture described in the region by Soares et al. (1998). These NE-SW structures exceed the limits of the Pantanal Basin, as shown by Curto et al. (2014), who described horsts and grabens northeast of the Pantanal, structures considered by the authors as LTB subsidiary fault zones. Among these, there is the General Carneiro shear zone which, prolonged to the SW, coincides with the lineament described in the present study that divides the northern from the central Pantanal.

The vegetation consists of evergreen forests in the NW portion of the lineament and of the savannas that cover most of the Pantanal in the SE portion. The NE–SW fault led to uplifting of the SE block over the NW block, as shown by the dominant patterns of surface water flow on the two sides of the fault (Assine et al. 2016). In the SE region, the runoff is essentially pluvial during floods, whereas in the NW region, in addition to the pluvial runoff, there is also the flow of fluvial and underground unconfined waters, associated with floods and perennial rivers.

A few studies have mapped out the various vegetation formations and habitats of the Pantanal (Conservation International 2009; Evans et al. 2014; Pott and Silva 2015). All of these studies have shown a notable discontinuity between different classes of vegetation in the northern Pantanal. This boundary is defined here as a lineament according to its linearity and dimensions. Conservation International (2009) described forest formations or vegetation under fluvial influence NW of the lineament and savannas SE of the lineament. Pott and Silva (2015) described pioneer woodlands NW of the lineament, highlighting the presence of *Tabebuia aurea* (Silva Manso) Benth.and Hook.f. ex S.Moore, *Copernicia alba* Morong ex Morong and Britton, *Vochysia divergens* Pohl, and savanna-like physiognomies SE of the lineament, where some of the common species are *Caryocar brasiliense* Cambess., *Dipteryx alata* Vogel, *Hymenaea stigonocarpa* Mart. ex Hayne, *Astronium fraxinifolium* Schott, *Buchenavia tomentosa* Eichler, *Qualea grandiflora* Mart., and *Tachigali aurea* Tul (common species of the Cerrado biome). Evans et al. (2014) proposed two habitat classes in the lineament region, with an area of prolonged flooding NW of the lineament. These authors observed monodominance of *Vochysia divergens* Pohl, a common tree of the Amazon Forest biome, and *Combretum laxum* Jacq NW of the lineament. SE of the lineament there are typical species communities from the Cerrado, with a well-defined grassy/herbaceous stratum mixed with shrubs and sparse trees, and forest fragments. The forested savannas mainly occur on ancient levees at slightly higher elevations than the floodplain (Fig. 1).

Remote sensing data

The most commonly used vegetation index is the NDVI. This index provides an indication of the greenness of the canopy of vegetation communities, which is a composite property of leaf chlorophyll content, leaf area, canopy cover, and canopy structure (Zhang et al. 2012). Plotting NDVI time-series data produces a temporal curve that summarizes the various stages that green vegetation undergoes during a complete growing season. These curves permit the extraction of key phenological variables, or metrics, about a particular season, such as the start, peak, and end of the growing season. These characteristics may not necessarily correspond directly to conventional, ground-based phenological events, but they provide indications of ecosystem dynamics.

To analyze regional phenological variability, we used 15 years of MODIS NDVI (November 2000 to February 2016, tile H12V10). Among the available MODIS products, we chose the MOD13Q1 product, which provides 16-day composite images (23 images per year) with a spatial resolution of 250 m. To improve data quality, the NDVI data were smoothed using the Savitzky–Golay filter (Savitzky and Golay 1964) implemented by TIMESAT software (Eklund and Jönsson 2016). The MOD13Q1 pixel reliability band was used to weight each point in the time series: value 0 (useful data) had full weight (1.0), values 1–2 (marginal data, snow/ice) had half weight (0.5), and value 3 (cloudy) had minimal weight (0.1). Function-fitting parameters were used in TIMESAT: a 5-point

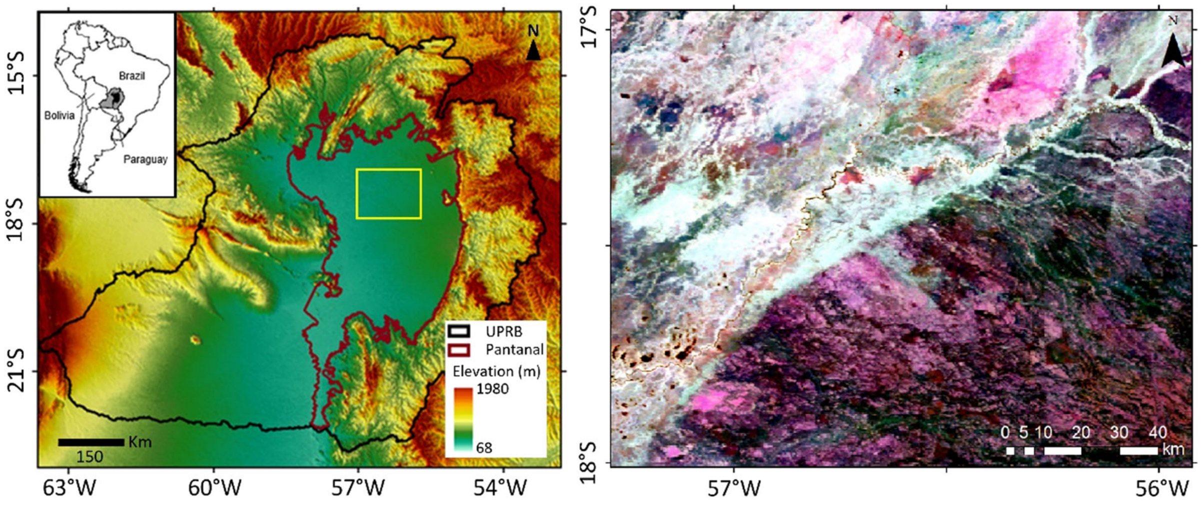

Fig. 1 Left: Location of the Pantanal and the Upper Paraguay River Basin on a map of South America and the studied area (yellow rectangle) and on a shaded relief map from Shuttle Radar Topography Mission data. Right: Color composition of Moderate Resolution Imaging Spectroradiometer Normalized Difference Vegetation Index from days of the year (DOY) 97(R) 241 (G) 289 (B) of the study area showing the vegetation lineament highlighted by the different plant phenologies. (Color figure online)

window over two appropriate steps, an adaptation strength of 2.0, and no spike or amplitude cutoffs. The MODIS NDVI filtered time series were used to derive the three phenological metrics, defined as:

- *Annual minimum NDVI value* This parameter, in an annual time series, represents the minimum level of photosynthetic activity in the canopy.
- *Seasonal amplitude* The difference between the maximum and minimum NDVI values in an annual time series, representing the maximum increase in canopy photosynthetic activity above the baseline.
- *Greenup rate* The rate of increase in NDVI at the beginning of the growing season, representing resprouting and increase in the vegetation greenness in response to local rainfall and water availability.

Data from the 3B43 product of the TRMM, from January 2001 to December 2015, provided estimates of mean monthly rainfall values for both sides of the lineament. These TRMM data, which were tested by Collischonn et al. (2011) in the UPRB, in an area located in the north of Pantanal, consistently estimated the rainfall in the region. The TRMM data were later used successfully by Penatti et al. (2015) to estimate precipitation in the entire UPRB and Pantanal. If the intensity and temporal distribution of the estimated rainfall were similar in the NW and SE regions, it would be possible to compare the seasonal behavior from both sides of the lineament. In this case, the application can indicate the relative independence of the vegetation greenness from local rainfall during the dry season. The application would also verify the dependence from the water table during dry periods on both sides of the lineament, since soil moisture is widely recognized as the key factor that links rainfall to vegetation growth (Jamali et al. 2011).

For the period from January 2001 to December 2015, the mean values of monthly NDVI were calculated for each side of the vegetation lineament, so that cross-correlations (r) between the NDVI and TRMM time series could be carried out to investigate the time lag between these events.

We then used the derived annual phenological metrics for the 15-year period to obtain average values of each metric that adequately reflected the general behavior on the two sides of the lineament. The use of NDVI time series data and derived phenological metrics has the potential of tracking vegetation cover dynamics and successional changes in response to drought. Ganguly et al. (2010) cite the importance of phenology for habitat studies. Thus, these phenometrics can complement floristic observations in the field. However, the phenological metrics do not contain information about the origin of the water available for plants, supplied here by the TRMM data application.

Field work and floristic data processing

To determine the location of plots for the floristic approach, we used a pair of Landsat satellite images (WRS2 226/072) from a TM sensor from 08/09/1986 and an OLI sensor from 09/01/2016 with 30 m of spatial resolution. The selected sites were those with dense vegetation (forest-like) on both dates to ensure the sampling of forests at least 30 years of age, reducing the possibility of imbalance between pioneer and climax species due to anthropogenic activities, once those forested fragments are primary formations or are in an advanced stage of regrowth.

We also used high-resolution multispectral images from the Pleiades and Rapid Eye sensors for field orientation and assistance in plot selection within forest fragments. Seventeen plots of 20 × 30 m were allocated in the study area in a stratified selective sampling manner.

The general disposition of plots considered the presence of two strata with different phenological patterns, previously verified by MODIS NDVI time series analyses, one on the NW side of the vegetation lineament and the other on the SE side. At the time, we considered the probable presence of two floristic strata associated with the two different phenological patterns. Initially, a visual analysis permitted the annotation of species present at the herbaceous and shrub strata. Later, all individuals with a diameter at breast height (DBH) $\geq$ 5 cm were sampled for taxonomic identification and collection of data such as the number of stems, DBH, and total height. The total height of the stems was measured with a Vertex IV hypsometer (Haglof, Madison, MS, USA). When necessary, photographs were used for later identification in books, journals, and virtual herbarium, with a zoom of branches, leaves, and reproductive organs when available.

To quantify the floristic similarity between field plots, we adopted the Jaccard Similarity Index (Jacc). This index, which is commonly used to analyze similarity between two sets of species, considers the species that are unique to each plot and those that are present in both. The following equation is used to calculate Jacc, where a is the number of species that occur in both plots, b is the number of species unique to one of the plots, and c is the number of species unique to the other plot:

$$\text{Jacc} = a/(a+b+c).$$

When no species occur in both plots, Jacc is equal to zero and the dissimilarity is maximal. When all species occur in both plots, Jacc is equal to one, and the floristic similarity is maximal. Classically, hierarchical methods of classifying elements could be agglomerative, in which individuals are progressively fused into groups of increasing size until the entire population is classified (Williams and Lambert 1966). Here we used the technique of hierarchical clustering with dendrograms grouping the most similar plots. This technique consists of grouping neighboring plots by establishing a hierarchy between the data. The distance metric for making the dendrogram was the Jacc index.

Results and discussion

Investigation of relationships between MODIS NDVI and local rainfall

Analysis of the spatial–temporal variability of precipitation estimates on each side of the lineament showed similar rainfall patterns on both sides ($r = 0.99$) (Fig. 2). Rainfall was concentrated between October and April and intense drought between June and August, a finding consistent with Pantanal hydrological dynamics.

Hydrologic variability affects the vegetation, since rainfall is the main factor that controls greenness in the Pantanal (Penatti et al. 2015). However, the NDVI of the NW and SE regions does not respond in the same way to the first rains, indicating some differences in local rainfall dependence. To test the phase difference between greenness and local rainfall for the period from 2001 to 2015, we used a cross-correlation function (Table 1).

The correlation between NDVI and rainfall estimates was the highest for the 1-month time lag in both regions of the lineament; however, the vegetation was strongly dependent on the local rains only in the SE region ($r = 0.68$). The correlation between NDVI and rainfall estimates was lower in the NW region ($r = 0.41$), indicating that the vegetation in this region was more independent of local rainfall and suggesting

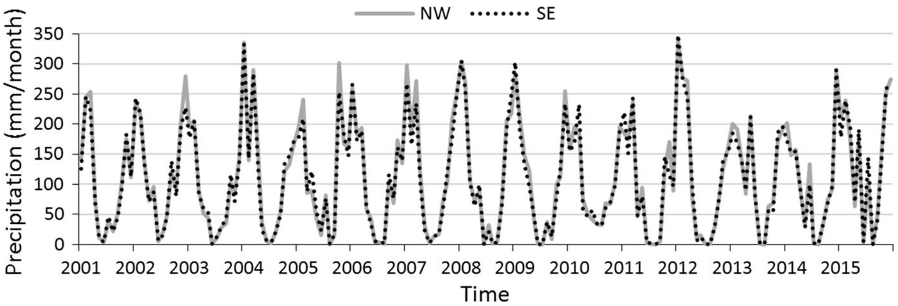

Fig. 2 Long-term monthly average of precipitation profiles of the NW and SE regions of the vegetation lineament, northern Pantanal, in central South America

Table 1 Correlation and time lag between NDVI and rainfall estimates in the NW and SE regions of the vegetation lineament

Region	Direct correlation	1-month time lag	2-month time lag
NW	0.38	0.41	0.36
SE	0.58	0.68	0.6

that water was not a limiting factor. This result indicates that a considerable portion of the water supplying this area is not from local rainfall. According to Assine et al. (2015), the major part of the superficial water flow consists of stream flow in the NW portion and pluvial runoff in the SE portion. Therefore, the hydrology dynamics proposed by these authors results in the absence of another significant water input into the SE system and in a major dependence of the vegetation on local rainfall, a result that corroborates our findings. In extreme situations, a significant increase in forest canopy greenness may coincide with the early drought season. This increase can occur if the increased availability of sunlight (due to decreased cloudiness) occurs when water is not limiting, as Saleska et al. (2007) describe for some parts of the Amazon Forest.

NDVI is always higher in the NW than in the SE portion because there is usually some soil exposed in the grassy savanna, which is associated with a decrease in leaf area and, consequently, in NDVI. The forested areas in the Cerrado are more characteristically semideciduous than the evergreen forest in the NW region of the lineament. Finally, the data demonstrate that drought has minor effects in the NW region compared with the SE region, with a smaller influence of rainfall on vegetation seasonality at NW (Fig. 3).

Phenological metrics

In all the derived metrics images, the vegetation lineament is well defined (Fig. 4). In general, the NW region had the lowest values of greenup rate and seasonal amplitude of NDVI and the highest values of annual minimum NDVI, whereas the SE region had the highest values of greenup rate and seasonal amplitude of NDVI and the lowest values of annual minimum NDVI.

The minimum NDVI values varied from -0.15 to 0.75, with the lowest values on both sides of the vegetation boundary refer to deforested areas, with pixel contamination by exposed free water during flooding periods. The presence of open water underneath the canopy reduces the spectral reflectance of a partly vegetated pixel in the near infrared, resulting in a decrease in NDVI, which in this case is not a result of lower photosynthetic rate due to water stress. Note that the free water response is absent or nearly absent from the NW closed-canopy forests in areas that flooded for 3–4 months a year. The dominance of high minimum NDVI values in the NW portion of the lineament indicates an area less subjected to water stress during the dry season. In the SE region, there are some high minimum NDVI values associated with closed forested savannas, as verified during the field campaign, but even these areas have lower NDVI values than the maximum values in the NW region, except in riparian vegetation, which occurs at the eastern end of the image.

The mean seasonal amplitude of NDVI varied widely, ranging from 0.13 to 0.56 (Fig. 4b), with the

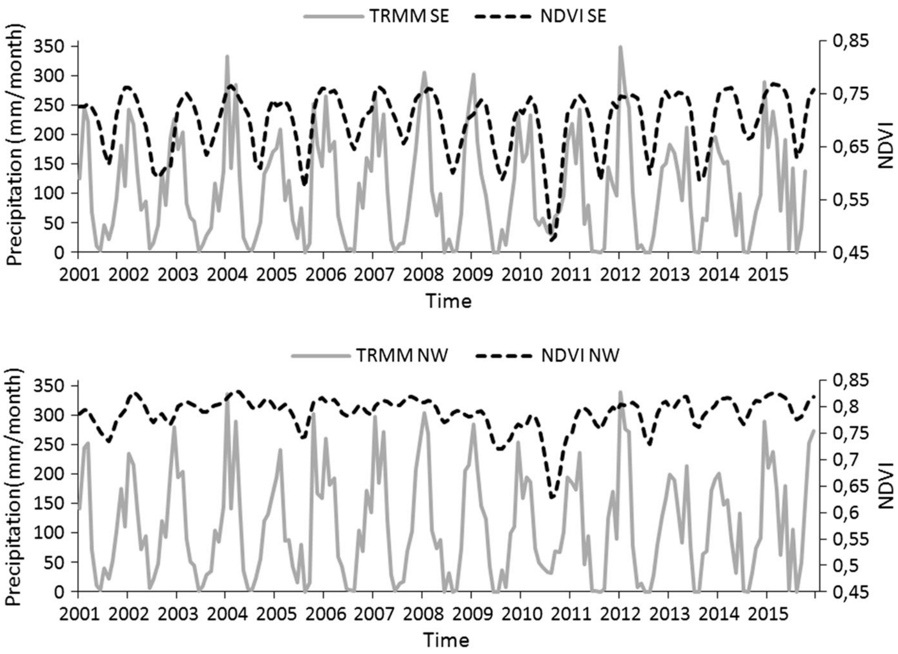

Fig. 3 Long-term mean monthly time series (2001–2015) of greenness (Moderate Resolution Imaging Spectroradiometer/ Normalized Difference Vegetation Index) and estimated precipitation (Tropical Rainfall Measuring Mission) on both sides of the vegetation lineament, northern Pantanal, in central South America

lowest values in the NW region and the highest values in the SE region. In natural areas, the amplitude should indirectly indicate water availability in the region throughout the year, including during the drier months. The amplitude should be higher in areas undergoing water stress during drought and lower in areas that remain moist. The higher amplitudes in the NW portion occur sparsely in grassy areas that are covered by water during the seasonal floods, resulting in a negligible greenness response. At the end of the floods, the grass grows and quickly covers the land, with an NDVI often exceeding that of evergreen forests due to the canopy geometry. In the SE region, however, the higher amplitude values predominate, except in riparian vegetation, which suggests a greater dependence on local rainfall.

The regrowth rate ranged from 0.04 to 0.31, with the SE region having higher rates than the NW region (Fig. 4c). Because of the scarcity of water in the SE region during the dry season, the rate of recovery of the vegetation at the beginning of the rainy season is high, with a rapid increase in greenness level, because the plants are making the most of the newly available water. In the NW region, however, the vegetation does not show a significant increase in greenness or in regrowth rate, since water is not a limiting resource for the plants during the dry season.

The different behavior of LSP on the two sides of the lineament indicates that, in the uplifted SE region, the availability of water is primarily from local rainfall, except in areas near streams. However, in the NW region, water is available throughout the year, thanks to the lowering of the base level by the fault and the perennial rivers that introduce water into the hydrological system even during droughts. This partial dependence on groundwater may occur in other wetlands, such as the Sian Ka'an Wetlands in Mexico, where most of the water input comes from groundwater (Gondwe et al. 2010). Therefore, the results show clearly that part of the maintenance of greenness on the NW side of the lineament during the months of drought is a response to the shallow water table.

Figure 4 shows the analyzed metrics and the corresponding area on the map of vegetation and land use in the region (Conservation International 2009). This map, updated to 2008, even with its flaws, allows the context of the study area concerning the vegetation covers to be seen. This view may make it easier to read the presented data set.

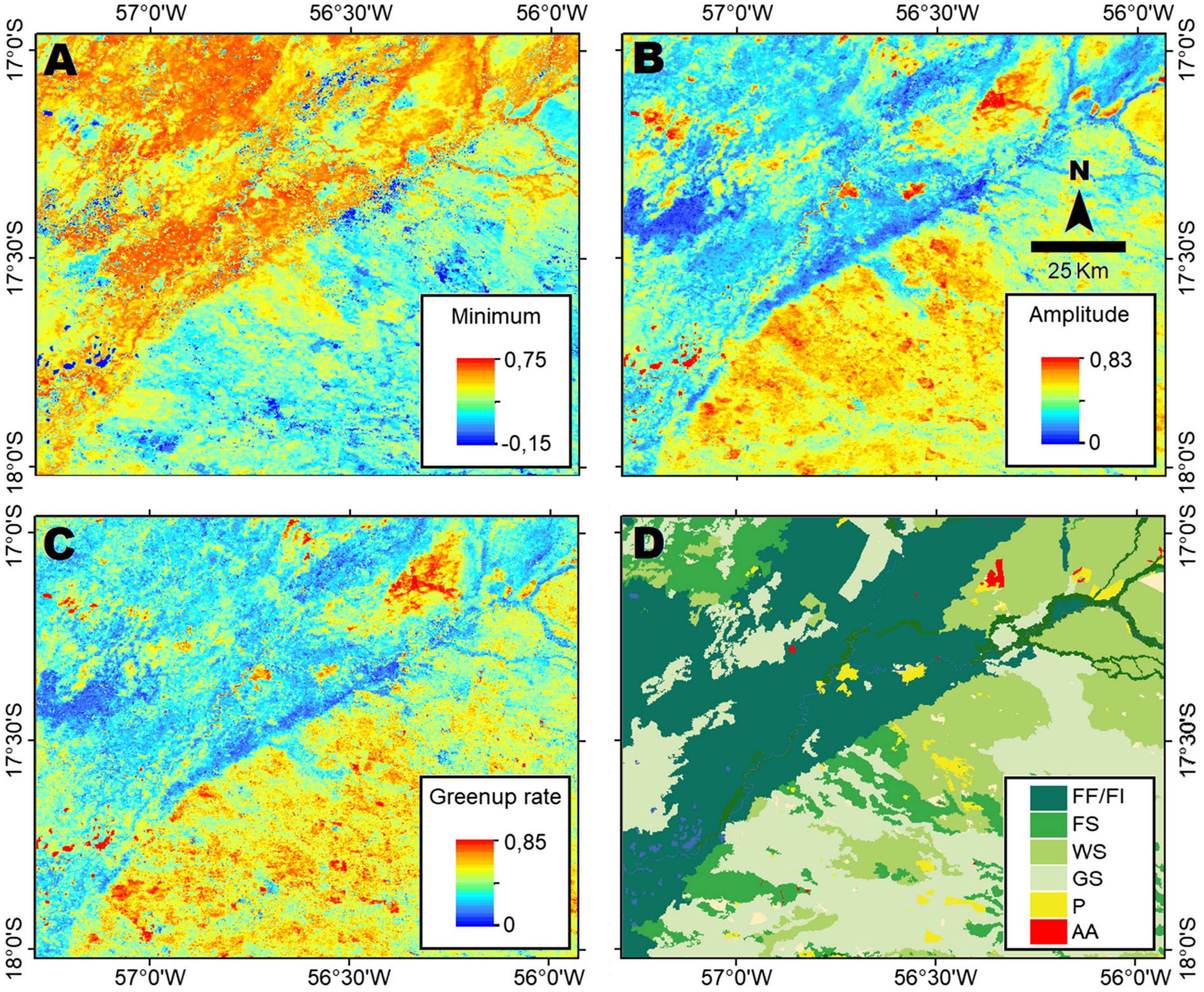

Fig. 4 Annual minimum value (**a**), seasonal amplitude (**b**), and greenup rate (**c**) averaged metrics derived over a 15-year Moderate Resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index (NDVI) time series. Vegetation map and soil use (**d**) are shown for comparison purposes (Conservation International 2009). *FF/FI* forest/vegetation with river influence, *FS* forested savanna, *WS* wooded savanna, *GS* grass savanna, *P* pasture, *AA* anthropized area

Floristic data

In order to verify the floristic variability in the lineament region, 17 plots 20 × 30 m were allocated in the field, 7 in the NW region of the lineament, 8 in the SE region, and 2 near the lineament. Among the plots in the NW region, one was located at an elevation of about 2 m on a temporary drainage levee that preserves the forest from the floods (plot 06). The plots in the SE region were located partly on the levees and partly on the plain in areas not prone to floods. The layout of the plots sought to cover the essential variability of the local forests, considering the possibilities of access and the relative position of the lineament (Fig. 5).

These plots permitted the recognition of 621 individual trees belonging to 32 botanical families, 63 genera, and 66 species. Because of similarities in the forests, indicated by the Jacc matrix (Table 2), there were two dominant strata of forests, one in the NW portion of the lineament, with dominance by seasonally flooded and evergreen forests (except for plot 06), and one in the SE portion. The latter comprised different phytophysiognomies and high floristic heterogeneity that could be considered, according to Nunes da Cunha et al. (2007), as ecotones

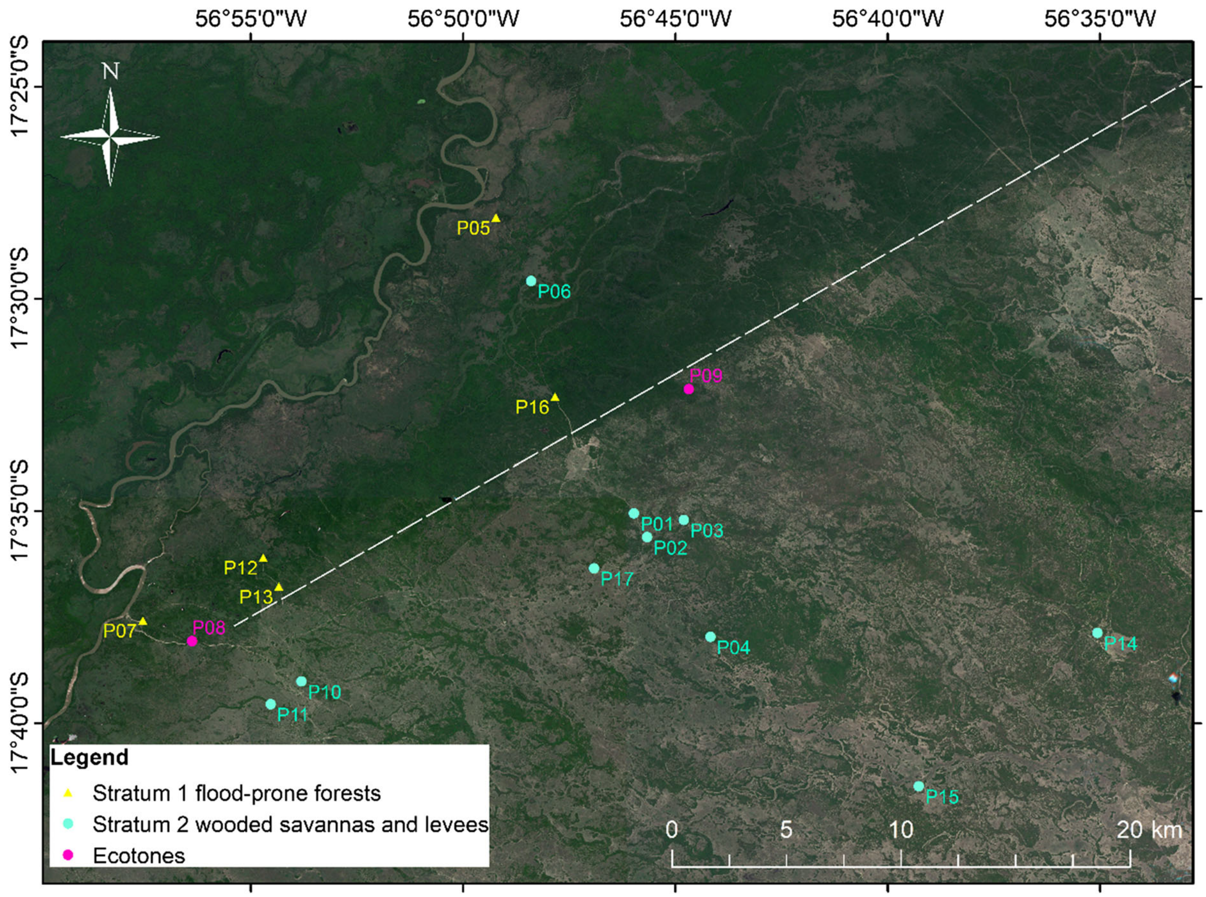

Fig. 5 Distribution of the 17 plots stratified by their Jaccard Similarity Indices, on a real-color RGB composition of a Rapid Eye images mosaic of the study region in the northern Pantanal showing the vegetation lineament

between grasslands (not sampled), forested savannas, and semideciduous forests. These forests occur over levees of ephemeral drainage, murundus, and older levees that are partially eroded but are higher than the surrounding terrain. The murundus are circular elevations in the terrain, up to 10 m in diameter each one, of still undetermined origin, possibly made by mound-building termites in particular environmental conditions (Souza and Delabie 2016).

It is important to note that there are some elongated areas 2 m in elevation in the NW strata, such as plot 06, that are covered by semideciduous forests preserved from flooding. The forest in these areas is entirely dissimilar from the forest in all other plots in the NW area, with Jacc values between 0 and 0.06. Plot 06 has only one species shared with plot 05 (*Triplaris gardneriana* Wedd.), one with plot 07 (*Unonopsis guatterioides* (A.DC.) R.E.Fr.), and none with the other four plots in the NW portion of the lineament. However, the forest in plot 06 has a relatively high similarity to forests in the SE area growing over levees, especially with the forest in plot 17, which is situated more than 10 km away (Jacc 0.42). The floristic similarity between distant plots, both preserved from floods, shows that a small change in elevation drastically overcomes the criterion of proximity in the regional distribution of species. This is a meaningful confirmation of the thesis here defended: the small vertical displacement of the fault is an important source of variability in the Pantanal, with phenological and phytosociological effects.

Two findings are evident in Table 2, which presents the Jaccard's similarity matrix: the distance between plots has no relevance to the distribution of species, and the similarity between the forests sampled is mainly determined by the presence and persistence of

Table 2 Jaccard's similarity coefficient matrix between vegetation plots at the study site in the northern Pantanal

	1	2	3	4	***5***	***6***	***7***	8	9	10	11	***12***	***13***	14	15	***16***	17
1	–	0.20	0.21	0.27	0	0.20	0	0.07	0.09	**0.25**	0.17	0	0	0.13	0.20	0	0.13
2	0.20	–	0.21	0.12	0.06	0.20	0.13	0.14	**0.26**	0.07	0.11	0.07	0.06	0.08	0.04	0.06	0.31
3	0.21	0.21	–	0.17	0	0.21	0	0.07	0.10	**0.27**	0.18	0	0	0.13	0.10	0	**0.33**
4	**0.27**	0.12	0.17	–	0	0.12	0	0.13	0.03	**0.25**	0.24	0	0	0.28	0.31	0	0.17
5	0	0.06	0	0	–	0.06	0.13	0.14	**0.26**	0	0	**0.25**	0.12	0	0.04	0.2	0
6	0.2	0.2	0.21	0.12	0.06	–	0.06	0.23	0.14	0.07	0.17	0	0	0	0.04	0	**0.42**
7	0	0.13	0	0	0.13	0.06	–	0.07	0.20	0	0.05	**0.36**	**0.27**	0	0	**0.29**	0
8	0.07	0.14	0.07	0.13	0.14	0.23	0.07	–	0.10	0	0	0.08	0.06	0	0.05	0.07	0.25
9	0.09	0.26	0.10	0.03	**0.26**	0.14	0.2	0.10	–	0	0.08	0.17	0.09	0	0.03	0.14	0.10
10	**0.25**	0.07	**0.27**	**0.25**	0	0.07	0	0	0	–	**0.38**	0	0	0.14	0.24	0	0.08
11	0.17	0.11	0.18	0.24	0	0.17	0.05	0	0.08	**0.38**	–	0	0	0.11	0.13	0	0.11
12	0	0.07	0	0	**0.25**	0	**0.36**	0.08	0.17	0	0	–	**0.45**	0	0.05	**0.5**	0
13	0	0.06	0	0	0.12	0	**0.27**	0.06	0.09	0	0	**0.45**	**–**	0	0.09	**0.73**	0
14	0.13	0.08	0.13	**0.28**	0	0	0	0	0	0.14	0.11	0	0	–	**0.38**	0	0.04
15	0.20	0.04	0.10	**0.31**	0.04	0.04	0	0.05	0.03	0.24	0.13	0.05	0.09	**0.38**	–	0.04	0.10
16	0	0.06	0	0	0.20	0	**0.29**	0.07	0.14	0	0	**0.50**	**0.73**	0	0.04	–	0
17	0.13	**0.31**	**0.33**	0.17	0	**0.42**	0	**0.25**	0.10	0.08	0.11	0	0	0.04	0.10	0	–

Plots in the NW region of the lineament are shown in italics. Values $\geq$ 0.25 (similar vegetation communities) are shown in bold

floods. The two plots characterized as ecotones are near the fault, reinforcing the importance of this structure as an environmental limit and corroborating the results of the phenological approach.

Plot 09 is an evident ecotone region, having erratic similarities with the two strata plots: a high Jacc (0.26) with the forest on levees of temporary drainage in the SE region of the lineament (plot 02) and with the plot on the long-term flooded forest (plot 05) in the NW region. Plot 08 is not precisely an ecotone, being floristically similar to plot 17 and quasi-similar to plot 06 (both over levees of temporary drainage) and having relatively high similarity scores to other SE region plots (plots 02 and 04) but also to a long-term flooded forest (plot 05), in an unexpected relationship. The remaining 14 plots are associated with floodable or non-floodable areas.

The use of dendrograms generated by hierarchical grouping using Jaccard's coefficient of similarity for the diversity of aquatic macrophytes in the Pantanal by Pott et al. (2011) permitted the classification of floristic similarity between the sampling sites. The authors used the Unweighted Pair Group Method with Arithmetic Mean (Kent and Coker 1992) as a clustering method, obtaining a dendrogram with a robust result from the statistical point of view. This method, applied to the plot data of Table 1, segregated the forests referred to the plots into four groups (Fig. 6):

- Semideciduous forests on levees of temporary drainage on both sides (i.e., including plot 06 in the NW region);
- Forests not associated with the main vegetation groups (the two plots in ecotone zones near the fault and plot 05, the closest to the São Lourenço River);
- Forested savannas, which occur only in the SE region; and
- Floodable evergreen forests, which occur only in the NW region.

Figure 6 Dendrogram of hierarchical clustering of the Jaccard similarity coefficient from plots allocated in the vegetation lineament region in northern Pantanal, Brazil. Note that plot 06 (highlighted) is the only one in a non-floodable area in the NW region of the lineament.

Considering the species accounting for more than 4% of the individuals sampled, the presence of two forest strata is clear. The most common species is *Attalea phalerata* Mart. ex Spreng., with 68

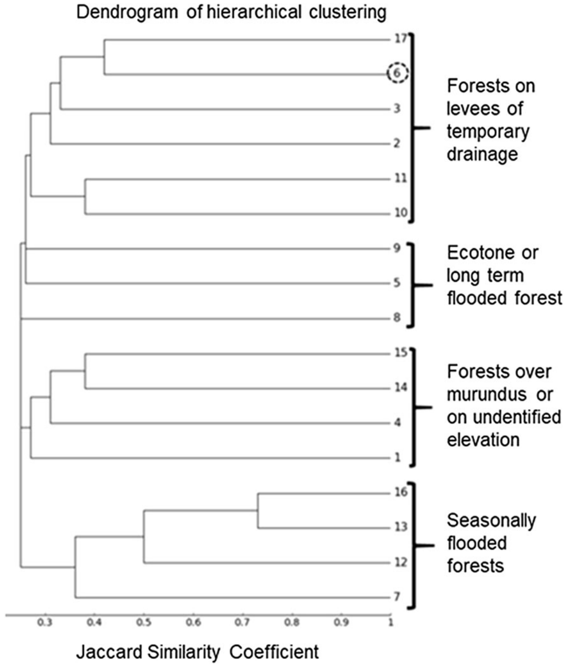

Fig. 6 Dendrogram of hierarchical clustering of the Jaccard similarity coefficient from plots allocated in the vegetation lineament region in northern Pantanal, Brazil. Note that plot 06 (highlighted) is the only one in a non-floodable area in the NW region of the lineament

individuals sampled in eight plots (01, 17, 02, 03, 04, 06, 08, and 09). This species is present in the two plots classified as ecotones but absent in the plots in floodable forests. *Licania parvifolia* Huber, which is the second most common species (53 individuals), is exclusively found in floodable forests in the NW region (plots 12, 13, 16, and 07) but is absent in the long-term plot 05. The third most common species is *Dipteryx alata* Vogel, which is present only in the SE region in the three plots associated with murundus (plots 04, 14, and 15), and plots with undetermined elevation or associated with levees of temporary drainage (01, 03, 10, and 11). The variety of subenvironments where *D. alata* is present suggests that it is a species generalist adapted to a variety of environmental conditions at the SE region. The fourth most abundant species, with 29 individuals, is *Astronium fraxinifolium* Schott, which is found in plots 01, 02, 04, 10, 11, 14, and 15 exclusively in the SE region and is associated with all the SE subenvironments. The fifth most common species is *Albizia inundata* (Mart.) Berneby and J.W.Grimes, with 26 individuals, which is found in all NW plots except plot 06 on the levee and plot 08 in the ecotone. The other species with a substantial presence, accounting for between 2 and 4% of sampled individuals, are also exclusive to the NW region (*Amaioua guianensis* Aubl. and *Couepia uiti* (Mart. and Zucc.) Benth. ex Hook.f.) or to the SE region over levees or murundus (*Handroanthus heptaphyllus* (Vell.) Mattos and *Protium heptaphyllum* (Aubl.) Marchand). The dendrogram of Jaccard's Similarity Index in Fig. 5, therefore, shows efficiency in the grouping of plots, including the detection of plots in ecotone areas (plots 08 and 09) or with characteristics not present in other plots (plot 05).

The dataset did not show an effect of the distance between plots on the degree of similarity, except when the proximity was simultaneously geographic and environmental. When the similarity between the plots closest to and belonging to the two forest strata is compared, there is a remarkable absence of common species between plots 4–5 km apart: plot 10 (SE side) versus plots 12 and 13 (NW side), and the 6-km-distant plots 01 (SE side) and 16 (NW side). However, plots 13 and 16, which were located more than 15 km apart, had the greatest Jacc (0.73).

The floristic data suggest that the lineament behaves as a limit to the extensive establishment of propagules of the Amazon biome. In the NW region of the lineament, species typical of the Amazon biome, such as *Vochysia divergens* and *Licania parvifolia*, are common or even dominant, whereas the species described from the SE region are all common to the Cerrado biome or are generalists.

Ecological significance of LSP and floristic data

The combination of data sets obtained in this research provides some advances in the knowledge of this remarkable region. The estimates of rainfall from January 2001 to 2015 show a severe seasonality, which is almost identical ($r = 0.99$) on the two sides of the lineament. The long-term observation of MODIS NDVI in the SE portion of the lineament shows an equilibrium between rainfall and greenness, whereas in the NW portion, it shows little or no influence of the local rains on greenness of the canopy. The phenological analyses naturally indicate this different behavior. In the process of colonization of a region by vegetation, the winning species in the competition for habitat occupation will not be the same on both sides of the lineament. Xeromorphic vegetation imposes its presence by surviving for months of drought each year in the SE region. On the other hand, in the NW region there are months of flooding every year, and in the dry season a shallow water table supplies the trees' need for water.

The interpretation of the two primary sources of data, the LSP and the floristic inventory, is direct. The most striking features in the differentiation of the two forest strata are the predominance of evergreen forests in the NW portion of the lineament and the intense drying of the vegetation in the SE portion, as demonstrated by the phenological metrics presented here. Forrest and Miller-Rushings (2010) argue that phenology is a significant structuring element that affects nearly all aspects of ecology and evolution. The same seems to be happening here. Viña et al. (2012) propose that the LSP is a valuable tool for mapping and monitoring floristic diversity patterns in ecosystems around the globe. The three most common species described in the SE portion of the lineament are typically xeromorphic or resistant to intense droughts. Likewise, in the SE portion, seasonal amplitude and greenup rates are high and plant species adapted to intense droughts are present. Thus, the xeromorphic species and the phenological metrics indicate the same environment, with droughts not relieved by water sources other than the local rains. The phenological metrics for the NW portion of the lineament showed an inverse situation, with the equally long dry seasons not affecting the vegetation severely, because the shallow groundwater provides water to the tree root systems. Pott et al. (2011) classified three of the four most prevalent species in the forests of the NW portion (*L. parvifolia*, *A. inundata*, and *C. uiti*) as vegetation of fluvial or lacustrine environments or heavily flooded areas. The fourth species, *A. guianensis,* is a generalist species that occurs in various environments.

Conclusions

Vegetation reflects in some way the nature and evolution of the environment by integrating the conditions of the environment and the functioning of the system. The present study has shown that the studied vegetation lineament in the northern region of the Pantanal, the world's largest continuous wetland, is a functional boundary between two different environments that are clearly marked by vegetation phenology (as indicated by the LSP analyses) and floristic inventory. The few meters of subsidence of the NW block of the geological fault allowed the region to have a shallow water table due to the change in the base level. The environment of the SE portion, not modified by neotectonic, is the same that occur in the central Pantanal. The prolonged droughts associated with a deeper water table favor savanna-like physiognomies and xeromorphic species. On the NW side of the lineament, thanks to the fault, there is an alternation between prolonged floods and availability of water to the vegetation even in prolonged droughts. This situation allows the permanence of predominant evergreen forests with species adapted to prolonged floods. Although there is no in-depth study of local faunal diversity in the area studied, some animal species are undoubtedly more adapted to one or the other side of this ecological boundary, which is the vegetation lineament. As there are no other differences in the physical environment to explain the presence of these two contiguous distinct habitats, it remains for neotectonics to explain the phenomena.

The advances obtained in this research regarding the presence of two such distinct and contiguous environments are relevant in several aspects. From the biological point of view, the advances are a stimulus to studies of the importance of this ecological boundary to the distribution of the fauna. With regard to forest sciences, it might be interesting to study in detail the changes in vegetation cover due to the alteration of the base level (from either natural or anthropogenic causes). With regard to preservation and management activities, the knowledge of two different neighboring habitats is essential information. Finally, with regard to science as the description and understanding of nature, the presented data indicating the separation of two habitats by reactivation of a fault assign to neotectonics the role of a not negligible driver in the environmental variability of the Pantanal.

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