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Long-term analysis of aquatic macrophyte diversity and structure in the Paraguay river ecological corridor, Brazilian Pantanal wetland

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ABSTRACT

Spatial and temporal variation in limnological variables, as well as local changes in the hydrological pattern, may affect inundation hydrology and alter biotic interactions and functional diversity of aquatic macrophyte communities in the Pantanal. The objectives of this research in the floodplain along the Paraguay River were to: 1) examine changes in the diversity of aquatic macrophyte communities over a ten-year period based on surveys taken in 2008 and 2018; and 2) evaluate the possible indirect relation of changes in rainfall patterns, which in turn affect lateral hydrological connectivity and limnological variables that directly affect the composition and productivity of the aquatic macrophyte community. Comparison of data taken in 2008 and 2018 revealed a change in the timing and a reduction in the number of rainy days. These changes in rainfall patterns coincided with limnological changes, including increases in transparency, pH, dissolved oxygen, ammonium, nitrate, total nitrogen, orthophosphate, and total phosphorus, as well as decreases in water temperature and connectivity. Species richness of aquatic macrophyte communities in three ecological zones of the Paraguay River floodplain increased between 2008 and 2018, with increases in emergent grasses, emergent non-grasses, and amphibious life forms, showing a trend that favors species that are more adapted to drought conditions. The seasonal pattern of inundation and desiccation, as well as dissolved oxygen and temperature, where correlated with macrophytes communities variations. The colonization and expansion of rooted emergent macrophytes over this period could be a response to local anthropogenic activities, hydrological trends, or may reflect interannual rainfall variability.

1. Introduction

Wetlands are among the most productive ecosystems in the world, supporting 10% of the global biodiversity and covering a wide range of hydrological characteristics (Mitsch and Gosselink, 2015; Darwall et al., 2018). Despite their importance, is well known that human activities have profoundly altered wetlands in many parts of the world. These anthropogenic alterations often entail changes in the quality and quantity of water, as well as seasonal patterns of inundation (Mahmoudi et al., 2010; Marengo et al., 2021).

In Brazil, Junk et al. (2014) reported that wetlands cover 20% of the country, including the extensive Amazon and the Pantanal floodplains, with specific flood pulse patterns that vary greatly in timing, duration, and amplitude. The Pantanal is one of the world's largest seasonally inundated floodplain wetlands (Hamilton et al., 2002). Lying within the watershed of the upper Paraguay River, the Pantanal is a vast complex of rivers, floodplain lakes, and seasonally inundated lands, with 80% of its total area of ~160,000 km^2 within the states of Mato Grosso and Mato Grosso do Sul, in Brazil (Da Silva and Girard, 2004; Brasil, 2020). The Paraguay River is the principal river that flows through and drains the Pantanal; together with its tributaries, it regulates the flood regime in adjacent floodplains (Da Silva, 2000; Fantin-Cruz et al., 2020).

The seasonal flood pulse is the primary driver that regulates the structure and function of the ecosystems of the Pantanal region (Da Silva

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and Esteves, 1993). A floodplain land that is subject to seasonal inundation and desiccation is known as the Aquatic-Terrestrial Transition Zone (ATTZ), which functions as an important ecological corridor and enhances the biodiversity of the floodplain ecosystem (Junk et al., 1989; Roberto et al., 2009; Kennedy and Turner, 2011; Quintela et al., 2019). The ATTZ along the margins of rivers and floodplain lakes commonly supports extensive stands of aquatic macrophytes, and these stands play important functions in the floodplain ecosystem, for example, by providing food and habitat for diverse organisms, retaining sediments, and mediating biogeochemical cycles (Pains da Silva et al., 2010; Ávila et al., 2019).

Globally, there are 3457 species of aquatic macrophytes distributed in 93 families, occurring in freshwater and marine environments (Murphy et al., 2019). In the Brazilian Pantanal, 280 species in 56 families have been recorded, with variable growth forms and life history strategies depending on the hydrological regimes in which they occur (Pott et al., 2011). The macrophytes morphophysiology and high ecological plasticity make them capable of inhabiting environments with different chemical and physical characteristics, such as nutrient concentration, water pH, dissolved oxygen, electrical conductivity, temperature, luminosity, flow, water level fluctuation, and lateral hydrological connectivity (Da Silva and Esteves, 1995; Esteves, 2011).

The seasonal dynamics of the flood pulse affect the diversity of macrophytes associated with floodplain lakes. During the period of retraction of water levels after the wet season, the shifting location of the land-water boundary of the ATTZ is, in fact, a “moving littoral zone” (Junk et al., 2020). The seasonal reduction in the extent of the flooded area and the depth of remaining standing water affect primary production, plant cover, and limnological variables, resulting in a local ecological succession from more aquatic to more terrestrial plant communities (Junk and Piedade, 1993; Lo et al., 2017). The high species richness and diversity of floodplain plant communities, as in ecosystems in general, are a function of spatial variability, temporal fluctuations, environmental heterogeneity, and colonization processes (Agostinho et al., 2009; Heino et al., 2015; Leibold and Chase, 2017; Schneider et al., 2019; Fernández-Aláez et al., 2020; Alahuhta et al., 2021).

During the rainy season, precipitation increases the transport of nutrients, to the water and benefits the establishment, composition, flowering and fruiting of aquatic macrophytes (Esteves, 2011; Campos et al., 2012; Aoki et al., 2017; Simão et al., 2021). In the Pantanal, although there is a no clear pattern, precipitation and temperature can be correlated with the flowering of emerging and amphibious species (Freitas et al., 2013; Catian et al., 2019). During the rainy season, the greater nutrients concentration in water, higher radiation and pollination processes can favor the flowering and fruiting of aquatic plants (Morellato and Leitão-Filho, 1992; Simão et al., 2021).

The ecosystem services offered by aquatic macrophytes can be associated with seasonality and rainfall patterns and, thus, be affected by climate changes in the Pantanal. According to some models proposed by Marengo et al. (2016), the reduction in the volume of rain and the increase in temperature has a direct impact on the flood pulse in the Paraguay River. In 2019, the reduced transport of hot and humid air from the Amazon to the Pantanal caused a strong reduction in precipitation in the region, generating impacts on the hydrology of the Paraguay River and intensifying wildfires in the region (Marengo et al., 2021; Silgueiro et al., 2021; Menezes et al., 2022).

An understanding of the controls on the biodiversity of floodplain macrophyte communities requires knowledge of the species pool, as well as functional characteristics and life histories of each species, and how individual species respond to environmental variation (Adler and Lauenroth, 2003; Dussault, 2019). On a local scale, it is essential to consider the composition and distribution of the species, and to identify how those characteristics may be affected by local, regional and historical environmental factors, including biotic interactions (Alahuhta et al., 2018). The concept of functional diversity provides a framework for analysis of how complex communities respond to environmental factors (Fu et al., 2014; Catian et al., 2018).

Aquatic macrophytes communities respond to the spatiotemporal environmental gradient of the flood pulse, and can indicate the variables that respond to an environmental change through their structure, diversity and organization. The objectives of this research in the floodplain along the Paraguay River were to: 1 - examine changes in the diversity of aquatic macrophyte communities over a ten-year period based on surveys taken in 2008 and 2018; and 2 - correlating the changes in rainfall patterns, which in turn affect lateral hydrological connectivity and limnological variables that directly affect the aquatic macrophyte community composition.

2. Methods

2.1. Study area

This study was carried out in four hydrological phases (dry season, rising water, flood and falling water) during 2008 and 2018. Macrophytes were surveyed in nine floodplain lakes with variable degrees of lateral hydrological connectivity distributed along a 155-km reach of the Paraguay River, between the coordinates 16°10'S, 57°47'W and 16°42'S, 57°45'W. The Paraguay River and the adjacent floodplain in this reach include four functional sectors, classified according to their hydrogeomorphological characteristics, in the meandering floodplain sector; straight sector; transition sector and fluvio-lacustrine sector (Wantzen et al., 2005).

The meandering channel zone (sector) includes the Retiro Velho (RV) and Simão Nunes (SN) lakes, on the left descending bank, and the Toma Vara (TV) lake, on the right bank. The Straight channel zone (sector) passes along a range of hills (*morros*) and includes the Canto Grande (CG) and Boca do Natalino (BN) lakes, on the left bank, and the Jauru Velho (JV) lake, on the right bank. The transitional channel zone (sector), which contains meanders of lower sinuosity, includes the Pacas (DP) and Morros (LM) lakes, on the right bank, and the Morrinhos (LMo) lake, on the left bank. The lateral connectivity of the floodplain lakes with the river varied: 1) directly connected at the highest water levels (Retiro Velho, Toma Vara); 2) directly connected all year (Simão Nunes, Canto Grande, Boca do Natalino); and 3) indirectly connected all year by narrow tie channels, locally known as *corixos* (Jauru Velho, das Pacas, Morrinhos, Morros (Fig. 1).

The climate of the region is humid tropical (Köppen type Awa), with a mean annual temperature of 26 °C, reaching 28 °C. The mean annual rainfall is 1335 mm, with most rain falling between October and March (Neves et al., 2011). Seasonal variation of rainfall in the upland and floodplain portions of the watershed, together with the attenuation of hydrological variability by extensive floodplains, results in a monomodal flood pulse of low amplitude along the Paraguay River axis (Da Silva and Esteves, 1995; Junk and Da Silva, 1999; Da Silva and Girard, 2004; Nogueira et al., 2011).

2.2. Data collection

Hydrological data (rainfall, water levels, and discharge) between the years 2000 and 2019 for a station along the Paraguay River, upstream of the study area (Cáceres DNPVN 01657003 and 66070004), were obtained from the Brazilian National Water Agency's Hidroweb - Sistema Nacional de Informações sobre Recursos Hídricos da Agência Nacional de Águas (Agência Nacional das Águas, 2019). Limnological variables were collected in the four hydrological phases each year, (at the same time as macrophyte surveys) including water temperature, pH, oxygen, turbidity, and conductivity, were measured using a multi-parameter checker (Horiba U-50) placed on the surface of the water column (20-cm depth) within stands of aquatic macrophytes, as well as at a point in the central region outside of the macrophytes stands of the lake. Measurements the water transparency (Secchi disk) and depth (sonar) were performed along the edge of the macrophytes stands.

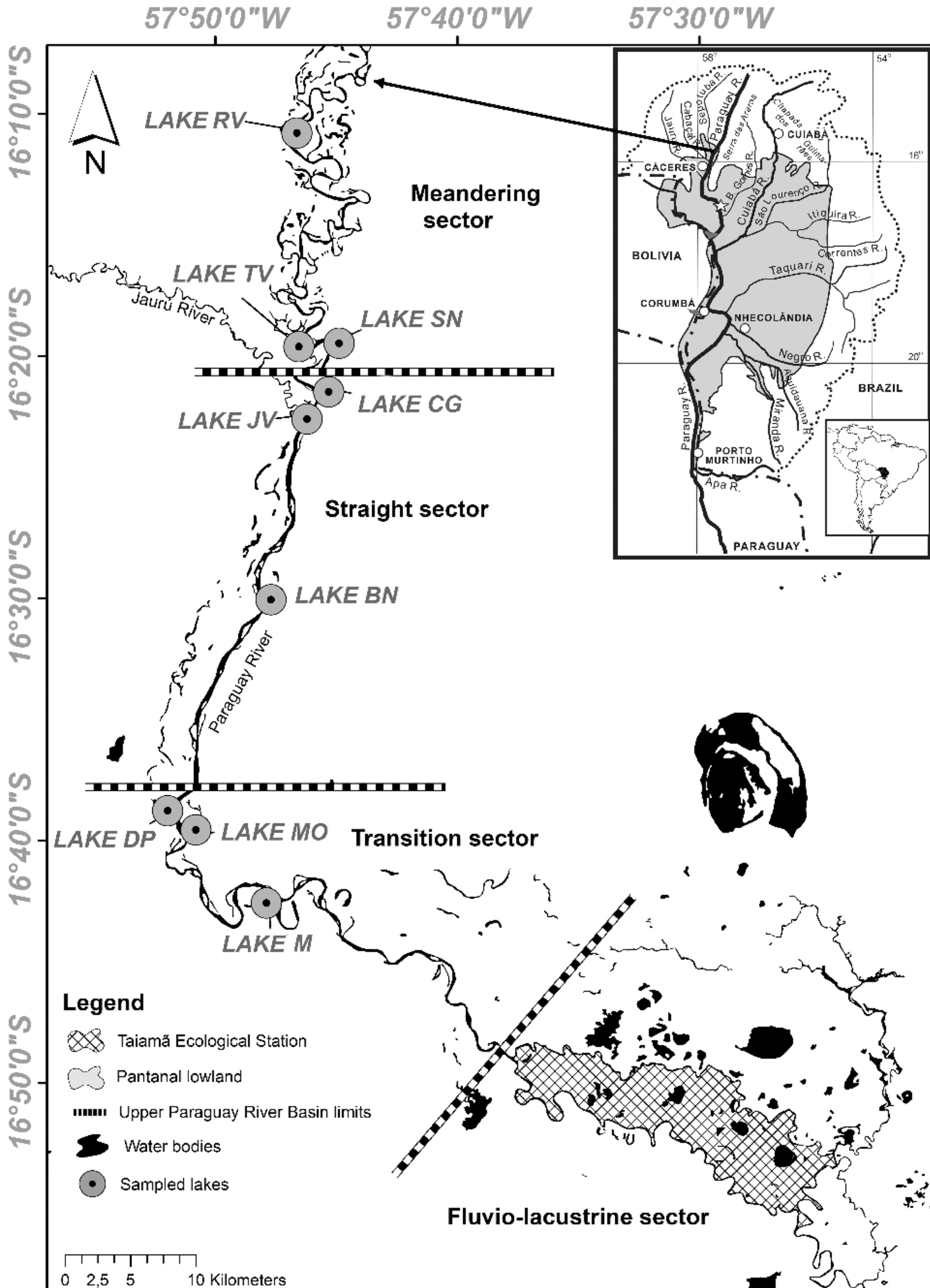

Fig. 1. Study area along the Paraguay River corridor in the Pantanal (municipality of Cáceres).

For the nutrient analysis, water samples (300 mL) were collected outside the aquatic macrophyte bank. The nutrients analyzed were ammonium, nitrate, orthophosphate, and total nitrogen and phosphorus, which were measured in the Laboratório de Limnologia at the Centro de Limnologia e Biodiversidade – CELBE using standard colorimetric methods and UV–VIS spectrophotometry (APHA, 2005).

The species composition and structure of aquatic macrophyte communities were surveyed in 2008 and in 2018 following the methods of Braun-Blanquet (1979), randomly placing a 0.50-m2 quadrant 20 times, totaling 10 m^2, in 20 randomly selected macrophyte stands, in each of the nine floodplain lakes and the Paraguay River. The species were identified, and the specimens were placed in the Herbário do Pantanal Vali Joana Pott (HPAN) and the Herbário da Amazônia Meridional (HERBAM), both at the UNEMAT, as well as at the Instituto de Botânica de São Paulo (IBt). The species were classified into seven life forms following Piedade et al. (2018). Submerged species were not considered since the proper methodology was not applied in the 2008 survey.

2.3. Analysis of inundation regimes

The temporal changes in inundated area of the nine lakes were determined through geometric editing of LANDSAT 5 TM and LANDSAT LC08 satellite images, in the same months for both years analyzed. A total of 124 images were aggregated, cut out, redesigned (WGS84, UTM, zone 21) and converted in a radiometric resolution from 16 to 8 bits. Pure pixels (from the medium infrared (MIR) and the blue band, for the vegetation, soil and water endmembers, respectively), were collected, and used to apply the Linear Spectral Mixing Model (MLME), followed by the slicing of water fraction images histogram ("water" and "non-water" classes). Once the classes were delimited, they were manually edited for errors in the classification. The analyses were carried out using the ConvGeoTif, SPRING and ArcGIS softwares. The spectral curves obtained for each MLME endmember fit with the standard spectral curves expected for the vegetation (Ponzoni, 2001), soil (Netto, 2001) and water (Novo, 2001) endmembers. The duration of the inundation between the years 2008 and 2018 was calculated based on the lateral hydrological connectivity of the lakes observed in the field, the amplitude of the flood pulse at the Cáceres station (DNPVN - 01657003 and 66070004), and the depth of the water column measured in each location over the cycle of inundation.

2.4. Statistical analysis

The limnological variables were subjected to Multivariate Analysis of Variance (MANOVA) and principal component analysis (PCA) to verify the differences and possible grouping of the samples. Normality and homoscedasticity of data were previously tested.

The species diversity and life forms, connectivity and functional sectors were subjected to permutational multivariate analysis based on the Bray-Curtis distance, and subsequently ordinated by Principal Coordinates Analysis (PCoA). Life forms were evaluated using the indicator value IndVal (Dufrêne and Legendre, 1997; De Cáceres et al., 2010) approach to determine whether a particular group tended to be more frequent or abundant in each of the study locations in the year of 2018.

The functional traits embodying the adaptation of macrophyte species to floodplain environments included the eight life forms described by Piedade et al. (2018), life cycle (annual or perennial), flowering period (annual, seasonal, or monthly), leaf architecture (hairy, leathery or herbaceous) and root structure (fasciculate or pivoting), biomass (g/dry weight) and specific length area - SLA (cm2/g) (Evans and Hughes, 1961). The association of hydrological phases and years on functional traits (community weighted mean - CWM) (Laliberté and Legendre, 2010; Laliberté et al., 2014) and functional diversity (RaoQ) was examined by redundancy analysis. Only the significant traits were retained for the examination. To determine the possible association of environmental variables on the selected traits and RaoQ, we choose to run Multiple Generalized Linear models. To identify the bestmodels in explaining the dependent variables we used the Akaike Information Criterion (AICc) for small samples andweight of themodels. All candidate models with values ≤ 2 ΔAICc were used as guides for choosing the best fit models for each situation. All analyses were conducted in the R platform, version 3.04 (R Core Team, 2011), at the 0.05 level of significance, using the ade4, fd, factoextra, glmulti, MASS and rJava packages.

3. Results

3.1. Landscape, hydrological and limnological variables

Between 2008 and 2018, there was a decrease of 199 mm of rainfall in the year. The range of variation between the maximum and minimum levels of the water column also changed over time, from 2.7 m to 3.3 m (Fig. 2).

Comparing the limnological variables (Supplemental Table 1), no significant variation between the years 2008 and 2018, or between the sample areas was observed ($F(3,72)= 1.455$, $p = 0.121$, Wilk's Lambda= 0.650). However, there are significant differences between hydrological periods of the flood pulse ($F(3,72)= 13.876$, $p < 0.05$, Wilk's Lambda= 0.320). The analysis of principal components (73.1% variation explained) was able to perform the ordering of groups of samples consisting of high waters (flood and rising water) and low water (dry and falling water). The group formation was regulated by depth, temperature, pH and oxygen values in the PCA1, that was the unique principal component to be statistical significant by the Broken-Stick procedure.(Fig. 3).

The results of the satellite images show that the sample areas (lakes) had lower water surface values in 2018 compared to 2008. Likewise, the levels of connection of habitats with the Paraguay River were not the same (Table 1). Four of the nine lakes had ~31% less water, and, therefore, less hydrological connectivity with the river, in 2018 (Supplemental Fig. 1).

Two of the nine lakes changed their lateral hydrological connectivity with the river during the dry season: In 2008, the lake RV in the meander channel zone was directly connected to the river, but lost that connection in 2018. The whereas the lake DP in the transition channel zone lost its direct connection and was instead connected only via a narrow and shallow tie channel.

3.2. Diversity index and life forms

The aquatic macrophyte communities increased in species richness and diversity between 2008 and 2018 (Supplemental Table 1). The 2018 survey recorded 80 species in 31 families, primarily represented by Poaceae (11 species), Onagraceae (9 spp.), Fabaceae (8 spp.), and Asteraceae (2 spp.) (Supplemental Table 2). Compared to 2008, there was an increase of 57 species and 13 families in 2018. The dominant species were relatively uniform in frequency and cover, including *Eichhornia azurea*, *E. crassipes* and *Salvinia auriculata*.

The structure of aquatic macrophyte communities, as reflected by life forms, varied across the years. In 2018, there was an increase in the number of species (Fig. 4A) in each life forms group and inside each life form group. From 2008–2018, the most frequent life forms shifted from free-floating (11 spp.) to emergent grasses and amphibious species (53 spp.) (Fig. 4B).

The test of permutation showed significant differences among the composition of life forms between phases, degrees of connectivity, or ecological zones only during the falling water phase (ecological zones – $p < 0.05$; connectivity – $p < 0.05$). These differences were apparent among the three ecological zones (meander, straight, and transition channels), and in the degree of lateral connectivity of the lakes with the river, although the PCoA indicated environmental homogeneity (Supplemental Fig. 2). This discrepancy could be explained by the species

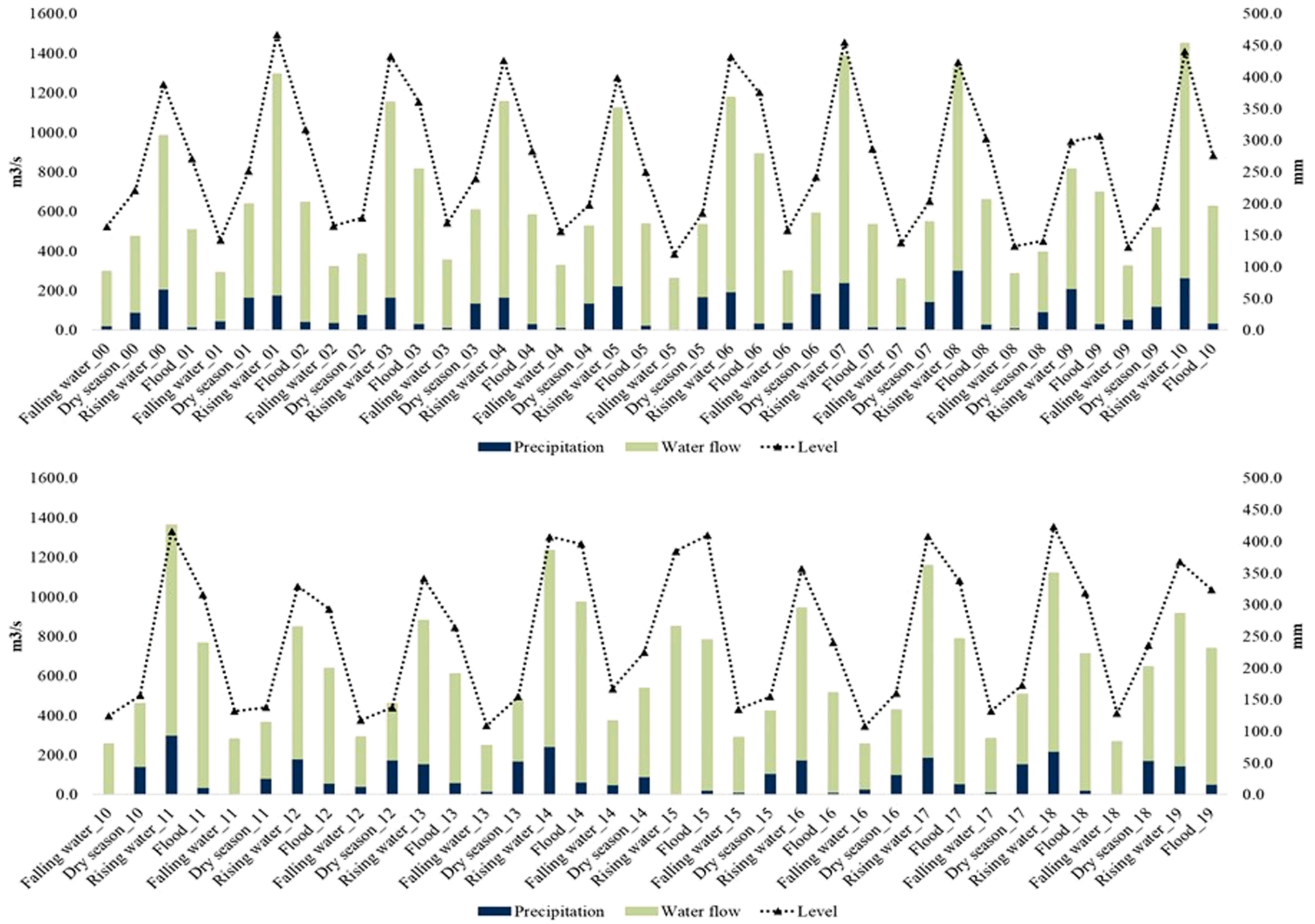

Fig. 2. Monthly average of rainfall and the water level and discharge in the Paraguay River from Falling water of 2000 through Flood 2010 (A) and from Falling water of 2010 through Flood 2019 (B), measured at the upstream National Water Agency station (Cáceres DNPVN).

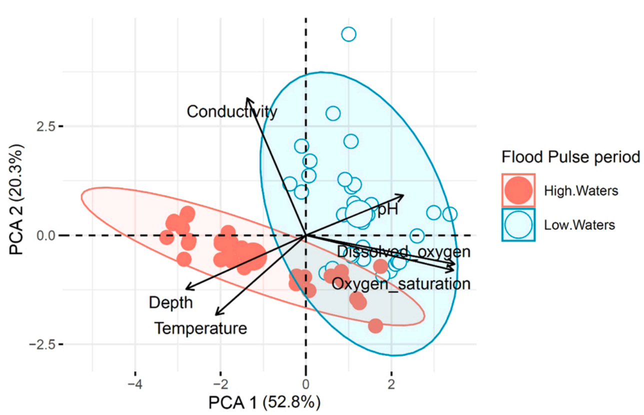

Fig. 3. PCA for the limnological variables between hydrological periods of the flood pulse (high waters –red, and low water - blue) of the Paraguay River, in the years of 2008 and 2018.

composition, which tended to show a substitution of species within the same life form. The indicator value (IndVal) approach also did not reveal a specific life form among the study sites. However, changes in the relative abundance of life forms were observed (Supplementary Figure 2).

The results of the redundancy analysis (RDA) showed that among the years analyzed, 2018 had the highest indices of functional diversity (RaoQ), biomass (CWM.Biomass), SLA (CWM.SLA) and the highest frequency among emerging (CWM.Emerg) and free floating (CWM. Float) life forms. (Fig. 5).

The dominance of certain life forms observed in 2018 when all sites were averaged was not apparent when the three ecological zones were examined separately. Depth was negatively correlated with functional diversity, SLA, and Biomass. The SLA, biomass, emergent and floating life forms were positively correlated with temperature. The Floating CWM and RaoQ were positively associated with total phosphorus (Table 2).

4. Discussion

Unlike other studies (e.g. Fu et al., 2014; Zhang et al., 2018), our data point to no association between the spatial (local, regional) variation of the taxonomic composition of aquatic macrophyte communities in the Paraguay River plain and limnological variables. Most aquatic macrophyte species are highly resilient, due to their functional traits, such as clonal growth and high capacity to produce easily dispersible propagules (Chambers et al., 2008; Viana et al., 2016), thus, it this pattern can be expected.

However, in relation to temporal variation (between years), the decrease in the depth of the studied lakes and higher temperature, seems to have favored both the species richness, the community biomass, SLA, as well as the diversity of life forms of the species. It can be assumed that shallow lakes harbour contrasting habitats for biologically and ecologically different macrophyte species and greater availability of shallow habitats for colonization. Only for the group of floating plants, there was an association with total phosphorus, which agrees with the theory of

Table 1
Total area inundated (km^2) in 2008 and 2018 during the four hydrological phases in the nine floodplain lakes. The degree of connectivity of each lake with the river is also shown. Boldfaced comparisons had less inundated area in 2018 than 2008.

Lakes	Connectivity	Falling water		Dry season		Rising water		Flood	
		2008	2018	2008	2018	2008	2018	2008	2018
Retiro Velho (RV)	DC	**0.0741**	**0.0553**	**0.0571**	**0.0401**	**0.1004**	**0.0852**	**0.1188**	**0.0966**
Toma Vara (TV)	DC	**0.2559**	**0.2458**	0.1842	0.2045	**0.3201**	**0.3160**	0.3331	0.3331
Simão Nunes (SN)	DCA	0.0983	0.1045	0.0606	0.0766	**0.1555**	**0.1421**	**0.1942**	**0.1762**
Canto Grande (CG)	DCA	**0.1584**	**0.1032**	**0.1158**	**0.0946**	**0.2029**	**0.1230**	**0.2259**	**0.1395**
Boca do Natalino (BG)	DCA	0.3672	0.4286	0.2945	0.3604	0.4945	0.5323	**0.6197**	**0.5891**
Jauru Velho (JV)	ICA	0.1783	0.2230	0.1094	0.1730	0.2524	0.2821	0.3067	0.3067
Pacas (DP)	ICA	0.6727	0.9556	0.5321	0.6068	0.9879	1.1383	1.2269	1.2318
Morrinhos (Mo)	ICA	**0.5275**	**0.4857**	**0.4019**	**0.3951**	**0.7283**	**0.5649**	**0.7969**	**0.6102**
Morro (M)	ICA	**0.3071**	**0.1803**	**0.2113**	**0.1222**	**0.3443**	**0.2103**	**0.4175**	**0.2379**

Lateral connectivity of the floodplain lakes with the Paraguay River: DC = directly connected at the highest water levels; DCA = directly connected all year; ICA = indirectly connected all year by narrow tie channels locally known as *corixos*.

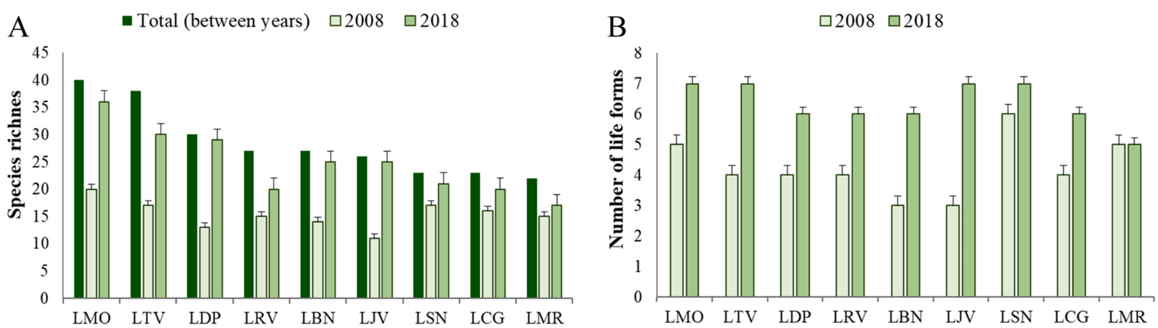

Fig. 4. Aquatic macrophyte species richness (Fig. 4A) and life forms (Fig. 4B) in 2008 vs. 2018, averaged across all nine study lakes. (LMO – Morrinhos Lake; LTV – Toma Vara Lake; LDP – Das Pacas Lake; LRV – Retiro Velho Lake; LBN - Boca do Natalino Lake; LJV – Jauru Velho Lake; LSN – Simão Nunes Lake; LCG – Canto Grande Lake; LMR – Morro Lake).

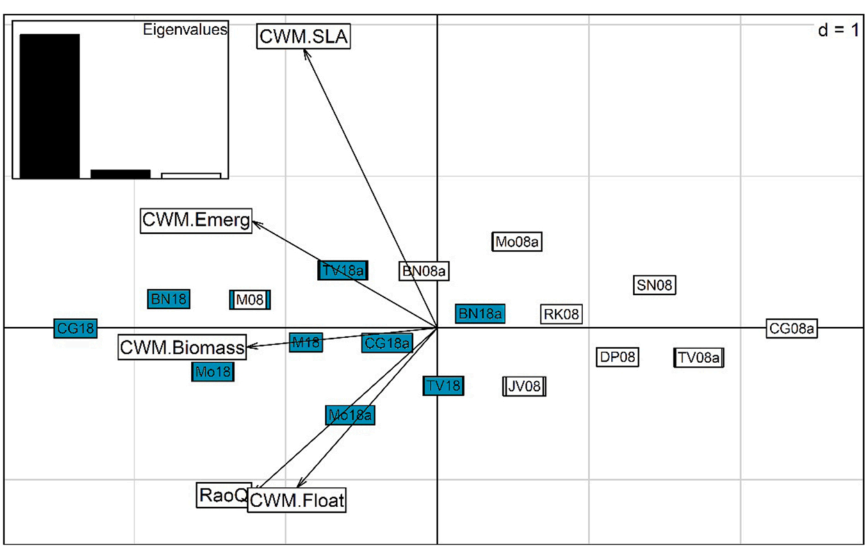

Fig. 5. RDA biplot showing the relationships between CWM values and RaoQ, for the aquatic macrophyte community in nine lakes of the Paraguay River, in the years of 2008 and 2018 (light blue). (CWM.Biomass=Community wheighted mean for biomass variable; CWM.Emerg= Community wheighted mean for emergent species coverage; CWM.Float = Community wheighted mean for floating species coverage; CWM.SLA = Community wheighted mean for single leaf area variable; RaoQ= Fucntional diversity as Rao's Quadratic Entropy.

stable states proposed by Scheffer et al. (2003).

In this sense, we hypothesize that one of the main structuring factors of aquatic macrophyte communities in this tropical plain can be habitat type and preference, with species substitutions within groups of similar life forms and functional traits, which shows a functional stability of the community (de Bello et al., 2021).

4.1. *Waterscape and limnological variables*

Studies in southern Amazonia and the northern Pantanal have provided evidence for a shift in the timing of the rainy season, starting later and ending earlier, reflecting a reduction in the number of rainy days and inundation areas in the floodplain (Debortoli et al., 2012; Lázaro et al., 2020). Brêda et al. (2020) noted that reductions in rainfall and increases in evapotranspiration in the Paraguay River watershed are impacting the hydrology of the Paraguay and Paraná rivers. In floodplain ecosystems, the changes in rainfall result in changes in the flood pulse, with consequent changes in the river discharge, floodplain water depth, and hydrological connectivity between the floodplain and the river.

Table 2
Candidate models (GLM) to explain the functional traits (CWM) and RaoQ variations for the aquatic macrophyte community in nine lakes of the Paraguay River, between the years of 2008 and 2018. (Variables in red are negatively correlated; in blue, positively correlated).

Dependent variable	Selected models	DF	AICc	Weight
RaoQ	Depth	76	304.8	0.36
CWM.SLA	Depth+temperature	77	346.5	0.44
CWM.Biomass	Depth+temperature	77	352.3	0.45
CWM.Emergent	Depth+temperature	75	301.3	0.65
CWM.Floating	Depth+temperature+TP	75	345.2	0.48

TP -Total Phosphorus; SLA – Specific leaf area

The landscape changes that we recorded did not interfere with the limnological variables between the years and points; however, the hydrological periods of falling water and flood showed relation between variables depth, temperature, pH and oxygen values. This pattern is expected for the Pantanal in the falling water season, since the flood pulse increases the concentration of compounds due to the transport of decomposing organic matter from the banks to the main channel of the river (Da Silva and Esteves, 1995; Rebellato and Cunha, 2005). The conductivity levels above 100 µS cm-1 in the transition sector may be directly related to the geological formation of the sector than to other environmental and landscape changes.

Among the limnological variables analyzed, only temperature was positively correlated with emergent and floating life forms, and TP with the floating life forms. For aquatic plants, temperature, light intensity and nutrient availability stand out as important abiotic factors (Bornette and Pujalon, 2011). Higher temperatures in the rising water and flood phases (generally from November to April) are associated with reduced dissolved oxygen concentrations due to high rates of organic matter decomposition (Abdo and Da Silva, 2004; Esteves, 2011; Abdo and Da Silva, 2012). In floodplain lakes of the southern Pantanal subregions of Abobral and Negro, Catian et al. (2018) found positive relationships between limnological variables (except pH) and the richness and composition of aquatic macrophyte communities and life forms. Pan et al. (2020) also showed a positive relationship of 19% of variance between bioclimatic variables and life forms, indicating a process of succession and adaptation of plants to environmental changes.

4.2. Changes in composition and life forms

Results of this study showed significant differences between the two years of survey in the composition of aquatic macrophyte communities, including an increase in the number of species, mainly in the families Poaceae and Onagraceae, in 2018. The changes in the composition of the life forms showed that these communities responded to the increase in the flow, with a negative relationship between functional diversity and water column depth. In this sense, edaphoclimatic conditions favored the establishment of emergent life forms (Junk et al., 2020).

Emergent and floating life forms were more prevalent and responsible for the observed biomass production in 2018 in the Pantanal. The expansion of emerging species due to habitat preferences and harsh conditions in temperate areas and tropics and was also recorded by other studies (Kors et al., 2012; Oyebanji et al., 2019).

The absence of dominance and the homogeneity of species distributions observed in 2008 and 2018 can promote, in the long-term, the loss of beta diversity, as has been found by Muthukrishnan and Larkin (2020). The hydroperiod is also a strong promoter of beta diversity, since the residence time and concentration of phosphorus interfere with environmental heterogeneity and replacement of aquatic macrophyte species in the landscape (Schneider et al., 2019; Fernández-Aláez et al., 2020).

Our analysis did not show the possible impact of human activities on the macrophyte diversity, but is possible to infer that the change in the environment, may be related to changes in the community, is a reflection of the expansion of human activities in the region. Some studies report that anthropogenic activities can alter the diversity, dominance, and functional characteristics of macrophytes (Alahuhta et al., 2011; Adeniyi et al., 2016). Prasad and Das (2019) emphasize that changes in the structure, composition, and abundance of macrophytes may be the result of indirect human activities, such as the discharge of nutrients from agricultural activities. Such work also demonstrated that the land use close to floodplain lakes and adjacent flooded areas can favor the establishment of rooted species.

For the Pantanal, Da Silva et al. (2015) identified the use of land and the energy matrix as important drivers affecting the state of biodiversity. Allied to these drivers, the climate change with a tendency to increase temperatures and decrease rainfall has been predicted since 2005 (Da Silva et al., 2015; da Silva, 2000) and has been documented in recent years by several authors (Debortoli et al., 2012; Marengo et al., 2018, 2021; Aparecido et al., 2020).

5. Conclusions

The spatiotemporal analysis of the structure of the aquatic macrophyte communities demonstrated that the observed changes may be related to the effects of climate change in the Pantanal, which has caused a temporal shift and shortened the duration of the rainy season. Specifically, this study reported a replacement of free-floating species by rooted emerging species in the nine studied floodplain lakes. The lateral hydrological connectivity between the Paraguay River and the floodplain lakes did not explain the observed changes in relative abundances of life forms, although the reduction in the water volume of the lakes between 2008 and 2018 may have favored the increase in frequency of the emergent and amphibious life forms. Dissolved oxygen, water temperature, year of survey, and the hydrological phases of drainage and dry season presented positive correlations with the functional diversity of aquatic macrophyte communities in the Paraguay River and floodplain lakes that were studied. The role of local anthropic impacts in affecting the dynamics of aquatic macrophyte communities remains unclear, although disposal of spoils from the dredging of the river could be contributing to an increase in substratum for the colonization by rooted emergent macrophytes along the Paraguay River. Climatic changes occurring in the region, which have been documented by other studies, could be contributing to the expansion of aquatic macrophytes that grow in the more terrestrial phases of the ATTZ.

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Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2022.103500.

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