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Relevant Phytogeographic Aspects of the Pantanal (Brazil) and Considerations on the Adaptive Strategies of the Vegetation of this Biome

Aspectos Fitogeográficos Relevantes do Pantanal (Brasil) e Considerações sobre as Estratégias Adaptativas da Vegetação deste Bioma

Aspectos Fitogeográficos Relevantes del Pantanal (Brasil) y Consideraciones sobre las Estrategias Adaptativas de la Vegetación de este Bioma

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Abstract
The Brazilian Pantanal, the largest tropical floodplain on the planet, forms an extensive ecotone. Recognizing the phytogeographic aspects of the Pantanal Domain is essential to understanding the ecological diversity and functional organization of its vegetation. The Paraguay River plays a central role in shaping vegetation physiognomies, controlling flood regimes and determining habitat distribution. This study aimed to analyze the phytogeographic characteristics of the Pantanal domain, seeking to identify possible adaptive strategies of vegetation to different habitats. A literature review was conducted between April and June 2025, using systematic searches in scientific databases such as ScienceDirect, SciELO, Scopus, and Web of Science. Publications from 2010 to 2025 addressing phytogeography, climate, soils, hydrology, and vegetation adaptation were prioritized. The floristic diversity of the Pantanal results from the overlap of adjacent biomes (Cerrado, Amazon, Chaco, and Atlantic Forest), topographic variability, and the hydrological regime. The vegetation is distributed among five major phytophysiognomic groups: forests, woody cerrado, herbaceous cerrado, monodominant formations, and Chaco-type vegetation, each with peculiar subdivisions. Each group exhibits specific adaptations, such as aerenchyma formation, specialized root systems, stem thickening, leaf deciduousness, and fire resistance. Additionally, the presence of endemic species in restricted microhabitats, such as saline lagoons and seasonally flooded fields, is noteworthy. It is concluded that understanding the phytogeographic patterns and adaptive strategies of Pantanal vegetation is essential to support public policies for conservation and sustainable management, especially in the face of climate change and intensified anthropogenic use.
Keywords: Ecotone; Pantanal Floodplain; Phytogeographical Formations.

Resumo
O Pantanal brasileiro, a maior planície tropical inundável do planeta, constitui um extenso ecótono. Reconhecer os aspectos fitogeográficos do Domínio Pantanal é essencial para compreender a diversidade ecológica e a organização funcional de sua vegetação. O rio Paraguai desempenha um papel central na modelagem das fisionomias vegetais, controlando os regimes de inundação e determinando a distribuição dos habitats. Este estudo teve como objetivo analisar as características fitogeográficas do domínio do Pantanal, buscando identificar possíveis estratégias adaptativas da vegetação a diferentes habitats. Foi realizada uma revisão bibliográfica entre abril e junho de 2025, por meio de buscas sistemáticas em bases de dados científicas como ScienceDirect, SciELO, Scopus e Web of Science. Foram priorizadas publicações de 2010 a 2025 que abordassem fitogeografia, clima, solos, hidrologia e adaptação da vegetação. A diversidade florística do Pantanal resulta da sobreposição de biomas adjacentes (Cerrado, Amazônia, Chaco e Mata Atlântica), da variabilidade topográfica e do regime hidrológico. A vegetação está distribuída em cinco grandes grupos fitofisionômicos: florestas, cerrado arbóreo, cerrado herbáceo, formações monodominantes e vegetação do tipo chaco, cada um com subdivisões peculiares. Cada grupo apresenta adaptações específicas, como formação de aerênquima, sistemas radiculares especializados, engrossamento caulinar, deciduidade foliar e resistência ao fogo. Além disso, destaca-se a presença de espécies endêmicas em micro-habitats restritos, como lagoas salinas e campos inundáveis sazonais. Conclui-se que compreender os padrões fitogeográficos e as estratégias adaptativas da vegetação do Pantanal é essencial para subsidiar políticas públicas de conservação e gestão sustentável, especialmente frente às mudanças climáticas e ao uso antrópico intensificado.
Palavras-chave: Ecótono; Formações Fitogeográficas; Planície Pantaneira.

Resumen
El Pantanal brasileño, la mayor llanura tropical inundable del planeta, constituye un extenso ecotono. Reconocer los aspectos fitogeográficos del Dominio Pantanal es fundamental para comprender la diversidad ecológica y la organización funcional de su vegetación. El río Paraguay desempeña un papel central en la modelación de las fisonomías vegetales, controlando los regímenes de inundación y condicionando la distribución de hábitats. El objetivo de este estudio fue analizar los principales aspectos fitogeográficos del dominio del Pantanal, con el fin de identificar posibles estrategias adaptativas de la vegetación a diferentes hábitats. Se realizó una revisión bibliográfica entre abril y junio de 2025, mediante búsquedas sistemáticas en bases científicas como ScienceDirect, SciELO, Scopus y Web of Science. Se priorizaron publicaciones de 2010 a 2025 sobre fitogeografía, clima, suelos, hidrología y adaptación de la vegetación. La diversidad florística del Pantanal resulta de la superposición de biomas adyacentes (Cerrado, Amazonía, Chaco y Mata Atlántica), de la variabilidad topográfica y del régimen hidrológico. La vegetación se distribuye en cinco grandes conjuntos fitofisionómicos: bosques, cerrado arbóreo, cerrado herbáceo, formaciones monodominantes y vegetación tipo chaco, cada uno con subdivisiones peculiares. Cada conjunto presenta adaptaciones específicas, como formación de aerénquima, sistemas radiculares especializados, engrosamiento caulinar, caducidad foliar y resistencia al fuego. Además, se destaca la presencia de especies endémicas en microhábitats restringidos, como lagunas salinas y campos inundables. Se concluye que comprender los patrones fitogeográficos y las estrategias adaptativas de la vegetación del Pantanal es esencial para apoyar políticas públicas de conservación y gestión sostenible, especialmente ante el cambio climático y el aumento del uso antrópico.
Palabras clave: Ecotono; Formaciones Fitogeográficas; Llanura del Pantanal.

1. Introduction

The Pantanal, located in the central-west region of Brazil and encompassing the states of Mato Grosso and Mato Grosso do Sul, is recognized as the largest tropical floodplain on the planet. It represents one of the most ecologically, biologically, and hydrologically significant ecosystems in South America (Mercante, Rodrigues, & Ross, 2011; Silveira et al., 2021). This phytogeographic domain is characterized by a mosaic of vegetation formations, resulting from the dynamic interaction among climatic, geological, hydrological, and geomorphological factors that profoundly shape its environments and determine its floristic diversity. The biome hosts a remarkable floristic convergence, incorporating elements from adjacent formations such as the Cerrado, Amazon, Chaco, and Atlantic Forest, which contributes to its high ecological heterogeneity and landscape complexity (Damasceno-Junior & Pott, 2021; Pessi et al., 2022).

The structure and distribution of vegetation in the Pantanal are directly controlled by seasonal hydrological processes, particularly by the periodic floods that act as the main ecological structuring factor (Caballero et al., 2025; Guimarães, Trevelin, & Manoel, 2014; Lo et al., 2023). Variations in the duration, depth, and extent of flooding generate ecological gradients that promote habitat diversification, ranging from permanently flooded areas to regions subject to prolonged droughts (Damasceno-Junior & Pott, 2021). In addition to this, the geology of the Upper Paraguay Basin—marked by crustal subsidence processes and the formation of megafans—directly influences the relief, drainage patterns, and, consequently, the configuration of plant communities (Assine et al., 2015; Silveira et al., 2021).

Given this dynamic environmental reality, the vegetation of the Pantanal has developed a remarkable set of adaptive strategies that ensure survival under extreme conditions of flooding, drought, and often seasonal fire (Silgueiro, Souza, Muller, & Silva, 2021). Among these adaptations are notable anatomical modifications, such as the formation of aerenchyma for respiration in waterlogged soils, the development of shallow or specialized root systems, as well as phenological and physiological adjustments that enable species to withstand both water stress and soil saturation. The distribution of phytophysiognomies directly reflects these adaptive responses, making it possible to identify forest, savanna, grassland, palustrine, and aquatic formations—each with its own floristic composition and structural patterns (Damasceno-Junior & Pott, 2021; Guimarães et al., 2014; Lourival et al., 2025).

In this context, understanding the phytogeographic aspects of the Pantanal, in light of the vegetation's adaptive strategies, becomes essential not only for botanical and ecological science but also for the formulation of public policies aimed

at the conservation and sustainable management of this ecosystem. This study aimed to analyze the phytogeographic characteristics of the Pantanal domain, seeking to identify possible adaptive strategies of vegetation to different habitats.

2. Methodology

This study is characterized as qualitative nature investigation (Pereira et al., 2018), a bibliographic research (Snyder, 2019), a narrative review (Rother, 2007), developed with the objective of gathering, analyzing, and synthesizing scientific knowledge related to the phytogeographic aspects of the Pantanal domain (Brazil), with emphasis on the adaptive strategies of vegetation in response to climatic, hydrological, and geological variables.

The systematic data search was conducted between April and June 2025, using major national and international scientific databases, including ScienceDirect, Scopus, Web of Science, SciELO, and SpringerLink, in order to ensure both breadth and quality in the selection of publications. The following descriptors were used, either individually or in combination, in Portuguese, English, and Spanish: “Pantanal,” “Phytogeography,” “Pantanal Vegetation,” “Plant Adaptability,” “Adaptive Strategies,” “Pantanal Flora,” “Phytogeography,” “Pantanal Wetland,” “Plant Adaptation,” “Vegetation Ecology.”

Inclusion criteria considered for selection included: original articles, reviews, and books published between 2010 and 2025, as well as classic works relevant to the topic, without language restrictions. Exclusion criteria comprised duplicate works, event abstracts without full text, and publications that did not directly address the phytogeographic or ecological aspects of the Pantanal. The material analysis process followed three methodological stages:

(1) identification and selection of relevant studies through the review of titles, abstracts, and keywords;

(2) analytical and exploratory reading of the full texts selected, with extraction of information on climate, hydrology, geology, phytophysiognomies, and vegetation adaptations; and

(3) critical synthesis and thematic categorization, allowing the organization of results into structuring axes of the Pantanal’s phytogeography, especially focusing on the environmental interactions that shape the composition and distribution of vegetation and on the adaptive strategies developed by plants in response to flooding regimes, drought, and edaphic variations. This methodological rigor seeks to ensure the consistency, credibility, and robustness of the data presented in this review.

3. Results and Discussion

3.1 General Geographical Aspects

The Pantanal is recognized as the largest continuous tropical floodplain on the planet, characterized as an extensive inland plain associated with the Upper Paraguay River Basin (Caballero et al., 2025; Soares et al., 2025). However, its geographic definition remains a topic of scientific debate, particularly regarding the criteria used to delineate its boundaries. Classical studies have established an area of approximately 140,640 km², a figure widely accepted (Figure 1) (J. D. S. V. Silva & De Moura Abdon, 1998; C. S. Miranda et al., 2018). This domain extends beyond Brazilian territory, encompassing portions of Bolivia (15,000 km²) and Paraguay (5,000 km²), consolidating itself as a transboundary ecological system of global importance (J. D. S. V. Silva & De Moura Abdon, 1998; Damasceno-Junior & Pott, 2021). The physiographic plain of the Brazilian Pantanal is located in the Central-West region of Brazil, between latitudes 15° 30' and 22° 30' South and longitudes 54° 45' and 58° 30' West, encompassing municipal areas within the states of Mato Grosso (MT) and Mato Grosso do Sul (MS) (Table 1) (J. D. S. V. Silva & De Moura Abdon, 1998; Gonzaga et al., 2022; Neto, Pereira, Helena Silva, Rosa Oliveira, & Alves Damasceno Júnior, 2024; Soares et al., 2025).

Figure 1 - Geographical location of the Brazilian Pantanal in South America, in the states of Mato Grosso and Mato Grosso do Sul.

Research source: Adapted from Miranda et al., (2018) e Marengo et al., (2021).

Table 1 - Pantanal with the participation of the municipalities in MT (Mato Grosso) and MS (Mato Grosso do Sul) that make up the area, with the subregions in which each municipality is located.

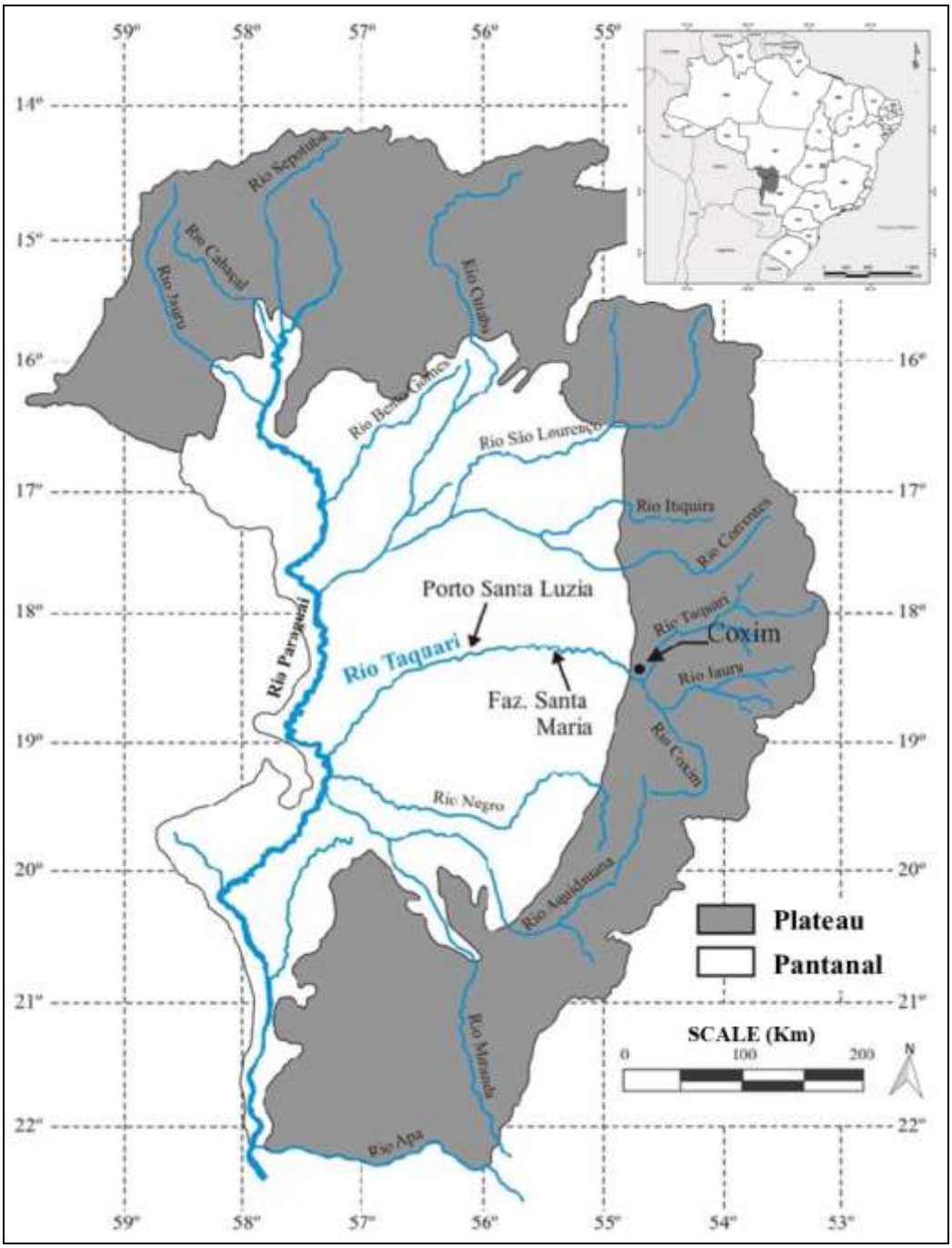
MUNICIPALITY	STATE	AREA IN THE PANTANAL (Km²)	ASSOCIATED SUBREGIONS
Barão de Melgaço	**MT**	10.782	Barão de Melgaço, Poconé
Cáceres		14.103	Cáceres, Poconé
Itiquira		1.731	Barão de Melgaço
Lambari D'Oeste		272	Cáceres
Nossa Senhora do Livramento		1.115	Poconé
Poconé		13.972	Poconé, Paraguai
Santo Antônio do Leverger		6.890	Barão de Melgaço, Poconé
Aquidauana	**MS**	12.929	Aquidauana, Nhecolândia, Abobral, Miranda
Bodoquena		46	Miranda
Corumbá		61.819	Paraguai, Paiaguás, Nhecolândia, Abobral, Nabileque
Coxim		2.132	Paiaguás
Ladário		66	Paraguai
Miranda		2.106	Miranda, Nabileque
Sonora		719	Paiaguás
Porto Murtinho		4.717	Nabileque, Porto Murtinho
Rio Verde de Mato Grosso		4.784	Nhecolândia

Research source: Adapted from Silva & De Moura Abdon (1998).

From a hydrological and geomorphological perspective, the Pantanal is a functional unit integrated into the Upper Paraguay Basin, which covers a total area of 496,000 km²—of which 363,442 km² are located in Brazil and 132,558 km² are distributed between Bolivia and Paraguay (Figure 2) (Caballero et al., 2025; Ivory, McGlue, Spera, Silva, & Bergier, 2019). This watershed not only supplies the Pantanal floodplain but also regulates its ecological processes, particularly the flood regime, which is the primary controlling factor of the system's ecological, phytogeographic, and hydrological dynamics. From a geomorphological standpoint, the Pantanal plain is not a homogeneous landscape. In addition to seasonally flooded areas, it includes prominent features known as residual hills or inselbergs—ancient geological formations consisting of outcrops that

rise above the floodplain (Damasceno-Junior & Pott, 2021; Nunes da Cunha et al., 2023). These elevations are subterraneously connected to peripheral mountain ranges, representing a structural continuity of the regional crystalline basement. This geomorphological configuration has profound phytogeographic implications. The residual hills, being above the flood line, host distinct vegetation types, often associated with Cerrado species, seasonal forests, and, in some cases, elements of the Atlantic Forest or the Chaco (J. D. S. V. Silva & De Moura Abdon, 1998; Lo et al., 2023; Silveira et al., 2021). Conversely, the surrounding areas subject to seasonal inundation exhibit phytophysiognomies adapted to flooding and drought cycles, resulting in environmental heterogeneity that promotes the coexistence of forest, savanna, grassland, and wetland formations, forming dynamic vegetation mosaics (Soares et al., 2025).

Figure 2 - Hydrographic basin of the Paraguay River, which feeds the Pantanal floodplain.



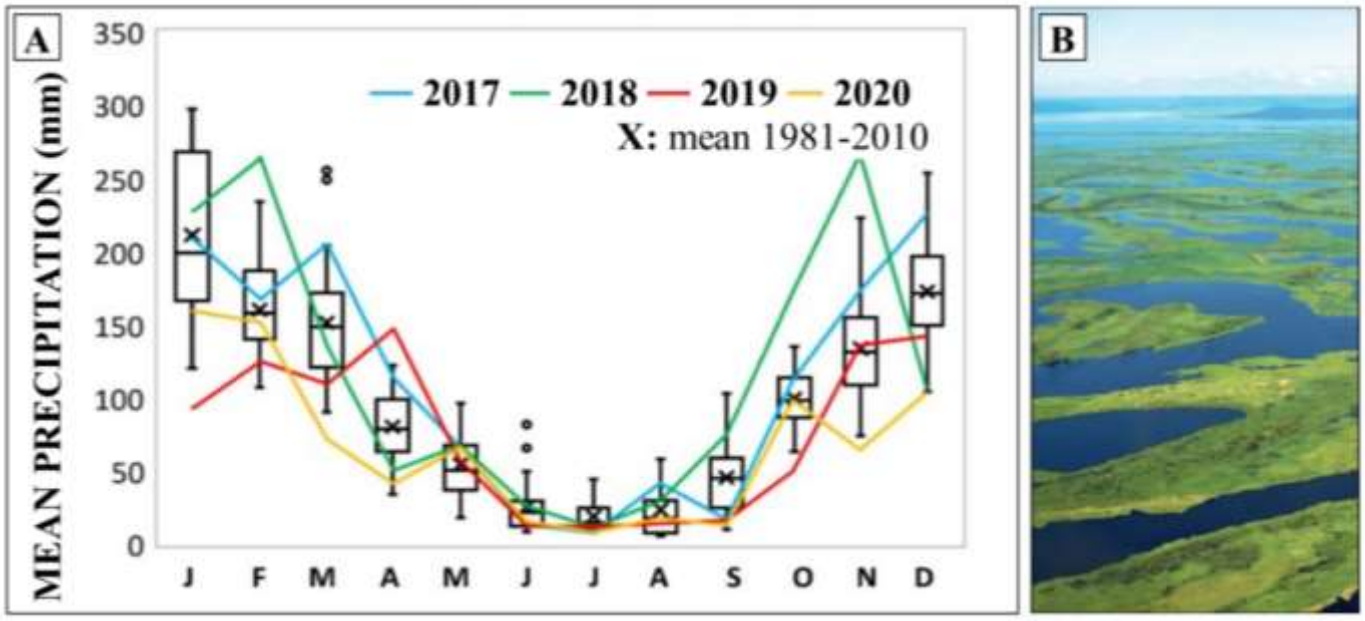
Research source: Adapted from Silva & De Moura Abdon (1998).

Therefore, the general geographic features of the Pantanal reveal not merely a vast floodplain, but a complex system in which the interaction among geomorphology, hydrology, topography, and drainage defines the ecological conditions and vegetation distribution patterns. Understanding these elements is essential for comprehending the phytogeographic processes that shape the biological diversity of the Pantanal, as well as the adaptive strategies developed by plant species in response to the environmental conditions imposed by the hydrological regime and the region's geomorphological particularities.

3.2 Climatic Aspects Influencing the Pantanal Domain

The climate of the Pantanal is classified as tropical continental with a well-defined dry season, according to the Köppen-Geiger classification (Cwa and Aw), characterized by hot and rainy summers and dry, mild winters (Caballero et al., 2025; Damasceno-Junior & Pott, 2021; Neto et al., 2024). The annual average temperature ranges between 24°C and 26°C, with summer highs exceeding 34°C and winter lows around 15°C (Bezerra, Encina, Figueiredo, Dalmas, & Paranhos Filho, 2021; Caballero et al., 2025). Annual precipitation varies between 1,000 mm and 1,400 mm, distributed in a highly seasonal pattern, with approximately 70% to 80% of rainfall concentrated between October and March, during the wet season (Figure 3) (Damasceno-Junior & Pott, 2021; Marengo et al., 2021; Neto et al., 2024). This climatic seasonality has a direct influence on hydrological processes, vegetation dynamics, and ecological cycles of the Pantanal floodplain, especially with regard to the flood and drought regimes that define the region's macro- and micro-habitats.

Figure 3 - Annual variation of rainfall in the Brazilian Pantanal. (A) Precipitation from 2017 to 2020. (B) Pantanal flood period.



Research source: (A) Adapted from Marengo et al., (2021). (B) Adapted from Zorzetto (2020).

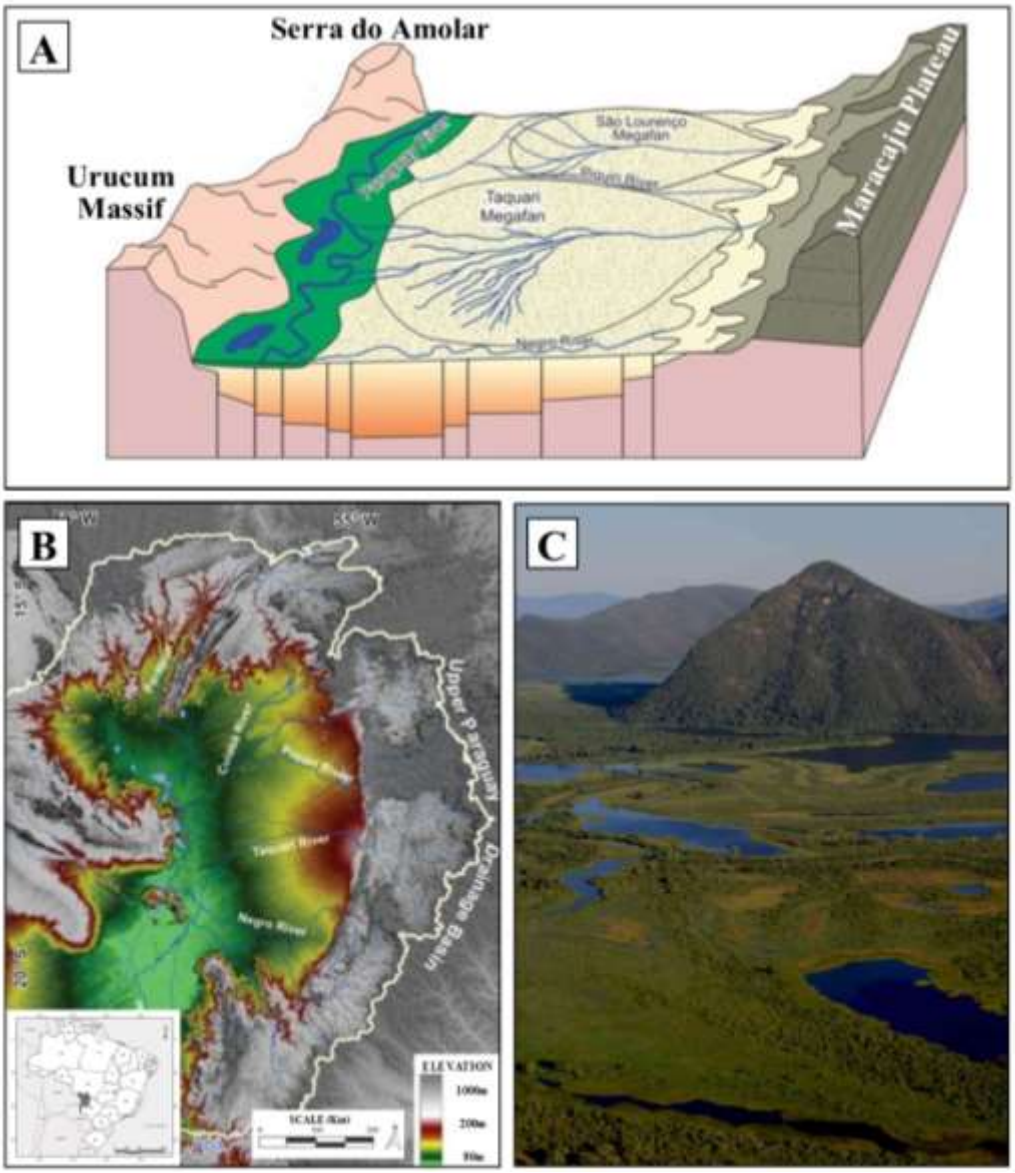
In addition to the seasonal distribution of precipitation, the spatial heterogeneity of the rainfall regime is a determining factor for the phytogeographic diversity of the Pantanal (Caballero et al., 2025). Studies have shown that the northern sector, which lies closer to Amazonian influences, receives higher rainfall volumes and exhibits greater regularity in its hydrological cycle, whereas the central and southern regions are more susceptible to interannual variability. This variability is associated both with topography and with the influence of climatic systems such as El Niño and La Niña (Damasceno-Junior & Pott, 2021; Marengo et al., 2021). Such variability directly affects the duration and intensity of flooding, altering vegetation

distribution patterns and promoting mosaics of phytophysiognomies adapted to different regimes of soil saturation, water availability, and drought duration.

3.3 Geology, Genesis and Soils of the Floodplain and Adjacent Areas

The geological origin of the Pantanal is directly related to tectonic movements associated with the uplift of the Andes Mountains during the Cenozoic, which caused the subsidence of the central region of the Upper Paraguay Basin (Assine et al., 2015; Mercante et al., 2011; Soares et al., 2025). This process led to the formation of a large intracratonic depression that has functioned as an active sedimentation basin since the Miocene, with increased activity during the Quaternary (Figure 4) (Soares et al., 2025). Throughout this period, vast quantities of alluvial, colluvial, and lacustrine sediments were deposited, shaping an extensive floodplain characterized by extremely flat morphology, with low altitudinal gradients ranging from 30 to 50 cm/km in the east–west direction and from 3 to 15 cm/km in the north–south direction.

Figure 4 - Geological aspects of the Pantanal. (A) Schematic block diagram illustrating the basin geometry. (B) Digital elevation model. (C) Amolar Mountain Range.

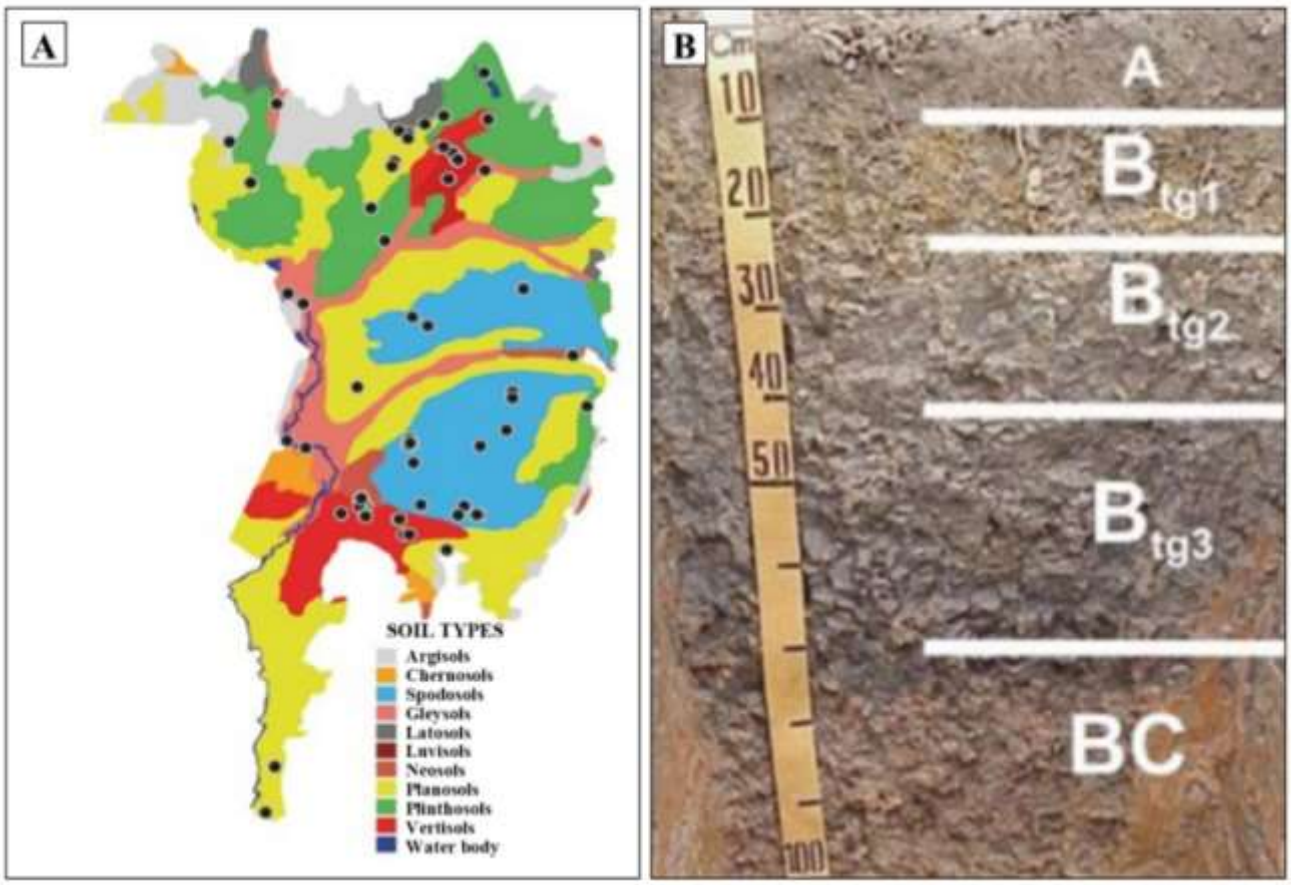


Research source: (A-B) Adapted from Assine et al., (2015). (C) Adapted from Olmos (2010).

This geomorphology consists of alluvial megafans, seasonally flooded plains, paleochannels, bays (lagoons), and floodplain drainage systems, with the Taquari River megafan standing out as one of the most prominent features, occupying approximately 50,000 km² (Mercante et al., 2011; Soares et al., 2025). These sedimentary environments are dynamic, constantly reconfigured by hydrological cycles and climatic variability, and they directly reflect the interaction between fluvial systems and the tectonic setting of the region. Parallel to the floodplain, residual hills (inselbergs) such as Amolar (Figure 4-C), Taiamã, Caracará, and Pão de Açúcar are noteworthy. These represent fragments of the crystalline basement or older sedimentary covers, resistant to erosive processes and functioning as ecological refuges (Assine et al., 2015; Schaefer, 2023).

The formation and distribution of soils in the Pantanal are directly conditioned by its geological origin and seasonal hydrological regimes (Schaefer, 2023; Soares et al., 2025). The landscape is dominated by young, poorly developed soils, strongly influenced by flooding processes and sediment deposition. The most common soil classes are Gleysols, associated with permanently or seasonally waterlogged environments; Planosols, found in areas with imperfect drainage; and Quartzipsamments (Arenosols), typical of sandy elevations and areas linked to alluvial fans and residual hills (Figure 5) (Damasceno-Junior & Pott, 2021; Novais et al., 2012). Additionally, Dystrophic Red-Yellow Latosols (Ferralsols) occur along the margins of the floodplain, in contact with adjacent plateaus, reflecting the direct influence of older geomorphic surfaces (Damasceno-Junior & Pott, 2021).

Figure 5 - Pedological map of the Pantanal. (A) Occurrence of the main soil types found in the Pantanal. (B) Gleysols, the most common soil type in flooded
areas.



Research source: (A) Adapted from Damasceno-Junior & Pott (2021). (B) Adapted from Schaefer (2023).

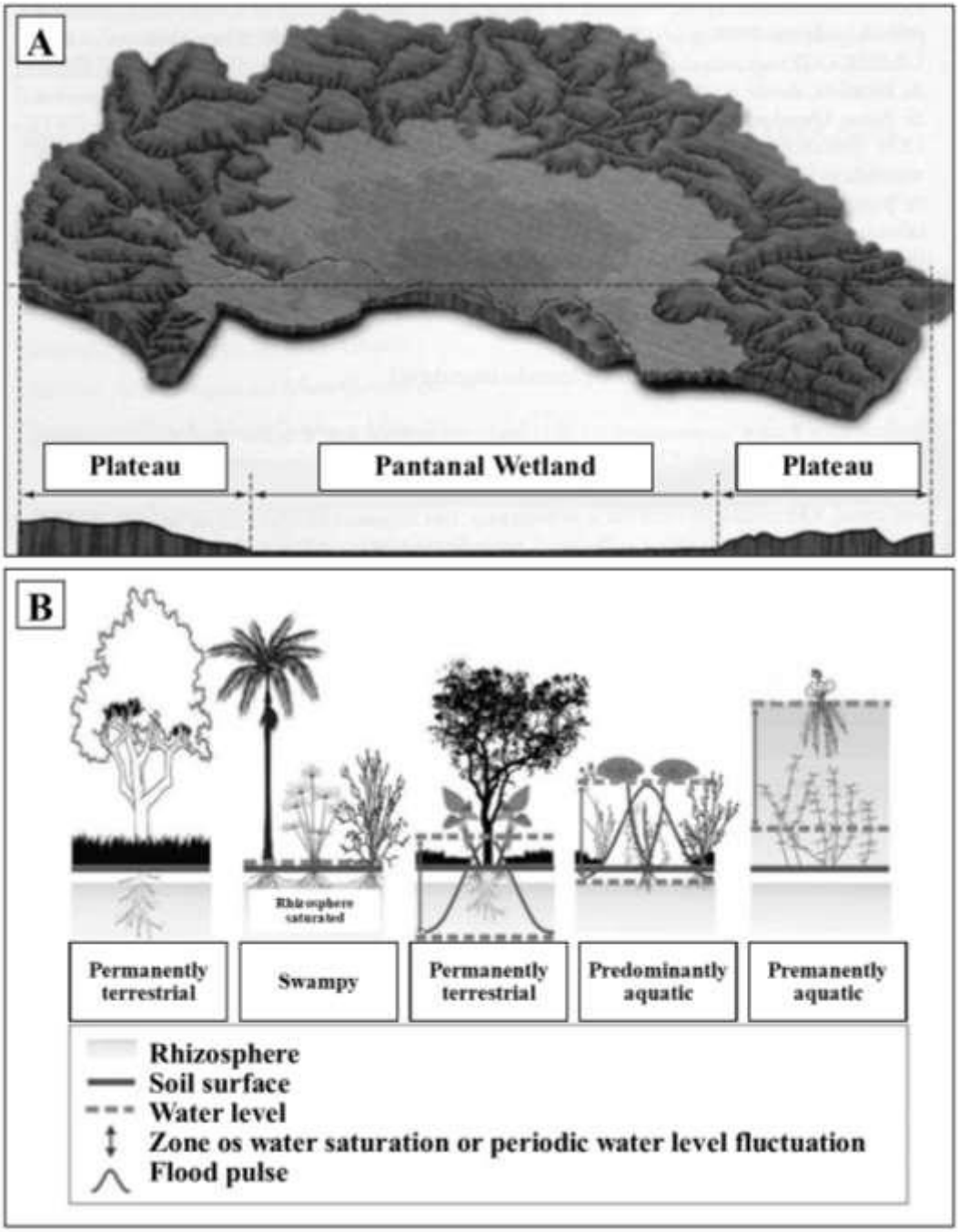
From a phytogeographic perspective, this pedological heterogeneity plays a crucial role in defining vegetation patterns. Poorly drained, hydromorphic soils rich in organic matter favor the development of palustrine phytophysiognomies, floodable grasslands, and vegetation adapted to periodic anoxia (Bezerra et al., 2021). Conversely, well-drained and sandier soils found on elevated areas, inselbergs, and sedimentary ridges support savanna formations, cerradões (wooded savannas), and seasonal forests (Guimarães et al., 2014; Ivory et al., 2019). Therefore, an integrated understanding of geology, floodplain genesis, and soil distribution is essential for explaining the spatial organization of vegetation mosaics in the Pantanal, as well as for understanding the adaptive strategies of plant species in response to the challenges imposed by environmental gradients of moisture, texture, and fertility (Pessi et al., 2022).

3.4 Hydrology and Inundation Cycle

The hydrological cycle of the Pantanal constitutes the primary ecological structuring factor of the landscape, profoundly influencing the dynamics of vegetation, fauna, and geomorphological processes (Luz, Stevaux, Parolin, & Silva, 2017; Schaefer, 2023). This system is characterized by a seasonal flooding regime, resulting from the combination of local rainfall and water inflow originating from the headwaters of rivers draining the adjacent plateaus. The rainy season, occurring from October to March, accounts for more than 70% of the annual precipitation, while the dry season, from April to September, features low rainfall indices (Damasceno-Junior & Pott, 2021; Luz et al., 2017). However, flooding of the plain does not occur simultaneously with the rainfall but follows a temporal lag, with the flood peak generally manifesting between February and May, when water accumulation in the basin is greatest (Marengo et al., 2021).

The lag between flooding and drainage can be explained by the hydrological dynamics of the Upper Paraguay Basin, where rainfall in the headwater regions—especially on the plateaus of Mato Grosso, Goiás, and parts of Bolivia—slowly drains into the Pantanal floodplain due to its gentle slope (Figure 6A) (Luz et al., 2017; Marengo et al., 2021; Mercante et al., 2011). As a result, water from accumulated rainfall in the upper basins takes weeks or even months to reach and inundate the floodplain. This phenomenon gives rise to four well-defined hydrological phases: (1) rising water (December to February); (2) flood peak (February to May); (3) falling water (May to July); and (4) dry season (July to November) (Figure 6B) (Marengo et al., 2021; C. S. Miranda et al., 2018). Each of these phases plays a determining role in shaping the phytogeographic components of the region.

Figure *6* - Correlation of the Pantanal flood and drought cycle with different vegetation gradients. (A) Representation of the relief of the Pantanal, with the marking of rivers and tributaries that are responsible for the flooding in the central plain of the image. (B) The five functional units in large floodplains defined according to their hydrological status.



Research source: (A) Adapted from Damasceno-Junior & Pott (2021).(B) Adapted from Mercante et al., (2011).

The drainage system of the Pantanal is highly complex, consisting of an interconnected network of rivers, corixos (seasonal channels), floodplains, bays, and lagoons that play essential roles in water storage, redistribution, and flow (Arruda et al., 2016; C. S. Miranda et al., 2018). During the flood phase, a large portion of the plain becomes submerged, with water overflowing from the main channels into adjacent areas, forming extensive flooded fields (Damasceno-Junior & Pott, 2021; Ivory et al., 2019). The floodplains channel excess water into depressions, bays, and swampy areas, while corixos act as temporary connecting channels between different water bodies. However, the Pantanal's flooding regime varies according to

the sub-region and the river that overflows. In the Paraguay River, it is seasonal, unimodal, and predictable, with the flood wave taking about three months to travel from the headwaters to Corumbá. The flooded area within the Paraguay River floodplain—the lowest part of the Pantanal—varies between 4,000 and 16,000 km² between low and high water seasons (Caballero et al., 2025). As a result, riparian forest vegetation may remain flooded from 11 to 220 days per year, depending on the maximum river level reached (Arruda et al., 2016; Ivory et al., 2019). This hydrological mosaic favors the formation of varied environments, ranging from permanent lakes to fields that remain flooded for weeks or months, directly shaping the structure and distribution of vegetation (Arruda et al., 2016).

The lacustrine system of the Pantanal is a fundamental component of the floodplain's hydrological and ecological dynamics, characterized by an extensive network of bays, permanent and temporary lagoons, wetlands, and seasonally flooded depressions, which play crucial roles in water storage, regulation of water flows, and biodiversity maintenance (Caballero et al., 2025). These water bodies are largely formed by sedimentation processes and fluvial dynamics, including meander abandonment (horseshoe-shaped lagoons) and water accumulation in interfluvial depressions (Lázaro, Oliveira-Júnior, Silva, Castrillon, & Muniz, 2020). The bays, a regional term used to designate lakes and lagoons, exhibit great morphological diversity and variable hydroperiods, functioning as essential habitats for aquatic species, migratory birds, fish, and a rich palustrine vegetation (Damasceno-Junior & Pott, 2021; C. S. Miranda et al., 2018). A notable aspect of the Pantanal lacustrine system is the presence of saline or brackish lagoons, especially in the subregions of Nhecolândia and Paiaguás, where intense evapotranspiration processes, salt accumulation, and drainage restrictions promote the natural salinization of some water bodies (Damasceno-Junior & Pott, 2021). These saline lagoons exhibit unique physicochemical compositions, favoring the development of highly specialized plant and microbial communities, distinct from those found in freshwater lagoons (Assine et al., 2015). The distribution and permanence of these lacustrine environments—both freshwater and saline—are directly associated with the floodplain's geomorphological features, seasonal flooding cycles, and their interaction with drainage systems such as corixos, floodplains, and main rivers, exerting a direct influence on the region's phytogeographic patterns and ecological diversity (Damasceno-Junior & Pott, 2021; Soares et al., 2025).

3.5 Characterization of the Component Phytophysiognomies

The vegetation of the Pantanal exhibits a highly heterogeneous composition and organization, resulting from the interaction of climatic, hydrological, edaphic, and geomorphological factors that shape the landscape dynamics (Bezerra et al., 2021; Lourival et al., 2025). This heterogeneity manifests as a mosaic of phytophysiognomies combining elements from different adjacent biomes, creating a synchronicity between the Cerrado, the Amazon Forest, the Chaco, and, to a lesser extent, the Atlantic Forest, conferring an ecotonal and transitional character to the Pantanal (Damasceno-Junior & Pott, 2021; Guerra et al., 2020; T. do N. Lima & Faria, 2021).

The constant variations in the flooding regime, associated with gradients of moisture, water table depth, soil texture, and surface stability, are determinants in the distribution and structuring of different vegetation formations (Lourival et al., 2025). Pantanal phytophysiognomies can be grouped into major structural sets, organized into five large phytophysiognomic groups that reflect the ecological diversity and adaptations of the flora to the extreme environmental conditions of the floodplain (Table 2) (Damasceno-Junior & Pott, 2021; Guglieri-Caporal, Pott, Felismino, Caporal, & Valls, 2018; Ivory et al., 2019): (1) Forest formations are composed of dense vegetation with a predominance of trees and well-defined vertical stratification, representing environments less subject to prolonged flooding; (2) Arboreal cerrado and (3) Herbaceous cerrado differ mainly in structure: the former presents sparse trees over grasses, while the latter is dominated by grasses with sparse shrubs; (4) The group known as Chaco includes woody savannas and grassy-woody savannas typical of drier and more arid environments, demonstrating the ecological transition with the Chaco biome; (5) Monodominant formations are characterized

by few dominant plant species, often associated with pioneer areas or grassy park savannas (Damasceno-Junior & Pott, 2021; Guglieri-Caporal et al., 2018; Guimarães et al., 2014; Lourival et al., 2025; Pessi et al., 2022; Pott, Oliveira, Damasceno-Junior, & Silva, 2011; Santos et al., 2020). These groups express the spatial variation of Pantanal habitats and constitute the basis for the phytogeographic analysis of the regional vegetation, which is strongly conditioned by hydrological, edaphic, and climatic regimes.

Table 2 - Phytophysiognomic Groups of the Pantanal and Their Characteristics.

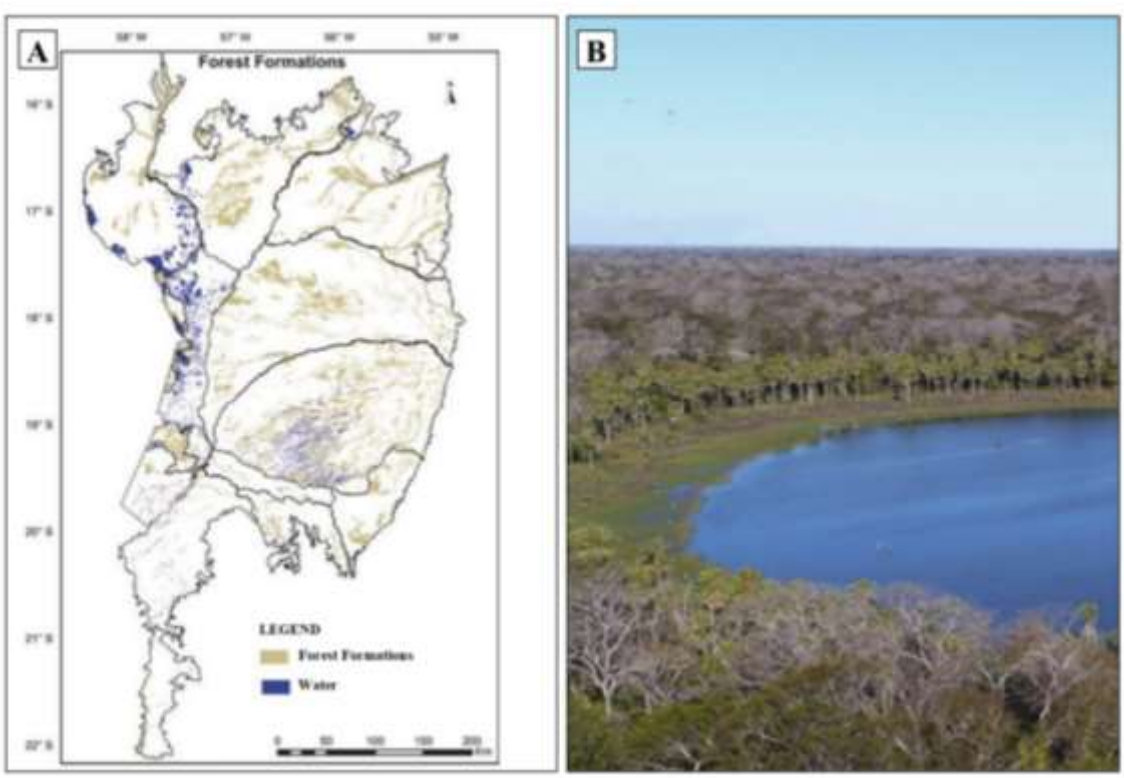
Nº	PHYTOPHYSIOGNOMIC GROUP	STRUCTURAL CHARACTERISTICS	TYPICAL ENVIRONMENTS / ECOLOGICAL CONDITIONS
1	**Forest Formations**	Dense vegetation, predominance of trees, and well-defined vertical stratification.	Less flood-prone areas, sedimentary levees, borders of residual hills.
2	**Woody Cerrado (Savanna)**	Woody savanna with scattered trees over grasses, including park-like savannas.	Well-drained soils or slightly waterlogged; transitional environments.
3	**Herbaceous Cerrado**	Dominated by grasses, sparse shrubs, and absence of a defined arboreal layer.	Open fields, areas with seasonal light to moderate waterlogging.
4	**Chaco**	Xeric woody savanna and xeric graminoid-woody savanna; vegetation adapted to dry conditions.	Dry areas or with low flood frequency, especially in the southwestern region.
5	**Monodominant Formations**	Composed of few dominant species; may include pioneer formations and xeric park savannas.	Unstable areas, lagoon margins, newly exposed fields, regenerating environments.

Research source: Adapted from Damasceno-Junior & Pott (2021).

3.5.1 Forest Formations

The forest formations of the Pantanal represent phytophysiognomic units of significant ecological, structural, and floristic importance, distributed in environments less prone to prolonged flooding, such as sandy ridges, residual hills, and river terraces. This group is composed of three main types: Seasonal Semideciduous Forest, Seasonal Deciduous Forest, and Forested Savanna (Cerradão) (Figure 7) (Table 3) (Arruda et al., 2016; Kohagura, Souza, Bao, Ferreira, & Pott, 2020; Meyer Oliveira et al., 2024). These formations are characterized by variations in leaf phenology, vertical structure, and floristic composition, and are directly related to gradients of edaphic moisture, altitude, and soil drainage.

Figure *7* **-** Distribution of phytophysiognomies of forests found in the Pantanal. (A) Distribution map. (B) Seasonal Semideciduous Forest.



Research source: (A) Adapted from Damasceno-Junior & Pott (2021). (B) Adapted from Santos et al., (2020).

Table 3 - Forest phytophysiognomies found in the Pantanal.

PHYTOPHYSIOGNOMIC GROUP	VEGETATION FORMATION	SUBTYPES / ASSOCIATED CLASSES	SUB-REGIONS OF OCCURRENCE
Forests	Seasonal Semideciduous Forest	Alluvial and Submontane	Cáceres, Barão de Melgaço, Poconé, Abobral, Miranda
	Seasonal Deciduous Forest	Alluvial, Lowland, and Submontane	Paiaguás, Porto Murtinho, Abobral, Nabileque
	Forested Savanna (Cerradão)	Mixed classes with characteristics of savanna and forest	Aquidauana, Miranda, Nhecolândia, Paraguay, Poconé

Research source: Adapted from Damasceno-Junior & Pott (2021).

The Seasonal Semideciduous Forest preferentially occurs in the higher and alluvial portions of the floodplain, such as areas near hills and well-established drainage systems, including the subregions of Barão de Melgaço, Poconé, and Miranda (Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021; Nunes da Cunha et al., 2023; Pott et al., 2011). This formation is characterized by having between 20% and 50% of species shedding leaves during the dry season, functioning as a transition between ombrophilous and deciduous formations. Among the most representative families are Fabaceae, Myrtaceae, and Lauraceae, with species such as *Bowdichia virgilioides* (Fabaceae), *Ocotea diospyrifolia* (Lauraceae), and *Eugenia uniflora* (Myrtaceae) (Damasceno-Junior & Pott, 2021). Floristic diversity is high, with composition influenced by elements from the Atlantic Forest and the Cerrado (M. S. de Lima, Takahasi, Damasceno-Junior, & Araujo, 2019).

The Seasonal Deciduous Forest occurs in even drier environments, on calcareous soils or soils with low water retention, such as in the subregions of Paiaguás, Porto Murtinho, and parts of Abobral (Damasceno-Junior & Pott, 2021; Nunes da Cunha et al., 2023). In this formation, leaf loss exceeds 50% during the dry period, reflecting adaptations to more restrictive

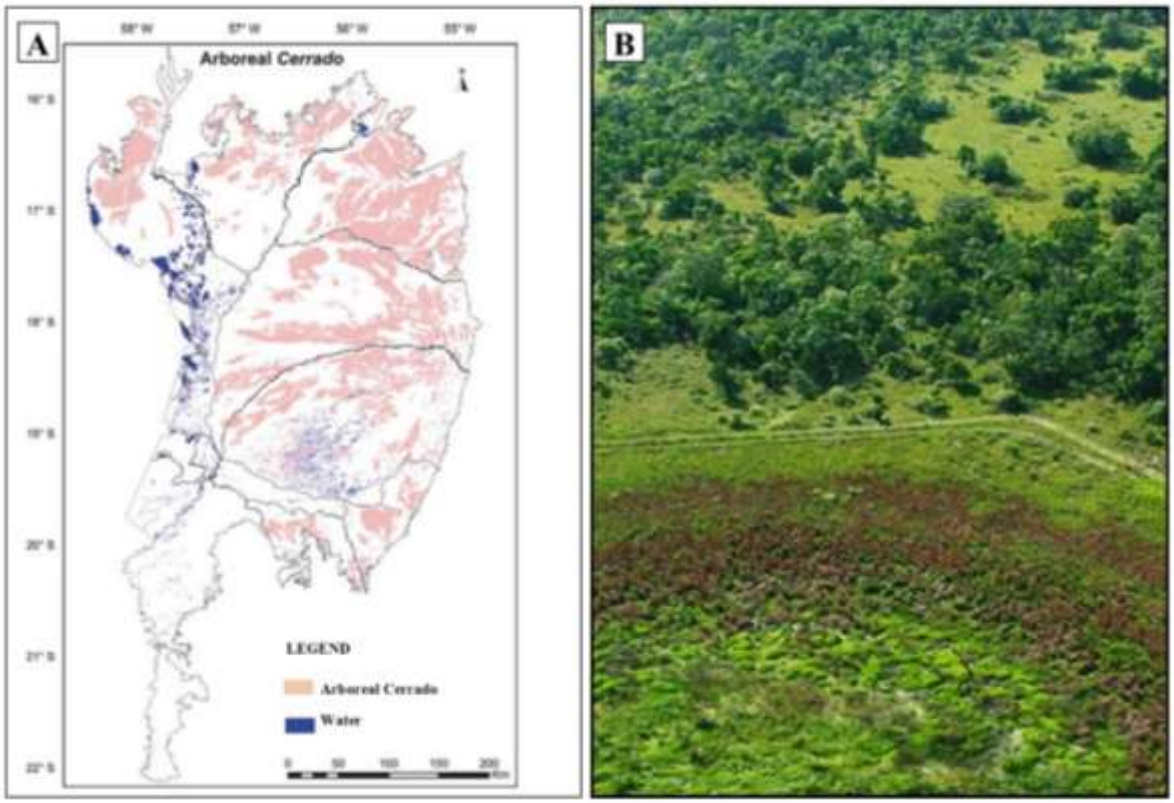
hydrothermal regimes. The dominant species are deciduous, with caducous leaves, thick trunks, and deep root systems. Among the most frequent species are *Tabebuia aurea* (Bignoniaceae), *Anadenanthera colubrina* (Fabaceae), and *Aspidosperma pyrifolium* (Apocynaceae) (Damasceno-Junior & Pott, 2021). The physiognomy is less dense, with lower vertical stratification, but with strong adaptive specialization of the flora (M. S. de Lima et al., 2019).

The Forested Savanna, known as Cerradão, represents an ecotone between savannas and forests and is common at the edges of the Pantanal, especially in regions such as Aquidauana, Miranda, Nhecolândia, and the elevated sectors of Poconé (Damasceno-Junior & Pott, 2021; Nunes da Cunha et al., 2023). It consists of dense vegetation with a continuous canopy and a predominance of xeromorphic and heliophilous species belonging to families such as Vochysiaceae, Malpighiaceae, and Fabaceae (T. do N. Lima & Faria, 2021). Cerradão hosts species such as *Qualea grandiflora* (Vochysiaceae), *Hirtella glandulosa* (Chrysobalanaceae), and *Bowdichia virgilioides* (Fabaceae), adapted to well-drained soils and periodic fire (Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021). Due to its combination of typical Cerrado elements with a forest structure, this formation is essential for understanding ecological gradients and floristic connectivity between adjacent biomes.

3.5.2 Woody Cerrado (Savanna)

The woody savanna physiognomies of the Pantanal, represented by the Arboreal Cerrado and the Cerrado Park, constitute transitional formations between open areas dominated by grasses and denser forest formations (Figure 8) (Table 4) (Damasceno-Junior & Pott, 2021; Guimarães et al., 2014; Nunes da Cunha et al., 2023). These physiognomies occur predominantly in well-drained areas with low flooding frequency, often on sandy or moderately fertile soils. Their structure is marked by the presence of spaced arboreal individuals and an understory of grasses and herbaceous plants adapted to seasonal cycles of drought and fire (Santos et al., 2020). They are physiognomic units that reveal the strong influence of the Cerrado biome on the Pantanal vegetation, especially in edge subregions such as Poconé, Cáceres, Aquidauana, and Miranda (J. D. S. V. Silva & De Moura Abdon, 1998).

Figure *8* - Distribution of phytophysiognomies of Woody Cerrado found in the Pantanal. (A) Distribution map. (B) Tree Cerrado.



Research source: (A) Adapted from Damasceno-Junior & Pott (2021). (B) Adapted from Santos et al., (2020).

Table 4 - Woody Cerrado (Savanna) Phytophysiognomies Found in the Pantanal.

TYPE OF WOODY CERRADO	CHARACTERISTICS	REGIONAL PHYSIOGNOMIES	SUB-REGIONS OF OCCURRENCE
Tree Cerrado	May occur with or without gallery forest; vegetation with sparse trees and a grass understory	Campo cerrado, cerrado, open cerrado	Poconé, Cáceres, Barão de Melgaço, Aquidauana, Miranda
Park Cerrado	Presence of isolated trees in open areas, generally without gallery forest	Campo cerrado, cerrado, open cerrado	Abobral, Nhecolândia, Paiaguás, Miranda

Research source: Adapted from Damasceno-Junior & Pott (2021).

The Arboreal Cerrado in the Pantanal encompasses regional physiognomies such as *cerrado campestre*, *typical cerrado*, and *open cerrado*, characterized by twisted trees with thick bark and coriaceous leaves, spaced over a continuous herbaceous-shrub layer. The presence or absence of gallery forests aids in the ecological distinction of these formations. Representative species include *Qualea grandiflora* (Vochysiaceae), *Annona coriacea* (Annonaceae), and *Byrsonima intermedia* (Malpighiaceae), all of which are adapted to well-drained soils and periodic fire occurrence (Damasceno-Junior & Pott, 2021; Nunes da Cunha et al., 2023). These formations are ecologically important due to their high functional diversity and their role in maintaining essential ecological processes, such as nutrient cycling, in environments that represent transitional zones between forests and grasslands.

The Park Cerrado exhibits an even more open structure, with isolated trees or small clusters of trees interspersed within extensive areas of herbaceous vegetation (Guglieri-Caporal et al., 2018; Nunes da Cunha et al., 2023). In general, it is not associated with gallery forests and occurs on flat or gently undulating terrain, more exposed to solar radiation and wind

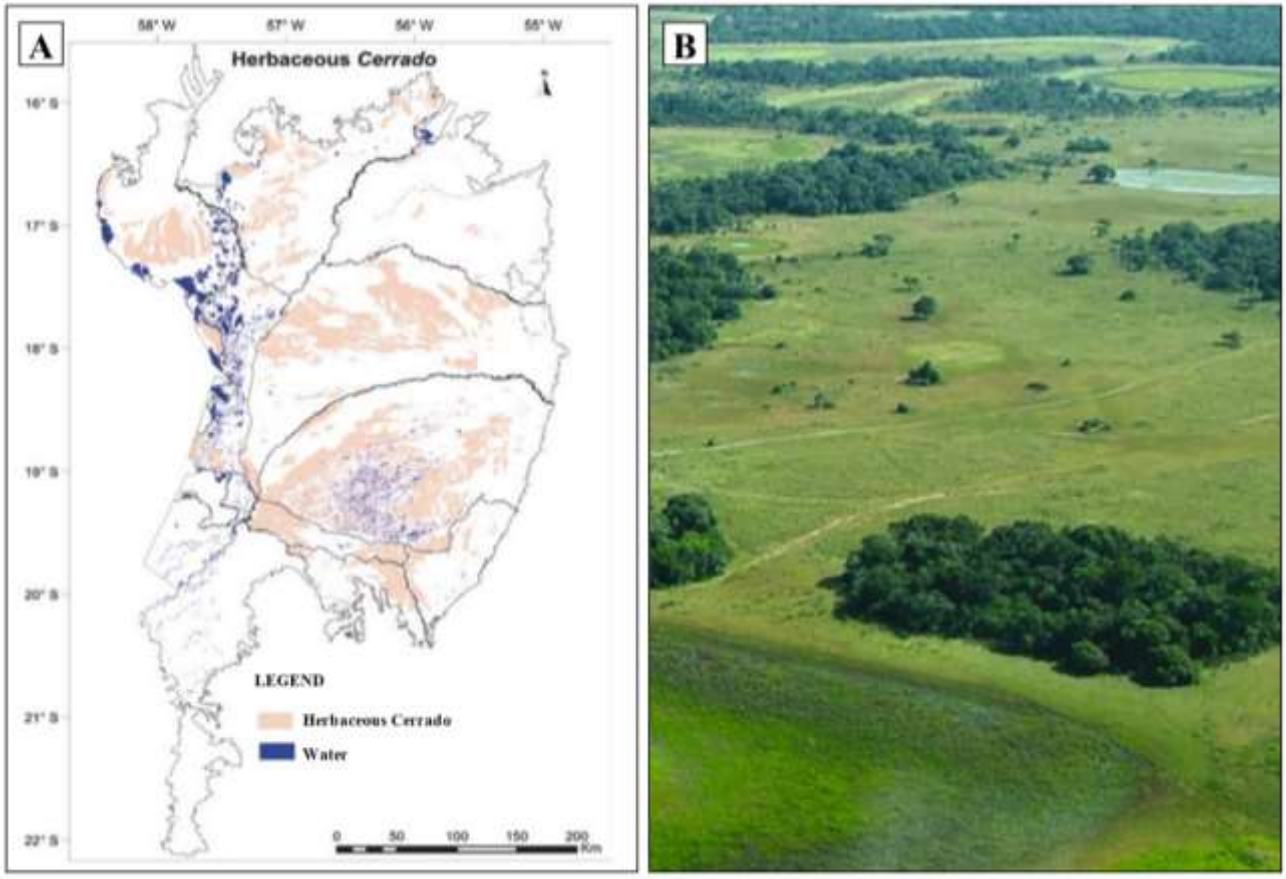
action. Its physiognomies include the so-called arborized grassland or woody open field, where species such as *Curatella americana* (Dilleniaceae) and *Byrsonima cydoniifolia* (Malpighiaceae) predominate, often associated with poor, well-aerated soils (Damasceno-Junior & Pott, 2021). This formation functions as an ecological transition zone and plays a fundamental role in ensuring ecological connectivity between floodable grasslands and denser Cerrado formations.

The woody savannas of the Pantanal thus reflect a combination of ecological resilience and adaptive plasticity, shaped by edaphic factors, fire regimes, and historical anthropogenic use. Their occurrence in peripheral areas with less influence from flooding reinforces the importance of these environments in maintaining floristic gradients and in mediating landscape responses to climatic and hydrological disturbances. Their floristic composition harbors a significant assemblage of endemic species and species of high ecological value, underscoring the need for the inclusion of these formations in conservation policies, detailed vegetation mapping, and ecosystem restoration programs in the Pantanal.

3.5.3 Herbaceous Cerrado

The Herbaceous Cerrado formations in the Pantanal, also known as grass-shrub savannas (savanas gramíneo-lenhosas), represent one of the most widely distributed physiognomic components of the floodplain (Figure 9) (Table 5) (Damasceno-Junior & Pott, 2021; Guimarães, Trevelin, & Manoel, 2014; T. do N. Lima & Faria, 2021; Nunes da Cunha et al., 2023). These vegetation types occur in areas dominated by grasses and subshrubs, where the tree canopy is absent or very sparse (T. do N. Lima & Faria, 2021). Two main variants are recognized according to their association (or not) with gallery forests: the grass-shrub savanna with gallery forest, which occurs near perennial watercourses, and the grass-shrub savanna without gallery forest, typical of seasonally floodable environments with low slope (Damasceno-Junior & Pott, 2021; Guglieri-Caporal, Pott, Felismino, Caporal, & Valls, 2018; Nunes da Cunha et al., 2023; Santos et al., 2020). Both variants host species adapted to hydric fluctuations, natural fire, and low soil fertility (Guglieri-Caporal et al., 2018; T. do N. Lima & Faria, 2021).

Figure 9 - Distribution of phytophysiognomies of Herbaceous Cerrado found in the Pantanal. (A) Distribution map. (B) Herbaceous Cerrado With Gallery Forest.



Research source: (A) Adapted from Damasceno-Junior & Pott (2021). (B) Adapted from Santos et al., (2020).

Table 5 - Herbaceous Cerrado Phytophysiognomies Found in the Pantanal.

TYPE OF WOODY-GRASS CERRADO	CHARACTERISTICS	PRESENCE OF GALLERY FOREST	REFINED SUB-REGIONS OF OCCURRENCE
With Gallery Forest	Herbaceous-woody vegetation with shrublands and associated riparian forests	Present	Northern and central Paiaguás; northeastern sector of Nhecolândia
Without Gallery Forest	Open vegetation dominated by grasses and sparse shrubs in wet areas	Absent	Western and southern Paiaguás; central and southern plains of Nhecolândia

Research source: Adapted from Damasceno-Junior & Pott (2021).

The grass-shrub savanna with gallery forest is frequently associated with higher or gently sloping environments, which favor surface drainage and the maintenance of riparian forests along streams and temporary watercourses (corixos) (Damasceno-Junior & Pott, 2021). The associated physiognomies include shrub fields and *Elionurus* grasslands, particularly featuring grasses such as *Elionurus muticus* (Poaceae), in addition to the occasional presence of shrubs and moisture-tolerant trees (T. do N. Lima & Faria, 2021; Santos et al., 2020). This formation occurs especially in the sub-regions of Paiaguás and Nhecolândia, where there is greater connectivity with riparian forests (Guglieri-Caporal et al., 2018; T. do N. Lima & Faria, 2021; Santos et al., 2020). The gallery forest functions as a transitional zone and a biodiversity refuge, influencing the surrounding floristic composition and favoring the emergence of more shaded and humid microhabitats (Santos et al., 2020).

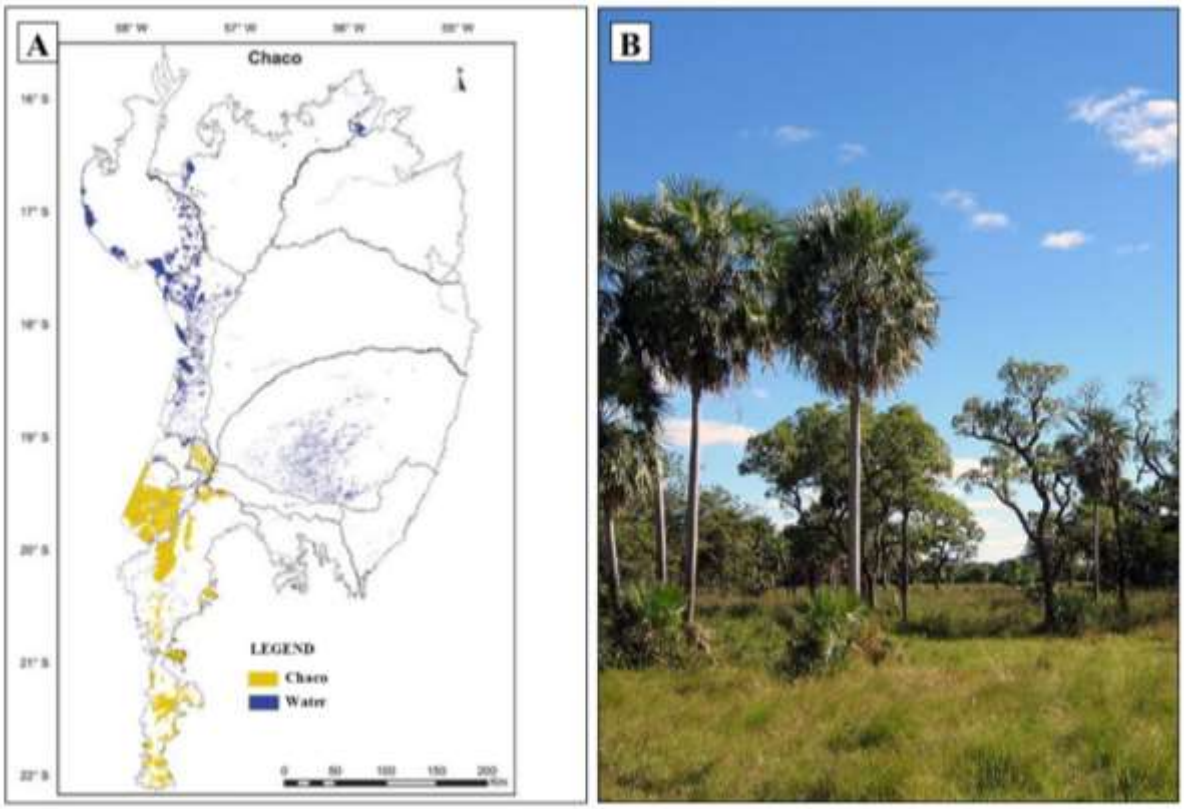
On the other hand, the grass-shrub savanna without gallery forest is characterized by extensive open areas dominated by grasses, often subject to seasonal flooding and with low tree cover (Santos et al., 2020). Physiognomies such as open fields,

campinas and flooded grasslands are common, with a predominance of species such as *Axonopus purpusii* (Poaceae), *Andropogon bicornis* (Poaceae), and *Paspalum carinatum* (Poaceae) (Guglieri-Caporal et al., 2018; Santos et al., 2020). This physiognomy occupies vast areas in the central sub-regions of Nhecolândia and southern Paiaguás, being absent in areas such as Nabileque and Porto Murtinho, where the topography and hydrological regime favor more shrubby or chaco-type formations (Guglieri-Caporal et al., 2018; T. do N. Lima & Faria, 2021). The absence of gallery forest in these areas exposes the vegetation to direct solar radiation and water stress during dry periods, which selects species with high tolerance to water deficit and fire (Guimarães et al., 2014).

3.5.4 Chaco

The Chaco-type physiognomies found in the Pantanal represent one of the most striking expressions of the transition between the humid tropical vegetation of the floodplain and the drier domains of southwestern South America (Figure 10) (Table 6) (Damasceno-Junior & Pott, 2021; M. S. de Lima, Takahasi, Damasceno-Junior, & Araujo, 2019; Nunes da Cunha et al., 2023). These formations are especially prominent in the sub-regions of Nabileque, Porto Murtinho, western Paiaguás, and to a lesser extent, around the Paraguay River (T. do N. Lima & Faria, 2021). They occur on poorly drained soils, sometimes saline, and under the influence of a climate regime marked by strong hydrological seasonality. Among the most representative physiognomic types are the Deciduous Seasonal Chaco Forest, the Chaco Woody Savanna, the Chaco Shrubland, and the Chaco Gallery Forests, each reflecting subtle variations in topography, edaphic conditions, and water availability (Damasceno-Junior & Pott, 2021; Silveira et al., 2021).

Figure 10 - Distribution of Chaco phytophysiognomies found in the Pantanal. (A) Distribution map. (B) Chaco Woody Savanna.



Research source: (A) Adapted from Damasceno-Junior & Pott (2021). (B) Adapted from Santos et al., (2020).

Table 6 - Chaco phytophysiognomies found in the Pantanal.

TYPE OF VEGETATION FORMATION IN THE CHACO	CHARACTERISTICS	REGIONAL PHYSIOGNOMIES	SUB-REGIONS OF OCCURRENCE (PANTANAL)
Seasonal Deciduous Forest of the Chaco	Forest with pronounced seasonal leaf loss, vegetation adapted to dry periods and soils with seasonal water availability	Deciduous forest, transition forest	Paiaguás region, Porto Murtinho, Nabileque
Woody Savanna of the Chaco	Vegetation with scattered trees, shrubs, and grasses adapted to arid soils and semi-arid climate	Dry savanna, open cerrado	Western sector of Paiaguás, Barão de Melgaço sub-region
Shrubby Field of the Chaco	Low vegetation dominated by spiny shrubs, grasses, and herbs	Open field, xerophytic shrubland	Central plains of Nabileque and areas near Corumbá
Gallery Forests of the Chaco	Dense riparian vegetation associated with watercourses, with high biodiversity	Riparian forest, gallery forest	Margins of the Paraguay River (regions of Miranda, Aquidauana, Corumbá)

Research source: Adapted from Damasceno-Junior & Pott (2021).

The Deciduous Seasonal Forest of the Chaco features dense arboreal vegetation that is seasonally leaf-shedding, with species that lose their leaves during the dry season to reduce water loss (Nunes da Cunha et al., 2023; Silveira et al., 2021). It is common on slightly elevated or well-drained terrains, dominated by species such as *Aspidosperma quebracho-blanco* (Apocynaceae), *Tabebuia aurea* (Bignoniaceae), and *Schinopsis brasiliensis* (Anacardiaceae), all adapted to calcareous or litholic soils (Damasceno-Junior & Pott, 2021; Nunes da Cunha et al., 2023). The vegetation structure shows a closed canopy but with a sparse understory and the presence of deep-rooted woody species, which gives these forests high hydric resilience (C. J. Silva et al., 2015). Its occurrence is strongly associated with areas less prone to flooding and with significant hydric deficit during winter (Silveira et al., 2021).

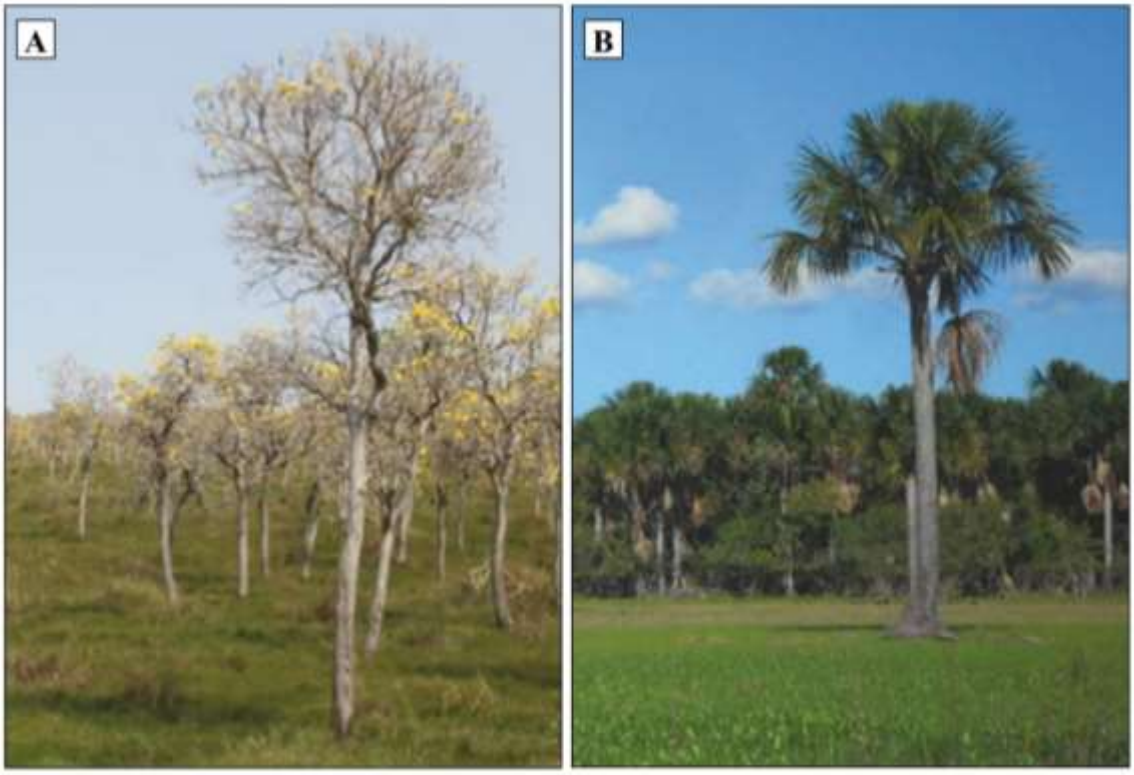
The Woody Savanna of the Chaco occurs in more open areas, with scattered trees and shrubs over a discontinuous herbaceous layer. This vegetation is typical of environments with alternating shallow floods and prolonged droughts, presenting species adapted to intense heat and surface salinization. Common species include *Prosopis rubriflora* (Fabaceae), *Capparis retusa* (Capparaceae), and *Cochlospermum regium* (Bixaceae) (Damasceno-Junior & Pott, 2021). This physiognomy is often overlain by fields of resilient grasses, such as *Trichloris crinita* (Poaceae), and by formations with xerophytic savanna characteristics (Damasceno-Junior & Pott, 2021). The soils, generally shallow and compacted, limit tree growth and favor vegetation adapted to water scarcity and extreme solar exposure.

The Shrubland of the Chaco represents a transition between woody savanna and open areas with low density of tree species (Guglieri-Caporal, Pott, Felismino, Caporal, & Valls, 2018; T. do N. Lima & Faria, 2021; Santos et al., 2020). It is a formation characterized by low height and woody biomass, yet ecologically relevant, as it hosts pioneer species and endemic components adapted to climatic seasonality and saline soils. Floristic elements include thorny shrubs, cacti, and some bromeliads, which exhibit adaptations such as thick cuticles, CAM metabolism, and resprouting capacity after fire events (Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021). In moist corridors and along intermittent drainage margins, the Chaco Gallery Forests also occur. These develop in narrow strips influenced by a high water table. Species such as *Triplaris americana* (Polygonaceae), *Ficus trigona* (Moraceae), and *Vitex cymosa* (Lamiaceae) are commonly found there. These formations exhibit a structure similar to riparian forests of other domains, but with a floristic composition adapted to extreme cycles of drought and flooding (Couto et al., 2024; Damasceno-Junior & Pott, 2021).

3.5.5 Monodominant Formations

Monodominant formations in the Pantanal represent phytophysiognomic units with low structural and taxonomic diversity, yet high ecological specialization (Curado et al., 2016; Manrique-Pineda, Souza, Paranhos Filho, Cáceres Encina, & Damasceno-Junior, 2021). In these formations, one or few taxa overwhelmingly dominate the arboreal or shrubby stratum, generally as a response to extreme edaphic conditions such as saline, poorly drained, or compacted soils, in addition to highly seasonal hydrological regimes (T. do N. Lima & Faria, 2021; Rocha, Santos Júnior, Damasceno-Júnior, Pott, & Pott, 2015). In the Pantanal context, this type of vegetation occurs both in forested areas and in savanna formations, characterizing specific physiognomies such as Codominant Seasonal Deciduous Forest and Codominant Woody Savanna, with a discontinuous distribution across distinct subregions of the plain, especially in areas of the Lower Paraguay, Nhecolândia, and Abobral (Figure 11) (Table 7) (Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021; Pott, Oliveira, Damasceno-Junior, & Silva, 2011; Rocha et al., 2015).

Figure 11 - Distribution of phytophysiognomies from Monodominant Formations in the Pantanal. (A) Tabebuia aurea (Bignoniaceae). (B) Mauritia flexuosa (Arecaceae).



Research source: (A-B) Adapted from Damasceno-Junior & Pott (2021).

Table 7 - Phytophysiognomies Monodominant found in the Pantanal.

CODOMINANT VEGETATION FORMATION	GENERAL CHARACTERISTICS	REPRESENTATIVE MONODOMINANT SPECIES WITH AUTHOR	SUB-REGIONS OF OCCURRENCE (PANTANAL)
Seasonal Deciduous Codominant Forest	Forest with seasonal leaf drop, diversified composition with co-dominant trees and shrubs	*Anadenanthera colubrina* (Vell.) Brenan *Astronium fraxinifolium* Schott *Tessaria integrifolia* Ruiz & Pav. *Tabebuia aurea* (Silva Manso) Benth & Hook ex S. Moore *Schinopsis balansae* Engl.	Paiaguás, Porto Murtinho, Nabileque
Woody Savanna Codominant	Vegetation with spaced trees and grasses, predominance of woody species	*Elionurus muticus* (Spreng.) Kuntze *Cyperus giganteus* Vahl *Curatella americana* L. *Byrsonima crassifolia* Kunth	Poconé, Cáceres, Barão de Melgaço, Aquidauana
Woody-Grass Field Codominant	Open areas dominated by grasses and sparse shrubs, often associated with wet or floodable soils	*Mauritia flexuosa L.f.* *Vochysia divergens* Pohl	Nhecolândia, Miranda, Nabileque

Research source: Adapted from Damasceno-Junior & Pott (2021).

The Seasonal Deciduous Codominant Forest is a low-diversity forest dominated by two or three deciduous tree species that respond synchronously to hydric seasonality. The physiognomy is characterized by a poorly stratified canopy, with predominance of species such as *Tabebuia aurea* (Bignoniaceae), *Astronium fraxinifolium* (Anacardiaceae), and locally *Anadenanthera colubrina* (Fabaceae) (C. J. Silva et al., 2015; Pott et al., 2011). This forest occurs on drier terrain or shallower soils, in alternating strips with dense cerrado forests (cerradões) or woody savannas (Arieira & Cunha, 2006). Monodominance is maintained by the competitive ability of the dominant species under limiting water and nutrient conditions and is also favored by natural disturbances such as fire, which eliminate less tolerant species (Arruda et al., 2016; Curado et al., 2016).

The Codominant Woody Savanna, in turn, develops in savanna fields with the presence of shrubs or small trees sparsely distributed, generally in environments with sandy soil, poor in organic matter, and subject to seasonal flooding (T. do N. Lima & Faria, 2021). Among the codominant species, *Curatella americana* (Dilleniaceae) and *Byrsonima cydoniifolia* (Malpighiaceae) stand out, forming extensive and relatively homogeneous populations, with a sparse understory and reduced herbaceous cover during dry periods (Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021). This formation is common in areas such as Nhecolândia, Paiaguás, and intermediate sectors between savannas and open fields, acting as an important ecological transition between different moisture zones and land use types (Schaefer, 2023).

From a phytogeographical perspective, monodominant formations are significant because they indicate restrictive and specific environmental conditions, functioning as ecological indicators of peculiar soils and hydrological regimes (Arieira & Cunha, 2006; Arruda et al., 2016; T. do N. Lima & Faria, 2021). Although these formations exhibit low diversity, they may harbor endemic or rare species and serve as important feeding areas for wildlife, especially during the dry season when other physiognomies enter ecological dormancy (T. do N. Lima & Faria, 2021). The management and conservation of these areas require special attention, as they are sensitive to changes in fire regimes, increased agricultural use, and climate change, which directly affect the flooding cycles that regulate their existence.

3.6 Considerations on the Flora of the Pantanal

The flora of the Pantanal represents one of the greatest examples of ecological convergence and floristic complexity among South American biomes (Damasceno-Junior & Pott, 2021; M. S. de Lima, Takahasi, Damasceno-Junior, & Araujo, 2019; Lourival et al., 2025; Moreira, Pott, Souza, & Pott, 2017). Situated in a floodplain with pronounced seasonal dynamics,

it is composed of elements originating from the Cerrado, the Amazon, the Atlantic Forest, the Chaco, and, occasionally, the Caatinga. This hybrid composition confers upon the Pantanal a remarkable floristic diversity, despite its relatively smaller area compared to other biomes (Guimarães, Trevelin, & Manoel, 2014; Nunes da Cunha et al., 2023). The highly heterogeneous Pantanal environment supports vegetation capable of responding to extreme variations in moisture and temperature throughout the year.

Recent studies indicate that the vascular flora of the Pantanal includes approximately 2,567 species, distributed across about 149 botanical families and more than 900 genera, with a predominance of angiosperms (Table 8) (Damasceno-Junior & Pott, 2021). Among the families richest in species are Fabaceae (344 species), Poaceae (302), Asteraceae (136), and Cyperaceae (117), which together represent about 30% of the recorded flora (Damasceno-Junior & Pott, 2021). These families are followed by Euphorbiaceae, Malvaceae, Rubiaceae, Apocynaceae, and Myrtaceae, confirming the dominance of taxa adapted to tropical environments with marked hydric variation (Arruda et al., 2016; Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021; Pott, Oliveira, Damasceno-Junior, & Silva, 2011).

Table 8 - Most representative botanical families in the Pantanal, Number of Genera and Most Diverse Genus.

BOTANICAL FAMILY	NUMBER OF GENERA	MOST DIVERSE GENUS	SPECIES IN MOST DIVERSE GENUS	TOTAL SPECIES IN FAMILY
Fabaceae Lindl.	72	*Mimosa* L.	32	344
Poaceae Barnhart	86	*Paspalum* L.	53	302
Asteraceae Bercht. & J.Presl	69	*Elephantopus* L. / *Stilpnopappus*	11	136
Cyperaceae Juss.	26	*Cyperus* L.	48	117
Euphorbiaceae Juss.	26	*Croton* L.	28	105
Malvaceae Juss.	22	*Sida* L.	12	105
Rubiaceae Juss.	24	*Coccocypselum* P.Browne	6	74
Apocynaceae Juss.	18	*Aspidosperma* Mart. & Zucc.	5	62
Convolvulaceae Juss.	10	*Ipomoea* L.	32	62
Myrtaceae Juss.	10	*Eugenia* L.	28	56
Malpighiaceae Juss.	8	*Byrsonima* Rich. ex Kunth	7	52
Bignoniaceae Juss.	8	*Tabebuia* Gomes ex DC.	4	45
Sapindaceae Juss.	9	*Serjania* Mill.	5	37
Solanaceae Juss.	7	*Solanum* L.	7	35
Orchidaceae Juss.	17	*Epidendrum* L.	5	31

Research source: Adapted from Damasceno-Junior & Pott (2021).

Regarding the most diverse genera, noteworthy examples include *Paspalum* (Poaceae), *Cyperus* (Cyperaceae), *Ipomoea* (Convolvulaceae), *Mimosa* (Fabaceae), *Croton* (Euphorbiaceae), *Eugenia* (Myrtaceae), *Arachis* (Fabaceae), and *Ludwigia* (Onagraceae), which together account for approximately 10% of the total species in the Pantanal (Damasceno-Junior & Pott, 2021; Pott et al., 2011). This floristic concentration reveals not only patterns of ecological adaptation but also reflects the presence of secondary diversity centers, where selective environmental pressures favored the diversification of groups with high phenotypic plasticity. Many of these genera, in turn, include species with broad pantropical or neotropical distributions,

suggesting historical dispersal processes associated with Quaternary climatic fluctuations (Alho & Sabino, 2011; T. do N. Lima & Faria, 2021).

The floristic diversity of the Pantanal is heterogeneously distributed among the five main phytophysiognomic groups composing the landscape: forest formations, arboreal cerrado (woody savanna), herbaceous cerrado (grass-woody savanna), monodominant formations, and chaco-type vegetation (Damasceno-Junior & Pott, 2021; M. S. de Lima et al., 2019). Each group reflects different flooding regimes, soil types, and topographical variations, factors that directly influence species richness and floristic composition (Guimarães et al., 2014; T. do N. Lima & Faria, 2021). Forest formations, especially those on sandy ridges or residual hills, concentrate a greater number of arboreal and epiphytic species, with families such as Fabaceae, Myrtaceae, and Apocynaceae being prominent, typical of seasonal forests and riparian woodlands. Woody savannas, represented by arboreal cerrado, shelter a large number of species adapted to water deficit and fire, including families such as Malpighiaceae, Vochysiaceae, and Melastomataceae (Damasceno-Junior & Pott, 2021; Nunes da Cunha et al., 2023).

Herbaceous cerrado and monodominant formations, in turn, exhibit a predominance of grasses and sedges, highlighting genera such as *Paspalum* (Poaceae) and *Cyperus* (Cyperaceae), strongly adapted to poorly drained soils and seasonal flooding (Damasceno-Junior & Pott, 2021; Guimarães et al., 2014; T. do N. Lima & Faria, 2021; Manrique-Pineda, Souza, Paranhos Filho, Cáceres Encina, & Damasceno-Junior, 2021). These phytophysiognomies show lower structural diversity but are ecologically important due to their resilience and rapid post-disturbance regeneration. In areas influenced by drier conditions, especially in the southwestern portion of the Pantanal, chaco-type formations bring together elements of xerophytic flora, such as species of *Aspidosperma* (Apocynaceae) and *Schinopsis* (Anacardiaceae), with morphophysiological adaptations to low water availability (Damasceno-Junior & Pott, 2021; T. do N. Lima & Faria, 2021). Thus, the five phytophysiognomic groups not only reflect the environmental variation of the Pantanal plain but also function as fundamental ecological units for maintaining the high species diversity observed in the regional flora (Guimarães et al., 2014; T. do N. Lima & Faria, 2021).

Phytogeographic analysis of the flora also highlights the importance of ecotones and vegetational enclaves present in the Pantanal landscape (T. do N. Lima & Faria, 2021). In these transition zones between different physiognomies, such as cerrado, chaco, and riparian forests, there is an overlap of species from distinct floristic origins (T. do N. Lima & Faria, 2021; Manrique-Pineda et al., 2021; Nunes da Cunha et al., 2023). Such contact zones act as natural laboratories of speciation, endemism, and adaptation, often harboring rare, monodominant, or even scientifically undescribed species (Manrique-Pineda et al., 2021). The aquatic and palustrine flora of the Pantanal, for example, is particularly rich and includes important macrophytes such as *Eichhornia crassipes* (Pontederiaceae), *Pistia stratiotes* (Araceae), and *Nymphaea amazonum* (Nymphaeaceae), among others, adapted to fluctuating water levels (Damasceno-Junior & Pott, 2021; Moreira et al., 2017).

Despite its ecotonal nature and strong floristic influence from adjacent biomes, the Pantanal harbors a significant set of endemic species, particularly associated with specialized environments such as saline lagoons, murundu fields, and palustrine vegetation enclaves. It is estimated that around nine vascular species occur exclusively in the Pantanal plain, many of them restricted to microhabitats with unique ecological conditions. Notable examples include *Stilpnopappus pantanalensis* (Asteraceae), *Ipomoea pantanalensis* (Convolvulaceae), *Arachis vallsii* (Fabaceae), and *Axonopus fusiformis* (Poaceae), whose distributions are linked to hydromorphic soils, natural salinization, or specific flooding cycles (Table 9) (Damasceno-Junior & Pott, 2021; Pott et al., 2011). These species represent not only important indicators of the Pantanal's ecological uniqueness but also vulnerable elements to habitat fragmentation and hydrological changes, demanding specific conservation strategies and ongoing floristic monitoring (Moreira et al., 2017).

Table 9 - List of Endemic Plant Species of the Pantanal.

BOTANICAL FAMILY	ENDEMIC SPECIES	SUB-REGION OF OCCURRENCE
Fabaceae	*Arachis appressipila* Krapov. & W.C.Gregory	Nhecolândia / Abobral
Fabaceae	*Arachis hoehnei* Krapov. & W.C.Gregory	Paiaguás / Nhecolândia
Fabaceae	*Arachis linearifolia* Krapov. & W.C.Gregory	Paiaguás
Fabaceae	*Arachis valida* Krapov. & W.C.Gregory	Abobral
Fabaceae	*Arachis vallsii* Valls & Simpson	Nhecolândia / Aquidauana
Poaceae	*Axonopus fusiformis* Silveira & Valls	Nhecolândia / Miranda
Boraginaceae	*Euploca pottii* Melo & Semir	Abobral / Porto Murtinho
Convolvulaceae	*Ipomoea pantanalensis* J.R.I.Wood, Scotland & S.Miranda	Nhecolândia
Asteraceae	*Stilpnopappus pantanalensis* H.Rob.	Nhecolândia / Paiaguás (saline lagoons)

Research source: Adapted from Damasceno-Junior & Pott, (2021).

The flora of the Pantanal reflects a remarkable combination of adaptive plasticity, phylogenetic diversity, and specialized ecophysiological responses, structured in mosaics that cyclically renew according to the pulses of flooding and drought (Arruda et al., 2016; Lima & Faria, 2021). The conservation of this floristic heritage requires the maintenance of natural hydrological regimes and monitoring of anthropogenic pressure on the most vulnerable sub-regions. Furthermore, deepening floristic knowledge through systematic inventories and functional ecology studies is essential to support management actions, restoration efforts, and public environmental protection policies within the Pantanal domain.

3.7 Morpho-Anatomical Adaptations of Vegetation to the Pantanal Domain

The environmental conditions of the Pantanal, characterized by alternating periods of flooding and drought, impose strong selective pressures on the local flora, resulting in a significant set of morphoanatomical adaptations (C. D. S. Miranda, Paranhos Filho, & Pott, 2018). These structural and functional strategies ensure plant survival in the face of challenges such as root hypoxia, soil salinization, intense solar radiation, prolonged periods of water deficit, and occasional fires (Leal Filho, Azeiteiro, Salvia, Fritzen, & Libonati, 2021; Manrique-Pineda, Souza, Paranhos Filho, Cáceres Encina, & Damasceno-Junior, 2021). The Pantanal vegetation has developed distinct adaptations both in permanently flooded environments and in edge and transitional areas, where poorly drained soils and extreme microclimates predominate (C. J. Silva et al., 2015).

In seasonally flooded areas, hydrophytic and marsh plants display notable features such as the development of aerenchyma—tissues with intercellular spaces that facilitate oxygen diffusion to roots—and stems with aquiferous parenchyma, which aid in water storage. Adventitious roots and floating stems are common in macrophytes like *Eichhornia crassipes* (Pontederiaceae) and *Pistia stratiotes* (Araceae), while plants such as *Nymphaea amazonum* (Nymphaeaceae) exhibit floating leaves with stomata concentrated on the adaxial epidermis, optimizing gas exchange in anoxic environments (Damasceno-Junior & Pott, 2021; Pott, Oliveira, Damasceno-Junior, & Silva, 2011). Such morphologies ensure physiological functioning even in soils saturated for long periods.

In higher regions subjected to prolonged drought, species with xeromorphic adaptations and pronounced sclerophylly predominate. Many trees and shrubs of the Pantanal savanna, such as *Curatella americana* (Dilleniaceae) and *Byrsonima intermedia* (Malpighiaceae), possess thick leaves covered with waxy cuticles and trichomes, as well as sunken stomata—features that minimize water loss through evapotranspiration (Damasceno-Junior & Pott, 2021; Resende & Pinho, 2011; Rocha Filho & Lomônaco, 2006). Secondary growth driven by the activity of the cork cambium produces a thick periderm that prevents excessive water loss through stem tissues. The deep or fasciculate root systems of these species allow access to declining water tables, while thick woody stems store water reserves and promote fire resilience—a recurrent disturbance in cerrado and chaco environments (Damasceno-Junior & Pott, 2021; Lima & Faria, 2021).

Besides physiological and anatomical adaptations, there are also phenological modifications such as seasonal leaf shedding, a common strategy in seasonal forests and chaco-type formations, which reduces leaf surface area during the dry period (Bezerra, Encina, Figueiredo, Dalmas, & Paranhos Filho, 2021; Souza-Lima, Sinani, Pott, & Sartori, 2017; Pott et al., 2011). Diurnal stomatal closure and C4 metabolism are also found in herbaceous species of the grasslands and flooded fields, resulting in large monodominant patches of Poales species, such as *Cyperus giganteus* Vahl (Cyperaceae), *Elionurus muticus* (Spreng.) Kuntze (Poaceae), and *Andropogon hypogynus* Hack. (Poaceae), among others (Guglieri-Caporal, Pott, Felismino, Caporal, & Valls, 2018; Lima & Faria, 2021; Santos et al., 2020). These adaptations allow the Pantanal's plant communities not only to survive but to maintain high primary productivity and biodiversity, even under fluctuating environmental conditions. Thus, the morphoanatomical traits of the Pantanal flora represent a remarkable model of adaptive convergence in tropical riverine landscapes (Guimarães, Trevelin, & Manoel, 2014; Kohagura, Souza, Bao, Ferreira, & Pott, 2020).

3.8 Consequences of Fire Incidence on Vegetation

The Pantanal biome, although predominantly shaped by hydrological cycles, has experienced a significant increase in fire incidence, especially during the dry season, which has become longer and more severe due to climatic variability and anthropogenic influence (Berlinck et al., 2022; Couto et al., 2024; Jesus, Rosa, Barreto, & Fernandes, 2020; Pelissari et al., 2023; P. S. Silva et al., 2022). Although fire is not a new phenomenon in the region, its frequency, intensity, and spatial extent have intensified in recent decades, shifting from a sporadic natural event to a large-scale ecological disturbance (Berlinck et al., 2022; Damasceno-Junior & Pott, 2021). In 2020 alone, the biome faced one of the largest wildfire outbreaks ever recorded, with more than 30% of the total Pantanal area affected, resulting in significant losses and alteration of vegetation structure (Kohagura et al., 2020; Lima & Faria, 2021; Neto, Pereira, Helena Silva, Rosa Oliveira, & Alves Damasceno Júnior, 2024).

The sub-regions most severely impacted by the fires include Nhecolândia, Paiaguás, and parts of the Paraguai and Abobral zones, where seasonally flooded fields, savannas, and monodominant formations proved particularly vulnerable due to the accumulation of dry biomass and low soil moisture during prolonged drought periods (Table 10) (Lima & Faria, 2021; Manrique-Pineda et al., 2021; Neto et al., 2024; Nunes da Cunha et al., 2023). In these areas, the transition zones between flooded and non-flooded environments, which normally act as buffer zones, become highly combustible under conditions of extreme dryness (Lima & Faria, 2021). Furthermore, fire spreads rapidly through extensive networks of dry channels, grass fields, and patches of herbaceous cerrado, overcoming natural barriers and affecting plant communities that are not adapted to recurrent burning (Kohagura et al., 2020).

Table 10 - Pantanal Phytophysiognomic Groups Most Affected by Fire and Their Associated Sub-regions

PHYTOPHYSIOGNOMIC GROUP	MOST AFFECTED SUB-REGIONS	ESTIMATED PROPORTION OF AFFECTED AREA (% OF THE GROUP)
Forest Formations	Barão de Melgaço, Poconé, Cáceres, Miranda, Nabileque	25% – 35%
Woody Cerrado (Savanna)	Poconé, Paraguai, Aquidauana, Nhecolândia, Abobral, Miranda	40% – 60%
Herbaceous Cerrado	Paiaguás, Nhecolândia, Miranda, Barão de Melgaço, Poconé	50% – 70%
Chaco	Nabileque, Porto Murtinho, Paiaguás	30% – 45%
Monodominant Formations	Paraguai, Paiaguás, Nhecolândia, Abobral	60% – 80%

Research source: Adapted from Pelissari et al., (2023).

Vegetation responses to fire in the Pantanal are varied and depend on the phytophysiognomy, ecological resilience, and life-history strategies of the species (Damasceno-Junior & Pott, 2021; C. S. Miranda et al., 2018). Herbaceous communities tend to exhibit rapid regeneration, favored by species with underground storage organs or seeds adapted for post-fire germination. However, in woody savannas and forest formations, fire causes canopy degradation, tree mortality, and floristic simplification, especially when fires are of high intensity and recurrence (Meyer Oliveira et al., 2024). The loss of tree cover reduces habitat complexity, facilitates the invasion of pyrophytic grasses (e.g., Andropogon spp.), and increases the system's vulnerability to new fires, creating a vicious cycle of ecological degradation.

From a phytogeographical perspective, the expansion of fire-prone environments alters the structure and spatial distribution of major vegetation units (Couto et al., 2024; Damasceno-Junior & Pott, 2021; P. S. Silva et al., 2022). Areas formerly dominated by closed-canopy forests or flood-tolerant formations are gradually replaced by more open, fire-adapted phytophysiognomies, especially in the transition zones between savannas and fields. The persistence of these changes can lead to shifts in species composition, local extinctions of sensitive taxa, and a reduction in ecosystem resilience (Pelissari et al., 2023). Thus, understanding the consequences of fire on Pantanal vegetation requires an integrated approach that considers the spatial heterogeneity of sub-regions, the interactions between fire and flooding regimes, and the adaptive capacities of native plant communities (Arruda et al., 2016; Manrique-Pineda et al., 2021).

4. Final Considerations

We conclude that the Pantanal exhibits great phytogeographical complexity, highlighting it as a dynamic ecosystem shaped by an intricate network of interactions among climate, geology, hydrology, and soils. The diversity of phytophysiognomies present in the Pantanal floodplain—including forest formations, woody and herbaceous savannas, monodominant systems, and Chaco components—reflects the flora's adaptability to seasonal hydrological regimes, natural salinization, and edaphic variations. This scenario results in a rich and heterogeneous flora, with the coexistence of elements from adjacent biomes and endemic species restricted to specialized microhabitats.

Understanding these existing dynamics is fundamental to underpin conservation strategies, sustainable management, and public policies aimed at protecting the Pantanal in the face of increasing impacts from climate change, anthropogenic pressure, and the recurrence of extreme events such as fires. Maintaining natural flooding regimes, preserving ecotones, and expanding taxonomic and ecological studies are essential measures to ensure the functional integrity and ecological resilience of this unique biome. Thus, the Pantanal stands not only as a natural heritage of continental relevance but also as a living model of interaction between vegetation and landscape, whose adaptive responses of the flora continue to provide valuable insights for environmental science and biodiversity conservation.

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