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Environmental drivers organize woody plant assemblages across a cerrado vegetation mosaic in Northern Brazil

The objective was to approach a mosaic of savanna vegetation (marginal-MS and disjunct-DS areas) in Brazilian Northern Cerrado to investigate the role played by environmental drivers as determinants of community organization at a spatial scale in order to understand the divergent patterns along an environmental gradient. We analyzed spatial, edaphic, and climatic predictors across 21 tree communities of Cerrado, comprising 235 species, 154 genera and 52 families. The results suggest significant spatial dependence among assemblages, despite their functioning as independent ecological systems. They also confirmed which although the effects of the concentrations of edaphic attributes were not homogeneous, they evidenced that climatic and spatial factors were responsible for greater explanation of the data. The ordination analyzes indicated an environmental gradient with high species turnover and a mosaic of individual floras along the spatial gradient. Eight species contributed with at least 70% of the turnover among the subgroups. The most influential drivers were precipitation, thermal amplitude, elevation, latitudinal-longitudinal spatialization of the areas and aluminum content.

Keywords: Brazilian Savanna; Environmental ecotone; Cerrado biodiversity.

Fatores ambientais determinantes das comunidades arbóreas dos cerrados do Meio Norte, Brasil

O objetivo foi abordar um mosaico de vegetação de savana (áreas marginais-MS e disjuntas-DS) no Cerrado Setentrional Brasileiro para investigar o papel desempenhado por fatores ambientais como determinantes da organização comunitária em escala espacial, a fim de compreender os padrões divergentes ao longo de uma gradiente ambiental. Analisamos preditores espaciais, edáficos e climáticos em 21 comunidades do Cerrado, compreendendo 235 espécies, 154 gêneros e 52 famílias. Os resultados sugerem uma dependência espacial significativa entre as assembleias, apesar de funcionarem como sistemas ecológicos independentes. Eles também confirmaram que embora os efeitos das concentrações dos atributos edáficos não fossem homogêneos, evidenciaram que fatores climáticos e espaciais foram os responsáveis pela maior explicação dos dados. As análises de ordenação indicaram um gradiente ambiental com alta rotatividade de espécies e um mosaico de floras individuais ao longo do gradiente espacial. Oito espécies contribuíram com pelo menos 70% do faturamento entre os subgrupos. Os drivers mais influentes foram precipitação, amplitude térmica, elevação, espacialização latitudinal-longitudinal das áreas e teor de alumínio.

Palavras-chave: Savana Setentrional Brasileira; Gradiente Ecotonal; Biodiversidade do Cerrado.

Topic: **Conservação da Biodiversidade**

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INTRODUCTION

The savannas of Brazil, Bolivia and Paraguay, and the llanos of Venezuela and Colombia are the largest representations of neotropical savannas (VELAZCO et al., 2018). The Neotropical Cerrado is the second largest biome in South America and, when compared to the savannas of the African, Asian and Australian continents, it has the richest biological diversity of the planet, with more than 12 thousand species of flowering plants cataloged (BFG, 2018). In Brazil, it is characterized as a tropical woody savanna and encompasses a complex of plant formations that includes grasslands, savannas and forests and they differ by the coexistence and densification of trees, grasses and herbs (BAUDENA et al., 2015).

The geophysiographic features of savanna have undergone changes throughout climatic fluctuations and glacial/interglacial cycles of the Pleistocene that led to the creation of mosaics of patches of different vegetations resulting from expansions and retractions of forests and savannas throughout the quaternary period (SANTOS et al., 2020). This process determined the genetic variability and subdivision, speciation, and distribution of different organisms (DURIGAN et al., 2006; SANTOS et al., 2020).

Knowledge about nature and range of ecosystem boundaries has important implications for the management and conservation of biodiversity (MARQUES et al., 2019), especially in the complex ecological condition of the Brazilian Cerrado, in large-scale contact areas. A central block occupies mainly the Brazilian Central Plateau, covering about 85% of the center-southeast area of the country and marginal or isolated fragments that extend to the north and northwest, towards the Amazon Forest; to the south and southeast into the Atlantic Forest; to the northeast into the Caatinga; and to the southwest into the Chaco and Pantanal (OLSON et al., 2001). Different from nuclear area, the cerrados of Northern Brazil reflect in particular the influence of edaphoclimatic, physiognomic and floristic transition conditions between the superhumid climate of pluvial and coastal Amazonian areas (ombrophilous forests), the northeastern semi-arid territory (steppe-savanna) and subhumid portions (seasonal forests) (CONCEIÇÃO et al., 2009; SANTOS et al., 2020).

Previously classified into three biodiversity centers (southern Southeast, Central Plateau and Northeast regions of the Cerrado), whose differences are characterized by two climatic barriers (drought and frost polygons) and by altimetric heights (400-500 m and 900-1000 m) (COUTINHO et al., 2019), the pattern of distribution of woody species is determined by elevation and latitude gradients (VIEIRA et al., 2019; SANTOS et al., 2020). Thus, the phytogeographic patterns of marginal and disjunct areas and the effect of the environment and spatial processes deserve to be more addressed to connect the different parts of this mosaic.

The environmental differences recorded in Cerrado are due to the action of several abiotic factors that interfere with the dispersion and growth of plant species and are, therefore, responsible for the distinct floristic formations and structures (MEWS et al., 2014, 2016; COUTINHO et al., 2019), especially in climatic variations influenced by latitudinal-longitudinal (CASTRO et al., 1999) and edaphic gradients (SANAIOTTI et al., 2002; DIONIZIO et al., 2018). The main factors that condition the transitions between savannas and other biomes are associated with natural gradients of seasonal precipitation, water deficit, low soil fertility, fire, herbivory, anthropogenic actions caused by fires, and environmental imbalances associated with the use of the soil (MURPHY et al., 2012; BUENO et al., 2018; SANTOS et al., 2020). In ecotone Cerrado-Amazonia, as important as the difference in tree diversity are the effects that higher temperatures and more significant precipitation drive on the soil and accumulation of biomass (MORANDI et al., 2020).

Consequently, divergent phytogeographic patterns have resulted in different types of Cerrado in Brazil, demonstrated through floristic-geographic comparisons (FRANÇOSO et al., 2016, 2019). Castro et al. (1999) subdivided the Cerrado *sensu lato* into eight physiognomic groups, in terms of mesoscale: Cerrados of the Central Plateau (three groups), Cerrados of São Paulo (two groups) and Cerrados of the Northeast, Cerrados of the Pantanal and Cerrados of the Coast (one group each). For these authors, the cerrados in Piauí and Maranhão are considered to be northern cerrados of lowlands (0-500 m) called "marginal distal cerrados" (MDC) because they are distributed peripherally, on the margins of the geographic space occupied by the Brazilian Cerrado.

It is noteworthy that Amazonian savannas do not exist in this subdivision. In turn, Ratter and associates (RATTER et al., 1996, 2011) divided the cerrados into seven geographic subgroups and disjunct areas in the Amazon, based on floristic distribution patterns (Southeast; Center-Southeast; North-Northeast; Midwest; Dispersed areas with strong mesotrophic features; Mesotrophic areas on the far western border, forming a group in Rondônia, Mato Grosso do Sul and Mato Grosso; and Amazonian savannas - Roraima and Amapá). This extensive sampling efort showed that the Amazonian Cerrado group presented the greatest floristic differentiation, and the peripheral areas of Cerrado presented phytodiversity indices equal to or greater than some hotspot areas. In an expansion of the database of Ratter et al. (2011) and Françoso et al. (2019) delimited seven biogeographic districts, and contributed to conservation planning of marginal districts in the south and southwest of the Cerrado.

Would complex ecological peculiarities in Brazil Northern Cerrado may have driven a distinct woody assemblages? Here in, we demonstrate that ecotonal areas present high environmental heterogeneity, high floristic richness, and specific clusters of "areais floras", showing a high diversity between assemblages and a spatial dispute with different adjacent biomes, as well as a recognized presence of Cerrado ecotonal mosaics. We aimed to describe phytogeographic patterns in marginal and disjunct areas in the northern portion of Brazil. We demonstrate that there is a gradual correlation of their floristic composition with spatial, edaphic, and climatic variables along a mesic-xeric gradient, and species co-occurrences with adjacent ecosystems.

METHODOLOGY

Study Area

Northern Cerrados include seasonal savannas (cerrado *sensu stricto*) of the North and Northeast regions in a segment (East-West) covering, respectively, six disjunct fragments in the Amazon region: CAm-Complexo Amapá (AP), CAr-Cachoeira do Arari (PA), Cam-Cametá (PA), Mar-Maracanã (PA), Sal-Salvaterra

(PA), Vig-Vigia (PA); and 15 marginal samples in the Northeast: BGr-Barão de Grajaú (MA), PNe-Paulino Neves (MA), Tut-Tutoia (MA), Tim-Timon (MA), Cax-Caxias (MA), Cas-Castelo do Piauí (PI), Red-Redenção do Piauí (PI), BJe-Bom Jesus (PI), CMa-Campo Maior (PI), Ber-Bertolínea (PI), Jat-Jatobá (PI), BHo-Boa Hora (PI), Pir-Piracuruca (PI), CTe-Cocal de Telha (PI) and Arr-Arraial (PI) (Figure 1).

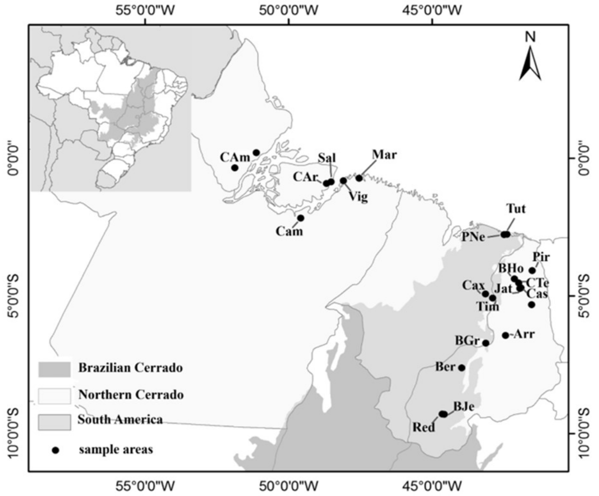

Figure 1: Location of the research areas (marginal and disjunct) in the Brazilian Northern Cerrado.

Samples from the mid-north of the Northeast are located at the northern margin of central block of the Brazilian Cerrado and correspond to the marginal cerrados (MS); the western areas of the Amazonian mid-north are isolated fragments of this block and are referred as disjunct savannas (DS), occurring outside of the Cerrado's boundary. Both exhibit variable environmental conditions and a gradient of savanna formations ranging from more grassy environments to more forested cerrados, maintaining contact with adjacent ecosystems such as caatinga, carrasco, deciduous/palmeiral forest, forests and sandbanks (AQUINO et al*.*, 2007).

According to the Köppen classification (KOTTEK et al., 2006), the climate between humid North and semi-arid Northeast is Aw, which is a tropical and humid climate type (tropical equatorial - Af, Tropical monsoon - Am, and tropical savanna - Am), with two distinct seasons (wet and dry), annual average temperature variation between 25 and 29 °C and total rainfall ranging from 95 mm (annual average of the last decade in Piauí) to 214.2 mm (in Pará and Amapá). Rainfall occurs between january and may, with highest concentration between february and april.

The soils are Dystrophic, sandy to clayey, acid Yellow Latosols, well drained, with moderate to high concentrations of aluminum (HARIDASAN, 2008) and low concentrations of organic matter and exchangeable bases such as calcium, magnesium, potassium, and phosphorus (SANAIOTTI et al., 2002) and fast water storage capacity and depth (ASSIS et al., 2011; SANTOS et al., 2017).

Phytosociological Analysis

A phytosociological analysis was carried out in 21 areas of Cerrado along an ecological gradient with different savanna physiognomies, in preserved landscapes without recent history of fires. The Protocol of

Minimum Phytosociological Assessment (PMPA) was adopted (FELFILI et al., 2002, 2004), whose minimum sampling is 1 hectare/area and at least 30 individuals per plot. Sampled individuals had their height and stem circunference measured and criterion included live woody individuals (including lianas) with stem diameter at ground level ≥ 3 cm ($SDGL_{3cm}$). The Mata Nativa 4 Software (CIENTEC, 2016) was used to analyze the structure of the vegetation and calculate the density, frequency, dominance and basal area (DOMBOIS et al., 2003). To facilitate comparisons between metadata the α-diversity was measured through the Shannon's diversity (H') and Pielou's evenness (J) indices (MAGURRAN, 2004). The botanical material was collected, herborized and incorporated into the herbariums of the Emílio Goeldi Museum of Pará (MPEG) and the Federal University of Piauí (UFPI). The scientific names, habits and distributions of the species was checked in the Flora do Brasil (http://floradobrasil.jbrj.gov.br) and Missouri Botanical Garden (www.tropicos.org) websites, which follows the APG IV taxonomy updates (APG, 2016).

Analysis of Environmental Variables

For the physical-chemical analysis of the soil of each area, one composite sample of five random samples per plot (center and vertices) were collected, no change in inclination, at 0-10 cm depth, following Lau et al. (2014). Samples were sent to Laboratory of soil analysis of the Brazilian Company of Agricultural Research and were analyzed for physicochemical properties, following the procedures recommended by the Brazilian Ministry of Agriculture for soil analyses (EMBRAPA, 1997). The investigated attributes are important factors for the spatial organization of plant assemblages and are associated with soil texture and fertility (coarse, fine, and total sand; silt; clay, Fe, Zn, Cu, Mn, pH (H_2O), Ca, Mg, Ca:Mg, K, Al, P, C, MO, N, C:N, Na, H+Al, SB, CTC (T), CTC (t), V and m).

The meteorological variables of the areas were based on the montly averages of minimum, mean, and maximum temperature (°C), relative humidity (%) and precipitation (mm) collected in automatic meteorological stations. These data were retrieved by accessing the Meteorological Database for Teaching and Research (MDTR) of the National Institute of Meteorology (INMet, http://www.inmet.gov.br). The annual averages were calculated from January 2005 to December 2017. The spatial coordinates and the average elevation were determined in the field with a Garmin GPS.

The analyses considered 25 structural parameters of communities, 39 environmental variables (edaphic and climatic) and 235 species in 21 areas (Tab.1 and Appendix 1). Univariate analyses were initially performed to test the significance of relationships of abundance, diversity, and richness with environmental variables. Normal distribution models were selected based on the Shapiro-Wilk test (SHAPIRO et al., 1965) for abundance data, richness and diversity, in order to investigate colinearities between variables and select more robust models. These models were adjusted to the biotic data using the Akaike criterion (AIC) (BURNHAM et al., 2004) and evaluated using generalized linear models (GLM) assuming a Poisson error distribution (CRAWLEY, 2013). They were categorized by environmental variable (latitude, longitude, climatic data, and physical-chemical composition of the soil) to facilitate the interpretation of the relations, opting for concurrent models with the smallest set of predictor variables and maximum explanatory values.

Analysis of Spatial Variables

In order to investigate the contribution of diversity in spatial scales and substitution of species along the areas to the regional diversity, additive partition analysis (APA) (CRIST et al., 2003) were performed, based on species richness and the Shannon’s diversity index. In this way, α-diversity represents the average number of woody species per area (local scale), β-diversity represents the mean difference (turnover) of species between areas, and γ-diversity represents the total number of species in the 21 areas (regional scale). The observed diversity values were contrasted with expected values in a null model ($\alpha = 50\%$ and $\beta = 50\%$) by means of statistical significance tests with 999 simulations in relation to total abundance.

Beta diversity turnover was investigated through differences in species composition and abundance among the sampled areas using the Sørensen (qualitative) and Bray-Curtis (quantitative) similarity indices (BRAY et al., 1957). β-diversity was decomposed using the indices of (di)ssimilarity of multiple sites of Sørensen ($\beta_{SØR}$) and Simpson (β_{SIM}), in order to identify the process that predominates in this spatial scale (turnover or nestedness) and replacement (β_{SIM}) and/or loss (β_{NES}) of species in this spatial gradient (*betapart* package) (BASELGA, 2010). The significance of Pearson correlations was calculated using Mantel permutation tests.

Analyses of similarity (ANOSIM) were applied on incidence data to evaluate the differentiation and interdependence of the species composition of the sites, and to point out the main shared and exclusive species that contributed to the segregation of groups. Non-metric multidimensional scaling (NMDS) was used to explore differences in species composition between communities, as well as to the ordination of the structural data and environmental variables, which is useful to check the relevance of the correlation of the variables and the fitness of the models (CLARKE, 1993). Candidate models also had their variances tested on compositional data by means of a PERMANOVA and illustrated through NMDS (BASELGA, 2010).

After adjusting the data to the ordination produced, we carried out a restricted ordination by Canonical Correspondence Analysis (CCA) (BRAAK, 1986; CRAWLEY, 2013) with the 12 most significant variables so as to detect relations between the variables and the composition of species occurring in the areas and infer the spatial heterogeneity of these communities. The significance of the CCA was verified using the ANOVA test with 999 permutations, considering $p < 0.05$. Rare species were kept in the CCA because they are considered to indicate relevant characteristics to the understanding of savanna ecosystems (BOCARD et al., 2011). The dataset studied through cluster analysis, using the Sørensen index to measure dissimilarity and the Ward's hierarchical method for agglomerative clustering. This index and clustering method proved to be the most valid (cophenetic correlation = 0.87). All analyses were performed in the Environment for Statistical R (R CORE TEAM, 2019) mainly using the *vegan* (OKSANEN et al., 2019), as well as RT4Bio, psych, AICcmodavg, MuMIn and betapart packages (BASELGA et al., 2018).

RESULTS AND DISCUSSION

Intra-habitat α-diversity and Structural Variations

The areas represent savannas of the following types: typical cerrado, sparse cerrado, dense cerrado, rocky cerrado and two samples of typical coastal cerrado (Table 1). The sparsest fragments (Maracanã and Vigia in coastal Pará, and Redenção and Bom Jesus in southwest Piauí) apparently responded to a greater predominance of anthropic disturbances. They are yellow latosols and quartzarenic neosols lands, with intense arboreal thinning and occupation by herbaceous plants. The waste disposal, fires, selective extraction, and logging have been clear causes of disturbances. In the 21 areas, 235 woody species distributed in 52 families, 154 genera and 30,835 individuals were registered. *Qualea grandiflora* and *Q. parviflora* had the greater number of individuals (3,713 and 3,172, respectively). *Byrsonima crassifolia* had 2,221 individuals and occurred in all areas. A total of 103 species were recorded in a single area and 42 of these were considered rare (in the sampling), with one occurrence each.

The Fabaceae, Malpighiaceae and Myrtaceae were represented in all areas. Another 20 families comprised the flora of more than 50% of the sampled areas, such as Vochysiaceae, Anacardiaceae, Apocynaceae, Bignoniaceae, Dilleniaceae and Sapotaceae. Seven families occurred in a single area; all were native and were present in both forest and savanoid vegetation. On the other hand, there were taxa, in the different taxonomic levels, restricted to the disjunct or marginal savannas. Hypericaceae, Lacistemataceae, Proteaceae and Symplocaceae occurred only in DS, and Cactaceae, Caryocaraceae, Celastraceae, Combretaceae, Ebenaceae, Lythraceae, Simaroubaceae, among others, which occurred only in MS. The richest families (Fabaceae, 51 species; Malpighiaceae, 13; Myrtaceae, 15) and genera (*Byrsonima*, 7; *Myrcia* and *Ouratea* (6, each); *Annona*, *Mimosa*, and *Mouriri* (5).

The structural parameters presented variable limits, evidencing a longitudinal (West-East) structural gradient. In the disjunct Amazonian savannas, the density (N: 630 ~ 979 ind.ha^{-1}), basal area (AB: 6.82 ~ 10.60 m².ha^{-1}), species diversity (H': 1.19 ~ 2.04 nats.indiv^{-1}) and species richness (S: 10 ~ 30, *exception Cachoeira do Arari-PA with 37 species) were lower than in the marginal savannas of Maranhão (N: 1114~1481, AB: 6.64~20.45, H': 2.29~3.07, S: 32~56) and Piauí (N: 1399~2996, AB: 15.65~27.60, H': 2.34~3.26, S: 38~70) with growing increases of these metrics towards the east, despite some peak trends in the middle of the gradient (Figure 2). The same was observed in the dominance (C) and evenness (J') of the communities, with greater diversity in the central-north areas of Piauí and Maranhão and smaller in coastal Pará. However, it is observed that the increase of these indices in mesoregion Marajó, northeast Pará and in the savanna complex of Amapá was mainly due to the high number of species with little or rare occurrence and the number of hyperdominant individuals per species (Figure 2).

Mean stem height, diameter and volume were quite different between the areas, exhibitingindividuals with many successional stages of the that independ on the physiognomic classification, although they correspond to natural landscapes under low anthropic impact. East Maranhão presented the highest mean (5.9 m) and highest SDGL (18.7 cm). Coastal Maranhão had means below 1.50 m and SDGL less than 9.5 cm; however, the lowest SDGL values were recorded in more open areas such as coastal Pará (5.65 cm) and southwest Piauí (5.85cm).

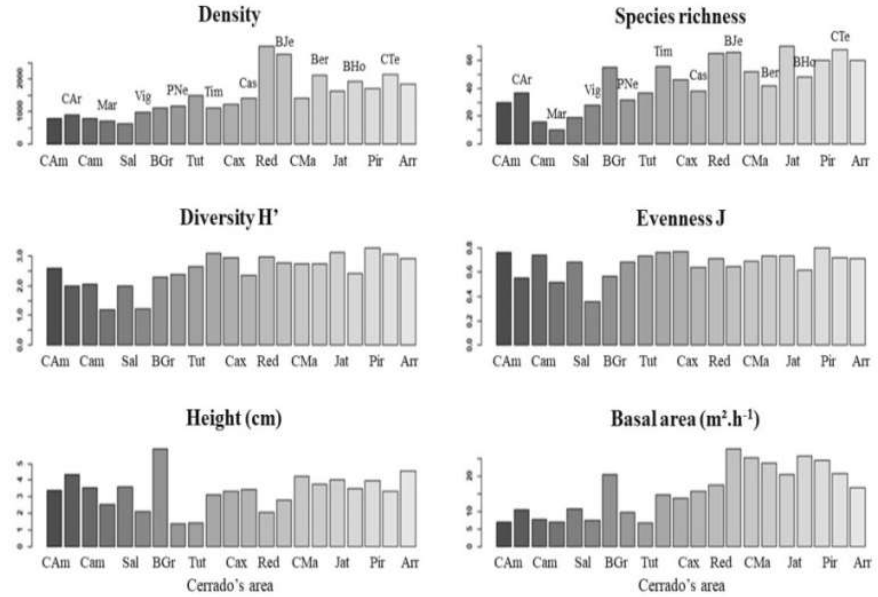

Figure 2: Density (total abundance), total species richness, species diversity (Shannon-H' index) and evenness (Pielou-J index), mean height (cm) and total basal area of woody species in the Northern Brazilian Cerrado. CAm = Complexo Amapá (AP), CAr = Cachoeira do Arari (PA), Cam = Cametá (PA), Mar = Maracanã (PA), Sal = Salvaterra (PA), Vig = Vigia (PA), BGr = Barão de Grajaú (MA), PNe = Paulino Neves (MA), Tut = Tutoia (MA), Tim = Timon (MA), Cax = Caxias (MA), Cas = Castelo do Piauí (PI), Red = Redenção (PI), BJe = Bom Jesus (PI), CMa = Campo Maior (PI), Ber = Bertolínea (PI), Jat = Jatobá (PI), BHo = Boa Hora (PI), Pir = Piracuruca (PI), CTe = Cocal de Telha (PI), Arr = Arraial (PI). Gray gradient represents the spatial gradient west east.

Table 1: Location (Latitude - Lat, Longitude - Long), elevation (Alt), structural parameters of the vegetation (abundance - N, richness - S, basal area - BA, mean height - HT), diversity (H'), evenness (J'), exclusive (Exc) and rare (Rar) species (Sp) by sampling, physiognomy of Cerrado *sensu stricto*, and mean annual precipitation (Prec) (2005 - 2017) in the six disjunct samples and fifteen marginal samples of the Northern Brazilian Cerrado.

Areas	Lat (N/S)	Long (W)	Alt (m)	N	S	BA (m^2ha^{-1})	HT (m)	H'	J'	Sp Exc/Rar	Physiognomy (Cerrado *s.s.*)	Prec (mm)
Complexo Amapá/AP	0º0'N	29º19'	16-81	787	30	6.951	3.39	2.57	0.76	7/3	Typical	211.3
Cachoeira do Arari/PA	0º54'S	48º40'	3-28	887	37	10.370	4.34	2.00	0.55	12/12	Typical	224.5
Cametá/PA	2º10'S	49º34'	6-16	784	16	7.651	3.56	2.04	0.74	0/1	Typical	217.4
Maracanã/PA	0º43'S	47º31'	26	704	10	6.821	2.52	1.19	0.52	1/2	Sparse	183.2
Salvaterra/PA	0º51'S	48º32'	10-22	630	19	10.599	3.58	2.00	0.68	2/5	Typical	224.5
Vigia/PA	0º48'S	48º05'	7-20	979	28	7.374	2.10	1.21	0.36	14/17	Sparse	224.5
Barão de Grajaú/MA	6°43'S	43°07'	130	1125	55	20.446	5.88	2.29	0.57	6/12	Dense	82.6
Paulino Neves/MA	2º46'S	42º29'	4-7	1177	32	9.693	1.38	2.36	0.68	1/8	Typical coastal	103.2
Tutóia/MA	2º46'S	42º22'	10-20	1481	37	6.641	1.42	2.64	0.73	2/3	Typical coastal	103.2
Timon/MA	5º04'S	42º52'	71-100	1114	56	14.672	3.12	3.07	0.76	6/5	Typical	117.6
Caxias/MA	4º57'S	43º07'	110-120	1227	46	13.722	3.36	2.93	0.77	3/1	Typical	117.6
Castelo do Piauí/PI	5º19'S	41º31'	170	1410	38	15.650	3.46	2.34	0.64	4/6	Rocky	52.2
Redenção do Piauí/PI	9º17'S	44º38'	560	2996	65	17.509	2.05	2.97	0.71	9/8	Sparse	81.9
Bom Jesus/PI	9º17'S	44º34'	350	2762	66	27.601	2.81	2.74	0.65	5/11	Sparse	81.9
Campo Maior/PI	4º43'S	41º55'	114-123	1399	52	25.069	4.24	2.71	0.69	4/14	Typical	100.7
Bertolínea/PI	7º36'S	43º57'	308-370	2111	42	23.707	3.74	2.72	0.73	2/4	Typical	86.1
Jatobá do Piauí/PI	4º42'S	41º53'	120-210	1630	70	20.380	4.03	3.12	0.73	7/16	Typical	118.5

Boa Hora/PI	4º22’S	42º07’	106-129	1913	48	25.750	3.49	2.40	0.62	4/9	Typical	118.5
Piracuruca/PI	4º04’S	41º30’	170-237	1718	60	24.491	3.98	3.26	0.80	4/9	Typical	110.9
Cocal de Telha/PI	4º31’S	41º58’	106-166	2155	68	20.527	3.32	3.05	0.72	4/18	Typical	118.5
Arraial/PI	6º25’S	42º25’	168-215	1846	60	16.563	4.55	2.90	0.71	6/15	Typical	82.6

β-Diversity in the Northern Cerrados

Composition varied substantially across the spatial gradient. The additive partitioning of total species richness differ α and β being statistically divergent from the expected in the null model. β-diversity accounted for 82% and α-diversity 18% of γ-diversity (total richness of woody species investigated). This revealed that γ-diversity was almost completely driven by the components β2 (85% - turnover) and β1 (4% - nesting).

The values for the local species (α1) were lower than expected by chance. In turn, the substitution of species from one area to the other (β1) was higher than expected by chance. Therefore, the differences in diversity were mainly caused by turnover of species, once that 90% of their renewal is due to total β- diversity ($\beta_{SØR}$ = 0.896), as seen in the decomposition of β-diversity, in which the representativeness of the processes of turnover (69.7% of beta diversity, represented by β_{SIM} = 0.85) and nesting (3.28%, β_{NES} = 0.04) was calculated. $\beta_{SØR}$ was equal to 0.89, and the nesting process explained 30.3% (Figure 3).

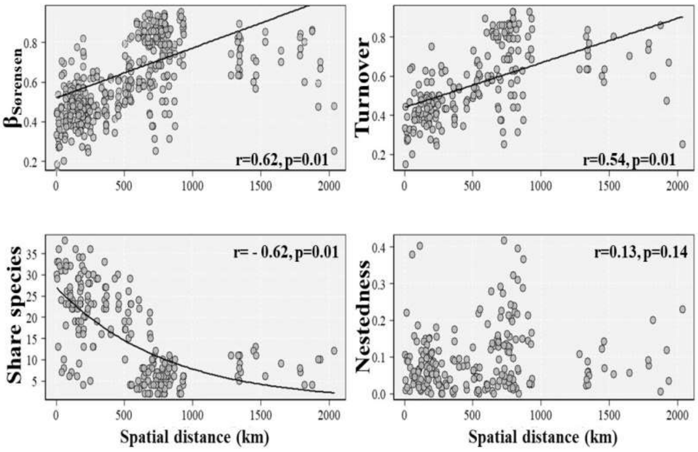

Figure 3: Relationship between spatial distance of species and dissimilarity of diversity ($\beta_{Sørensen}$ = total beta diversity; Turnover = replacement of species; Shared species = number of shared species; Nestedness = disaggregation of assemblages with species lost in the nesting process).

The lower turnover (β_{SIM} = 14%) and total β-diversity ($\beta_{SØR}$ = 18%) occurred in the coastal areas. The highest dissimilarity ($\beta_{SØR}$ = 95%) occurred between mesoregion Marajó (PA) and southwest Piauí (PI), and the highest β_{SIM} (92%) occurred between coastal amazon (PA), southwest Piauí and Castelo, in Piauí, indicating them as areas with more distinct assemblages. The highest nested diversity (β_{NES} = 41%) occurred between northeast Pará and eastern Maranhão and 10 areas showed no subtraction in their biota by nesting (β_{NES} = 0%). Despite the marked spatial turnover, there was a proportion of shared species (least 11 areas shared more than 30 species), suggesting a strong relation between the vegetation. On the other hand, different areas on the coast Pará shared only two species. This leads us to believe that the variation in turnover is more related to the connectivity of floras than to spatial proximity.

Spatial inferences of the species richness and geographic distance of the areas based on Pearson correlations (r) and significance (p) were assessed from Mantel test showed a direct relationship of total beta diversity ($r = 0.6193$, $p = 0.01$) and of the turnover subcomponent ($r = 0.5403$, $p = 0.01$) with spatial distance, since the number of shared species decreased with the distance of the samples. The subcomponent of disaggregation of assemblages with species lost in the nesting process ($r = 0.127$, $p = 0.144$), this had no significant relation through this spatial scale (Figure 4).

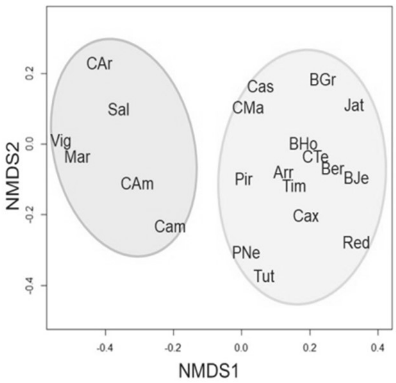

Figure 4: NMDS biplot of areas (n=21) indicating clustering and dissimilarity in the cluster analysis of the Brazilian Northern Cerrado.

The dissimilarity, based on richness diversity (Sørensen index) and abundance (Bray-Curtis index), followed by ordination and cluster analyses, reinforced the existence of discontinuous a composition in the communities, forming of two large floras: disjunct patches of cerrado pre-Amazonian (Pará and Amapá) and the component of the marginal cerrados (Maranhão and Piauí), with floristic subgroups. The minimum dissimilarity was 0.18 and the maximum 0.99 (Figure 5).

The floristic composition indicated significant diferences through the vegetative gradient. The independence between the areas was confirmed by the ANOSIM similarity analysis ($r = 0.841$, $P < 0.001$), despite the confirmation of a spatially structured ordination. It can be inferred that despite the spatial strong influence on the floras, they are independent ecological systems. The ordination represented in the dispersion plots of abundance and composition data using the NMDS method (Figure 5) showed the spatial formation of phytogeographic patterns in the areas and highlighted the segregation of two larger groups: mesic savannas (disjunct phytophysiognomies - DS) and xeric ones (marginal phytophysiognomies - MS) (Figure 6). Dissimilarity between DS assemblages was observed, which were sub-grouped in three distinct "areal" communities. Other significant predictors for the differentiation of diversity were pointed out in the canonical correspondence analysis, as presented below.

The marginal savannas, in turn, subdivided into two other subgroups, showing a floristic connection maintained between the areas of the northeastern coast and a greater homogeneity between these marginal areas. The grouped units of Tutoia and Paulino Neves, in the state of Maranhão, and the isolation of Castelo do Piauí-PI stood out, because they were grouped but differed from the rest of the grouping (Figure 6).

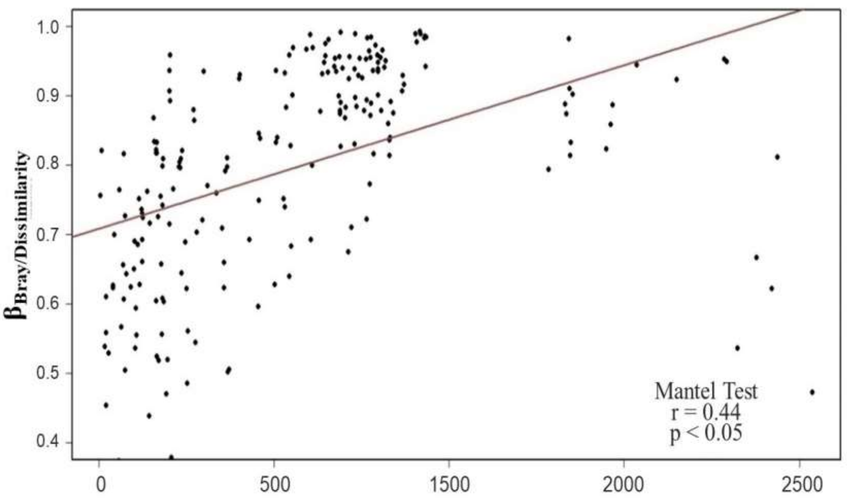

Figure 5: Relationship between spatial distance and species dissimilarity in the Mantel test showing significant spatial dependence between species of the Brazilian Northern Cerrado.

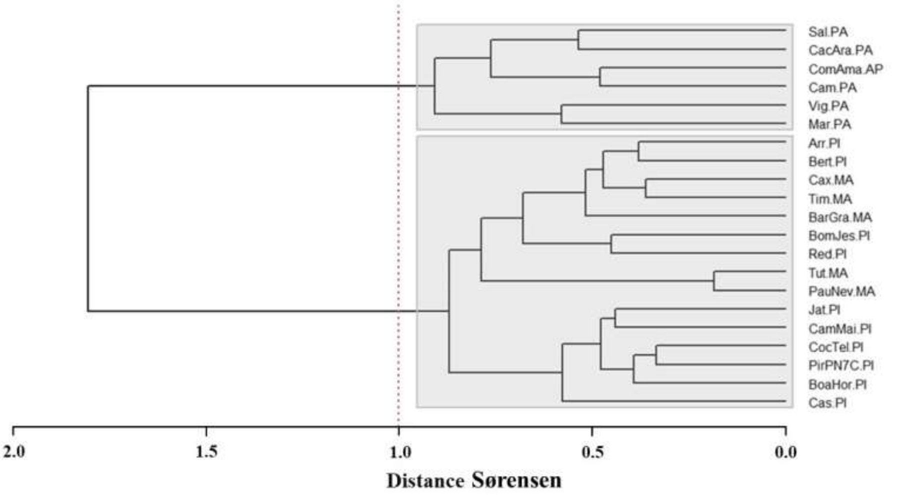

Figure 6: Dendrogram of the 21 woody communities of the Northern Brazilian Cerrado using Ward's hierarchical method. The gray areas represent the groups separated at value 1 of Sorensen distance represented by line: disjunct savannas (DS) in the upper cluster and marginal savannas (MS) in the lower cluster.

All the marginal assemblages presented exclusive species. Regarding the individual contribution to the general dissimilarity, the species that stood out in the Amazonian communities were *Annona paludosa, Annona sericea, Casearia arborea, Chloroleucon acacioides, Chrysophyllum sparsiflorum, Ficus guianensis, Guatteria schomburgkiana, Matayba arborescens, Miconia albicans, Psidium guineense, Sapium marmieri, Vachellia farnesiana*. In coastal floras, there was only *Manilkara zapota* as differential. In Southwest Piauí, nine species were exclusive (*Banisteriopsis gardneriana, Dioclea virgata, Jacaranda jasminoides, Myrcia multiflora, Ouratea oleifolia, Pterocarpus* sp., *Pyrostegia venusta, Styrax pohlii* and *Waltheria indica*).

Environmental hypothesis was tested to understand the savannas ecological gradient of diversity and structure. As expected differences in the abiotic variables affected the physiognomy and floristic representation of these communities. It is noteworthy that every environmental factor has a relevant influence on each individual, but some are representatively colinear while others have more explanatory power. Thus, two topographic variables (mean elevation and spatial clustering of savannas), two climatic variables (thermal amplitude and precipitation), two physical aspects (sand and silt), and seven chemical variables (pH in the water, Al, Cu, Fe, Ca and saturation by base) of the soil were statistically important in the selection of models in a differentiated way for abundance, richness and diversity (Tables 2 and 3).

Table 2: Concurrent models selected by empirical evidence (Δ ≤ 2) that predict with less uncertainty the abundance, richness, and diversity of woody communities in an environmental gradient in the Northern Brazilian Cerrado. Explanatory variables include soil elements (Cu: copper, Fe: iron, P: phosphorus, silt, Ca: calcium, sand, Al: aluminum, pH in water, saturation by base - Sat), climatic variables (thermal amplitude - TA, precipitation - Prec), topographic variables (mean elevation - Alt), and savanna phytophysiognomies (phyto).

Model *(error = Poisson)*	df	LogLik	AIC$_c$	Δ	Weight
y = woody abundance					
Cu/Fe/P/AT/Silt/Alt	7	-138.11	298.8	0.00	0.06
Ca/Cu/Fe/AT/Sand/Alt	8	-135.79	299.5	0.75	0.04
Ca/Cu/Fe/Sand/Alt/Phyto	8	-135.91	299.8	0.99	0.04
Fe/AT/Alt	5	-143.22	300.4	1.60	0.03
AT/Alt	4	-145.09	300.6	1.84	0.02
Ca/Cu/Fe/AT/Silte/Alt	8	-136.53	301.0	2.22	0.02
y = woody richness					
Prec/Alt/Phyto	5	-70.88	155.7	0.00	0.03
Al/Phyto	4	-72.70	155.9	0.15	0.03
Al/pH/Phyto	5	-71.05	156.1	0.35	0.03
pH/Prec/AT/Alt/Phyto	7	-66.84	156.2	0.54	0.03
Prec/AT/Alt/Phyto	6	-69.24	156.49	0.73	0.02
pH/Prec/Alt/Phyto	6	-69.54	157.0	1.32	0.02
Al/Sand/Phyto	5	-71.62	157.2	1.49	0.02
Al/Alt/Phyto	5	-71.70	157.40	1.65	0.01
Al/Prec/Alt/Phyto	6	-69.81	157.61	1.86	0.01
pH/Phyto	4	-73.63	157.76	2.01	0.01
y =woody diversity					
Fe/Sat/Prec/Sand/Phyto	7	2.92	16.78	0.00	0.08
Fe/Sat/Prec/Sand/Alt/Phyto	8	4.84	18.32	1.54	0.04
Fe/Sat/Sand/Phyto	6	-0.53	19.07	2.29	0.03

Table 3: Permutational Multivariate Analysis of Variance in the Bray-Curtis distance of the composition sampled in the Northern Brazilian Cerrado, verified by group of environmental drivers.

Climate Variables	df	SS	MS	F	R2	P
Precipitation	1	1.5176	1.51762	6.5047	0.23103	0.001 ***
Humidity	1	0.4544	0.45437	1.9475	0.06917	0.044 *
Maximum temperature	1	0.5318	0.53179	2.2793	0.08096	0.019 *
Thermal amplitude	1	0.3322	0.33218	1.4238	0.05057	0.124
Residual	16	3.7330	0.23331		0.56828	
Topographic variables						
Mean elevation	1	0.9074	0.90737	3.6997	0.13813	0.001 ***
Savannah phytophysiognomies	1	1.3331	1.33310	5.4356	0.20294	0.001 ***
Mean elevation: Savannah phytophysiognomies	1	0.1591	0.15915	0.6489	0.02423	0.844
Residual	17	4.1693	0.24525		0.68502	
Physical edaphic variables						
Coarse sand	1	0.9995	3.5538	3.5538	0.15215	0.001 ***
Fine Sand	1	0.2859	0.28592	1.0166	0.04353	0.373
Silt	1	0.3241	0.32414	1.1525	0.04934	0.256
Clay	1	0.4596	0.45959	1.6342	0.06996	0.094 .
Residual	16	4.4998	0.28124		0.68502	
Chemical Variables						
Cu	1	0.6850	0.68504	2.6196	0.10428	0.012 *
Organic C	1	0.5546	0.55455	2.1206	0.08442	0.028 *
Saturation (V%)	1	0.4133	0.41333	1.5806	0.06292	0.090 .
Zn	1	0.3262	0.32619	1.2473	0.04966	0.214
Na	1	0.4772	0.47717	1.8247	0.07264	0.044 *
K	1	0.3712	0.37121	1.4195	0.05651	0.130
Al	1	0.2697	0.26971	1.0314	0.04106	0.381
P	1	0.3336	0.33364	1.2758	0.05079	0.187
Residual	12	3.1381	0.26151		0.47772	
Total	**20**	**6.5689**			**1.00000**	

* P < 0.05, ** P < 0.01, *** P < 0.001

The environmental predictors that most influenced the species composition and abundance patterns in the northern savannas were precipitation (Prec: F=7.69, P=0.001), thermal amplitude (TA: F=3.09, P=0.003), elevation (Alt: F=1.85, P=0.045), latitudinal-longitudinal spatialization of the areas (phyto: F=2.28, P=0.023), and aluminum content (Al: F=1.61, P=0.088).

The eigenvalues of the first two CCA axes were 0.69 (axis 1) and 0.56 (axis 2) and explained 14.4% and 11.6%, respectively, of the total variance. The residual fraction of variation was 74% (Tab.4; Figure 7). These eigen values, relatively high for the two axes, indicated a marked gradient, with a wide variation and high species turnover, as verified in the partitioned variation. On the other hand, the small eigenvalues of soil attributes indicated that few areas stood out by the presence of an element, such as Al, since the concentrations of elements such as Ca and Mg did not show a significant variation.

The highest correlations between the environmental variables and the first two axes of the ordination showed that the variables that correlated most strongly and positively with the first axis were TA, Fe, Alt, and negatively with Cu, Precipitation and sand, whereas the second axis was related more strongly and positively with Sat.V, pH, silt, Ca and negatively with Al and Alt. Thus, the ordination led to infer a variation of salinity, texture, and climate in the first radius and fertility in the second (Table 4 and Figure 7).

Table 4: Results of the Canonical Correspondence Analysis (CCA) of the abundance of 235 woody species in 21 samples from the Northern Brazilian Cerrado, showing correlation values between the environmental variables and the first and second axes.

Variables	Axis 1	Axis 2	R2	P
Elevation	0.795	-0.605	0.523	0.018 *
Precipitation	-0.998	-0.057	0.787	0.001 ***
Thermal amplitude	0.988	-0.152	0.807	0.001 ***
Total sand	-0.995	0.094	0.082	0.574
Silt	-0.276	0.960	0.171	0.212
Cu	-1.000	-0.001	0.211	0.141
Fe	0.932	0.359	0.160	0.275
Ca	0.341	0.939	0.051	0.527
Al	-0.212	-0.977	0.284	0.085 .
Saturation V (%)	-0.115	0.993	0.043	0.724
pH (H_2O)	-0.252	0.967	0.023	0.792
Physiognomy/environment (phyto)			0.454	0.001 ***
DS	-2.191	-0.316		
MS	0.406	0.058		
Eigenvalue	0.696	0.561		
Explained variance (%)	0.144	0.116		
Cumulative variance (%)	14	26		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

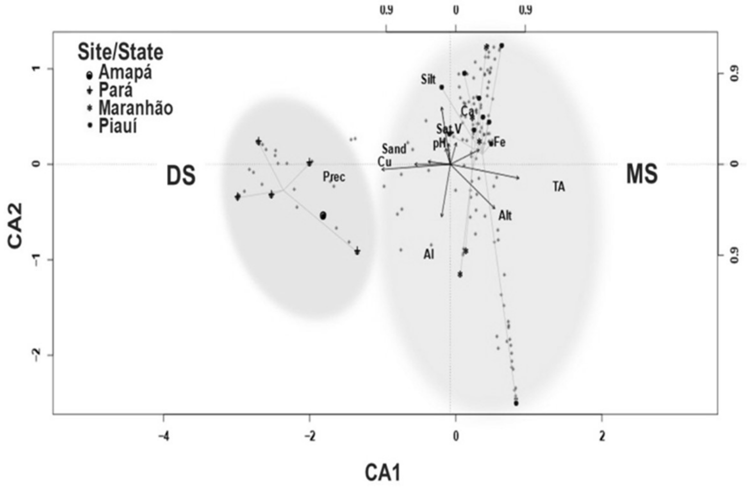

Figure 7: Canonical Correspondence Analysis (CCA) of the distribution of abundance of 235 woody species in 21 savanna areas in an environmental gradient in the Northern Brazilian Cerrado and their correlations with precipitation (Prec), elevation (Alt), thermal amplitude (TA), sand (Sand), soil pH in water (pH), aluminum (Al), copper (Cu), iron (Fe), calcium (Ca), saturation by base (Sat.V), and physiognomic aspects (DS: disjunct cerrados, MS: marginal cerrados).

Most of the communities (mainly those of MS) were positively correlated with Fe and Ca, and negatively with Al, forming a clustering, in terms of abundance of plants, in the axis 2 and comprising most of the areas of Piauí (12) and Maranhão (3) (Figure 7). In turn, the Amazonian samples (DS) were positively correlated with precipitation (Prec), Cu, sand (Sand) and Al, and negatively correlated with elevation (Alt) and thermal amplitude (TA); they were ordered in a small group on axis 1, including disjunct floras from Pará and Amapá, strongly influenced by higher precipitation, high percentage of total sand and higher concentrations of Cu and Al, associated with lower thermal amplitudes and low elevations.

Regarding altitudinal variations, they had an important effect, in general terms. Elevation is fundamental for the understanding of variations in the floristic composition. The effect was, however, indirect because the areas with lower elevations also had lower thermal amplitudes, the higher precipitation rates, and higher saturation of elements such as Cu, related to the white sand banks of Amazonian and coastal fragments whose soils are sandy, poor and leached, and the vegetative cover shows a marked scleromorphic structure.

Only two samples in the coastal cerrado of Maranhão and one sample in a mountain range in southwest Piauí were positively correlated with elevation (Alt) and thermal amplitude (TA) and negatively correlated with soil pH in water (pH), saturation by base (Sat.V), and silt (Silt). These were more dispersed and represent the extreme of the gradients obtained for the analyzed variables, such as the maximum amplitude of elevation, thermal and humidity variation, potential acidity (H + Al), Al and Fe contents, and soil pH.

As expected in an ecotonal gradient, the structure of the communities responded significantly to climatic and spatial drivers and these prevailed over the other environmental descriptors in the joint analysis of the variables, even after weighting. Despite the lower correlation in the CCA method, some edaphic variables also had an influence on the vegetation, as pointed out in previous analyses of variance, although their effects were not homogeneous along the gradient.

Intra-habitat α-diversity and Structural Variations

It is a historical cycle of anthropogenic disturbances and changes in environmental conditions that lead to the ecological inheritance of local niche change (WERNECK et al., 2012; MORANDI et al., 2016; ALBUQUERQUE et al., 2019), which cause mortality, thinning and secondary degradation in the region's savannas (AQUINO et al., 2007; ASSIS et al., 2011).

At the same time, the coastal areas presented floras and physiognomies of typical cerrado, but with inferior aspects (diversity, height and diameter) in comparison to the others, which was due to the effects of climate and low altitude (5-15 m). These areas are surrounded by coastal sandbanks of the state of Maranhão and mainly characterized by highly dystrophic conditions from quartz sandy and markedly drained soils, which have low natural fertility and offer a low reserve of nutrients for the plants (EMBRAPA 2006; SOUSA et al., 2008; SANTOS et al., 2017). The possibility that these physiognomic characteristics have been worsened by long-term and secondary effects of fires previous to this research is not ruled out, because they increase the flammability of the cerrado and its dependence from it (SILVA et al., 2013; SOARES et al., 2015; DIONIZIO et al., 2018; SANTOS et al., 2020).

The presence of rare species is common in tropical environments because populations occur with different abundances (COUTINHO et al., 2019; SANTOS et al., 2020). Rare species were kept in the analyses to infer the presence of "areal floras” and conservation in savannas, since according to Assis et al. (2011) and Baudena et al. (2015), most species occur in small populations. Marginal savannas had the richest families and genera. In the disjunct savannas, the richness taxonomic was not significantly different along the areas.

There was a wide variation in species richness (from 10 species in coastal Pará to 70 in eastern Piauí) and in other structural characteristics. These values are below the range commonly found in the central cerrado (between 55 and 97 species) (FELFILI et al., 2004), but within previously reported ranges for marginal areas of the biome (MIRANDA et al., 2002; COUTINHO et al., 2019, SANTOS et al., 2020). The woody flora of the disjunct savannas with lower richness presented species indicators of transition to the Amazonian domain and a typical flora of Amazonian savannas. The composition was different from that of the central cerrado, as predicted by Sanaiotti et al. (2002); Miranda et al. (2002) and Feitosa et al. (2016).

Contrary to the expectations, the geographical position of the pre-Amazonian DS did not contribute to increase the richness and diversity of species, contrary to the findings of Felfili et al. (2004) in marginal savannas of Mato Grosso in transition with forests in Água Boa (MT). Based on the afore mentioned parameters, studies point out to a pattern observed in the central cerrados where only about 10 species respond to more than 50% of the structural aspects of these communities (FELFILI et al., 2004). In the areas investigated, this margin was smaller, while at most seven species responded to the general aspect of the communities, with few dominant species remaining. This may be related to ecological differences such as adaptation to higher thermal amplitudes in lower latitudes and elevations, limited soil fertility and disturbances, considering that most of the areas are not protected, although they consisted of natural vegetation under low anthropogenic impact.

β-Diversity in the Northern Cerrados

According to the analysis, the average richness per area (α1) was 42 species and the average variation was 192 species, indicating substantial turnover of species across communities and many species had limited local distributions, composing "areais flora” (COUTINHO et al., 2019; SANTOS et al., 2020). As detected in other savannas (MEWS et al., 2014), the assemblages indicates complementary but not equivalent floras, regarding the individualization of the synareal assemblages as floristic sub-centers, or districts, with abiotic conditions confluent with their own flora (COUTINHO et al., 2019; SANTOS et al., 2020). This low floristic similarity and high species turnover reinforces typical floras of each area (areal floras), confirming and amplifying the communications on the marginal and disjunct savannas.

According to the Refuge Theory, savannas and forests expanded and retracted during the last glacial period, or last inter-glacial period (BUENO et al., 2016), as a consequence of the climatic dynamics during the Quaternary (HAFFER et al., 2002; MARIMON et al., 2014). The current distribution patterns of Neotropical savannas are related to a set of environmental (climatic, biotic and pedological) variations linked to these events (PENNINGTON et al., 2000; SANAIOTTI et al., 2002; BUENO et al., 2016).

A strong literary base reinforces the theory that the savannas reached wide extensions during the mid-Holocene, and thus the northern portions of savanna consisted in continuous vegetation through the country. However, as the climate became more humid and hotter, they would have retreated due to the expansion of forests and remained connected only by narrow stretches. Following the main savanna corridors proposed by Silva et al. (2002), it is possible that the 21 areas investigated were interconnected by the coastal corridor, a fact that would explain the sharing of 10% of the species between the areas. However, based on the high beta diversity recorded, vicariance and/or environmental effects strongly influenced gene disruption among the plant populations of these communities.

This corroborates the ecotonal hypothesis that adjacent phytogeographical domains influence differently the northern Cerrado region. It also extrapolates the premise of Castro et al. (1999) "areais flora", which respond to latitudinal patterns associated with high spatial heterogeneity. In this sense, when Vieira et al. (2019) and Oliveira et al. (2016) evaluated local endemic areas within the Cerrado of the Northeast, regional differences were detected with endemic areas of the coast, north and southwest.

Diverging from the core region of Brazilian savannas (MEWS et al*.*, 2016), climatic and spatial factors were clearly more important in the explanation of the distribution of species and physiognomic types than edaphic factors, although the former are dependent from each other and synergistic. This confirmed the predicted predominance of the climatic gradient, although not discrete, as it can be inferred from the differences in the direction of environmental drivers (arrows). Similarly, in the transition from the Amazonia to the Cerrado, Dionizio et al. (2018) found through modeling a heterogeneity and synergy of environmental effects along the latitudinal-longitudinal gradient, especially of the climate, the limitation of phosphorus, and the occurrence of fires. Similarly, Miranda et al. (2002) showed a certain independence of edaphic factors with the phytodiversity of savannas from Roraima, except for the aluminum content in the upper layers of the soil.

Our results agree with Marimon et al. (2014) and Coutinho et al. *(*2019), who argued that the climate acts on the physicochemical conditions of the soil and, therefore, the distribution of vegetation is in a general and indirect way more related to the effects of the climate and to the synergy of the other variables in function of thermal amplitude and humidity, which are stronger factors responsible for the limiting conditions of the soil (in the upper layers). This is partially opposite to the effects detected by Neri et al. (2012), Abreu et al. (2012), Bueno et al. (2013), Dionizio et al*.* (2018) and Santos et al. (2020), who showed that in the absence of fires, nutrient limitation would outweigh the effects of climate variability on the dynamics of transitional ecosystems.

Although sharing similar environmental preferences, assemblages from the DS did not appear spatially close in the ordination, which confirms their floristic dissimilarities previously pointed out, due to their high number of rare and exclusive species. This resumes the discussion of the genesis and distribution of savannas in Amazonia, despite the fact that most have a climatic origin (HAFFER et al., 2002; COUTINHO et al., 2019; SANTOS et al., 2020).

Therefore, in order to improve research on the separation of species niches, the evaluations also pointed to the soil, silt, Cu, Fe, Ca, Al, pH and saturation base influences on the abundance, diversity and richness of species. They indirectly reflect the influence of the water regime, inseparable from the observations of Oliveira Filho et al. (1989) and Santos et al. (2020) about gradients in cerrados on sandy soils, where the soil water regime and slope, associated to topography and presence of rocks, have reflections on the variation observed in the vegetation.

After removing the collinear variables, Cu, Ca, P, pH, and total sand and silt concentrations proved to be the soil attributes that best explained the abundance of the assemblages ($p > 0.05$). The attributes with greater explanatory power over the configuration of richness were organic matter (OM), cation exchange capacity at pH 7.0 (CEC.T), saturation by base (Sat.V), pH, total sand, and silt. In the case of diversity, the most influent attributes were the same, with addition of Fe and clay.

The high concentration of Cu (ranging from 2.4 to 3.1 mg/kg in the DS and from 0.11 to 3.1 mg/kg in the MS) in the superficial layer of the soil (0-10 cm) was the individual characteristic with higher factor load (score), followed by Al (DS: 0.4-1.6 cmolc/dm^3 and MS: 0.1-1.4 cmolc/dm^3) and Fe (DS: 23.4-55.7 mg/kg and MS: 16.2-134.3 mg/kg). The high levels of these elements certainly contributed to the lack of essential nutrients and to the acidity of the soil, because of the imbalance in Ca and Mg uptake or cation leaching caused by competition for cation exchange complex sites. This fact has already been argued by Haridasan (2008); Lilienfein et al. (2001) and Santos et al. (2020), that the edaphic factor is limiting for the development of native plant species in this ecosystem, but which, on the other hand, did not prevent them from developing adaptive and coevolutionary strategies.

The soils demonstrated sandy texture, little presence of rocks (except for the rocky cerrado), strong acidity (pH 4.6-5.1 in the DS and 4.3-5.6 in the MS), and low fertility. The essential nutrients P (DS: 0.3-1.0 g/kg, MS: 0.1-1.2 g/kg), N (DS: 0.3-1.0 g/kg, MS: 0.1-1.2 g/kg), Ca (DS: 0.05-0.26 cmolc/dm^3, MS: 0.07-1.11 cmolc/dm^3), and Mg (DS: 0.12-0.25 cmolc/dm^3, MS: 0.04-0.83 cmolc/dm^3) were present in low amounts and unbalance ratios, especially in the case of the bases (Ca, Mg, K). The soils and physiognomies of DS and MS did not presente significant differences in the values of the attributes, which were very variable and irregular due to very specific interactions, possibly related to differences in Zn, Cu, Na and Al contents, in which a slight latitudinal-longitudinal gradient was observed.

These conditions occurred more strongly in the DS, and seemed to be repeated in other patches, as predicted in the savannas from Roraima by Miranda et al. (2002) and Morandi et al. (2016, 2020), where only Al levels in the superficial layers and soil texture indicated floristic and physiognomic diferences.

Soils of the northern cerrados were found to be poor in nutrients (SANAIOTTI et al., 2002; MIRANDA et al., 2002; COUTINHO et al., 2019; SANTOS et al., 2020), what was expected for neotropical savannas. However, the distal areas were more fertile than the marginal ones, with higher content of organic matter (18.7-31.0 g/kg) and N, P and Ca, although their richness and density of plants were inferior. In this case, other abiotic factors such as the rainfall regime and the unbalanced relationships between the elements (Na, Ca, Mg, P and K) possibly alter the local soil conditions regarding cation exchange capacity at pH 7.0, saturation by base, and soil pH in water. Furthermore, the high saturation of Cu (2.38-3.7 mg/kg), Zn (3.7-5.02 mg/kg) and Al occurred at more critical levels in these areas and potentially promoted changes in the absorption of essential elements by plants and may explain this variation in species performance.

CONCLUSION

It is not new that phytogeographic patterns of the northern Cerrado are different of those found in the central region. Here, the topographic and climatic drivers are confirmed as the main determinants in the modelling of the northern savannas. The edaphic aspects were subordinated to climatic variations, especially to the high rainfall regime in the region of the Amazonian savannas, and to the drought and marked thermal amplitude in the northeastern savannas. Climatic adversity, either due to excess or scarcity of precipitation or to thermal amplitude, acted on the aspects of the soil and filtered the most adapted species. In consonance with other natural aspects, this phenomenon differentiated the woody assemblages generating the disjunct and marginal savannas.

The low floristic similarity and high species turnover between the areas reinforces the theory of the areal floras (typical of each area) in the cerrados, confirming and expanding the communications on the marginal and disjunct savannas. It still reinforces the individualization of these nine synareal assemblages as floristic sub-centers with abiotic conditions confluent with their own flora and physiognomy, and also demonstrates the ecosystemic specificity of disjoint fragments ecologically resistant to forest occupation, whose origins and evolution are explained by the theory of forest refuges, requiring a more delayed reflection to correlate new information and mature discussions.

Although the lack of stable or homogeneous environmental parameters in ecological transition zones renders the understanding of these communities imprecise, the present study provides a background for further research of savanna communities in the long term, in relevant sites and types of Cerrado for the purpose of monitoring species, environmental factors, and the dynamics and ecological delimitation of species as part of the of the process of natural succession (and expansion) or suppression by anthropogenic pressures.

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