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ECOSYSTEMS

Soil-vegetation relationship in savanic formations of the Jalapão, Brazil

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Abstract: Understanding the influence of fine-scale abiotic filters on plant communities can provide important insights into floristic patterns of the Brazilian Cerrado. We aimed to evaluate the interactions of the soil and the plant community composition with their distribution in different sandy environments of Brazilian Cerrado, the Jalapão region. Eight environments were sampled, each with ten plots of 20 × 50 m. All woody individuals presenting circumference at soil height ≥ 10 cm were sampled. Subplots of 5 × 15 m were demarcated, where woody individuals with a circumference at soil height ≥ 5 and < 10 cm were sampled. Subplots of 2 × 2 m were also demarcated to sample herbaceous individuals. Soil samples varying from 0 to 20 cm of depth were collected for each plot (20 × 50 m). Overall, 20000 individuals that belong to 338 species and 76 families were sampled. The dominant family was Fabaceae. There were significant differences among the environments regarding species richness and soil. The analyzed soils are extremely poor and with a tendency to sandy texture, small chemical and/or physical variations imply differences in the distribution of vegetation. Our study revealed abiotic filters exerted crucial fine-scale effects on plant community in the Jalapão region.

Key words: Cerrado, community composition, sandstone, soil filters.

INTRODUCTION

Understanding the influence of the environmental filters on the composition, structure and distribution of plant communities is key to predicting how the dynamics of biodiversity will impact on ecosystem processes (Loreau et al. 2001, Bello et al. 2013). At a local scale, the soil's physical-chemical properties are among the main determinants of the spatial structure of tropical plant communities (Keddy 1992, Lortie et al. 2004, Peña-Claros et al. 2012, Rodrigues et al. 2019, Campos et al. 2021). Several studies in worldwide savanna point to the soil as a driver of local scale vegetation distribution (Neri et al. 2013, Lehmann et al. 2014, Bueno et al. 2017), representing one of the main physical components that influences the species diversity (Neri et al. 2013, Rodrigues et al. 2019).

The main extent of Neotropical savanna is largely found within Brazil, often termed as Cerrado (Ab'Saber 2003, Ribeiro & Walter 2008). Originally, it covered about 2 million km^2, or 22% of the national territory (Bueno et al. 2013), mainly on the Brazilian Central Plateau, under seasonal climate, with wet summer and dry winter (Ratter et al. 1997). The Brazilian Cerrado is highly heterogeneous, it includes numerous grassland and savanna formations as well as different types of forest (Eiten 1978, Ab'Saber 2003, Haidar et al. 2013). Considered the tropical savanna with the world's greatest species richness (Silva et al. 2006), the Brazilian Cerrado has more than 11000 known species (Mendonça et al. 2008), out of which 4400 are endemic (Myers et al. 2000). Past climate changes (Oliveira-Filho & Ratter 2002), variations in soil attributes, geomorphology, topography, fire regime and water availability are associated with a high beta diversity for vegetation (Lehmann et al. 2014, Bueno et al. 2017). Most soils of the Brazilian Cerrado are acidic, well-drained, dystrophic, deep, with low cation exchange capacity, low organic matter content, and high levels of exchangeable aluminium (Furley & Ratter 1988, Ratter et al. 1997, Haridasan 2000). According to Gottsberger & Silberbauer-Gottsberger (2006) these soil attributes determine the occurrence of the Brazilian Cerrado and its physiognomic variations. This mosaic of different phytophysiognomies may be accompanied by changes in floristic composition and community structure (Haridasan 2000, Neri et al. 2013).

Most of the research in Brazilian Cerrado areas was carried out in Ferrasols (Latossolos), mainly because they comprise the greatest extent (46%), in contrast to the Arenosols (Neossolos Quartzarênicos) with only 15.2% (Goodland 1971, Reatto et al. 1998). The vegetation of the Brazilian Cerrado shows a close dependency not only to the chemical atributes of the soil, but also to the physical ones (Neri & Camargos 2007). Sandy texture may limit the establishment and development of certain species (Abreu et al. 2012). For example, many authors recorded lower plant species richness on Arenosols, when compared to Ferrasols (Lindoso et al. 2009, Amaral et al. 2022). In Arenosols, the low amounts of clay and organic matter reduce the capacity for particle aggregation and nutrient adsorption, making the soil very susceptible to erosion and nutrient loss by leaching (Reatto et al. 1998, Spera et al. 1999). Furthermore, according to Maia et al. (2006), texture effects on plant communities mainly occur through their influence on the soil's water retention capacity, in which species in habitats with higher sand percentages experience low water availability.

Floristic and phytogeographic studies conducted in Brazilian Cerrado areas on sand soils have focused particularly on States of Piauí (Oliveira 2004, Lindoso et al. 2011), Maranhão (Medeiros et al. 2008), Bahia, Minas Gerais (Felfili & Silva Júnior 2001, Rodrigues et al. 2019), Mato Grosso (Oliveira-Filho et al. 1989) and São Paulo (Durigan et al. 2002, Teixeira et al. 2004). In the State of Tocantins, only one work was carried out in *Campo Úmido* in the Jalapão (Rezende 2007). The lack of knowledge regarding the dynamic between environmental filters and vegetation on sand soils in Brazilian Cerrado areas is remarkable. The Tocantins State is located in the most preserved portion of the Brazilian Cerrado (Sano et al. 2009) and in the zone of contact with three important Brazilian biomes (Cerrado, Caatinga, and Amazon Forest), this area becomes a relevant source of scientific information (IBGE 1992). However, few studies have been conducted on the relationships between environmental conditions (e.g. soil properties) and plant communities in the region (Lemos et al. 2013). Most studies have focused on environmental diagnosis (Brito et al. 2002, Carvalho 2009), floristic composition and vegetation structure (Santos et al. 2006, Rezende 2007, Martins et al. 2011). Information about the flora, including species composition and interactions between vegetation and edaphic factors, is scarce in the Jalapão region of Tocantins State. In this context, we aimed to evaluate the soil and the plant community composition and distribution in different sandy environments of Brazilian Cerrado, the Jalapão region.

MATERIALS AND METHODS

Study area

The study was carried out in the northeast portion of the Brazilian Cerrado, Jalapão region, Tocantins State (10°08’ - 10°36’ S and 46°24’ - 46°56’ W; Figure 1). The set of protected areas of the Jalapão is located on the eastern portion of the State of Tocantins. The region is considered the largest continuous expanse of original Brazilian Cerrado and is recognized as a priority area for biodiversity conservation (Cavalcanti & Joly 2002). Most of the vegetation is formed by savanic formations (Cerrado) with patches of veredas (wet areas). It covers three integral protection conservation units: Jalapão State Park, with 154,000 ha; Serra Geral de Tocantins Ecological Station, with 716,306 ha in the state of Tocantins; and the Parnaíba National Park, with 729,813 ha in the states of Tocantins, Piauí, Maranhão and Bahia, with limits close to the Jalapão State Park. According to Köppen’s classification, the climate is Aw - Tropical with wet summer, and presents two seasons: a dry season, from April to September, when it rains less than 10% of the annual total (±1300 mm/year); and a rainy season, from October to March (Consórcio CTE/MRS 2003).

The Jalapão region is characterized by the contact between two contrasting relief components: the elevated Serra Geral plateaus (700 - 1,000 m), and depositional plains (300 - 600 m) covered with quartzitic sands, formed by the erosion of the sandstone plateaus (locally

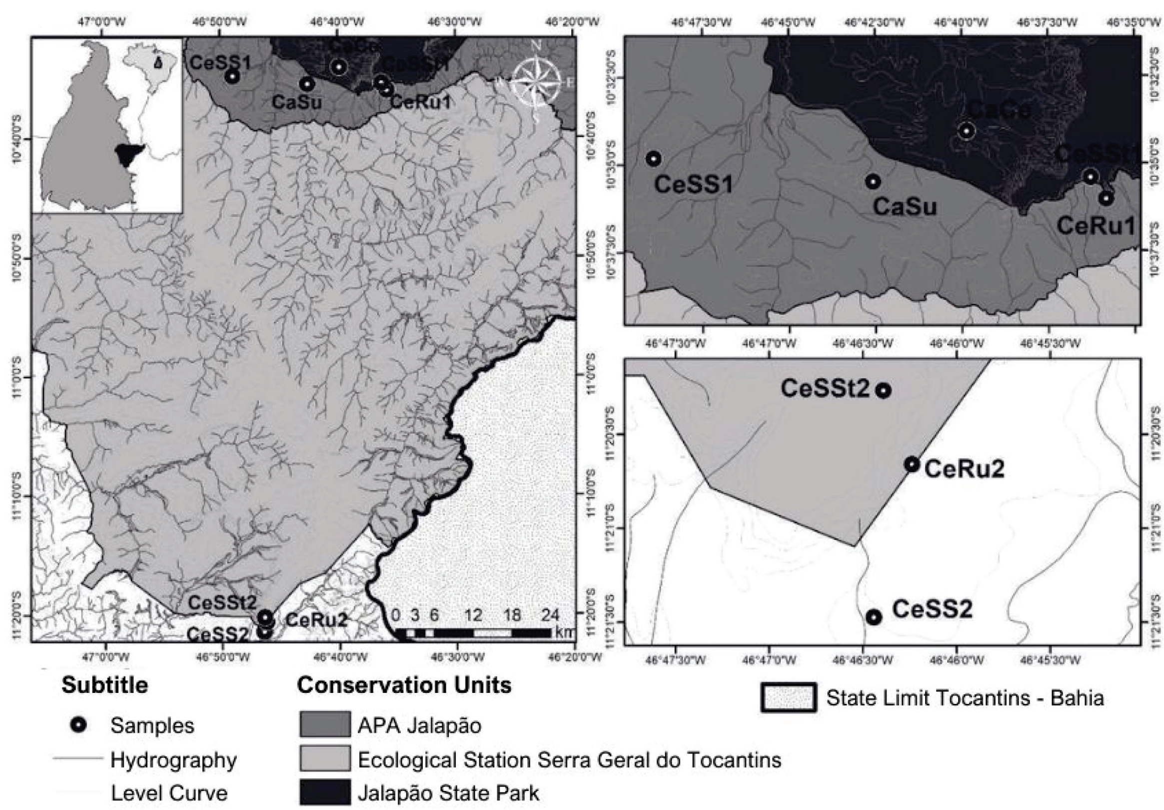

Figure 1. Study area located in the Savanic Formations of the Jalapão, state of Tocantins, Brazil. CeSS1 = Cerrado *sensu stricto*; CaSu = *Campo Sujo*; CaCe = *Campo* Cerrado; CeRu1 = Cerrado rupestrian fields in slopes; CeSSt1 = Cerrado *sensu stricto* in top of the tablelands; CeSS2 = Cerrado *sensu stricto*; CeRu2 = Cerrado rupestrian in slopes; CeSSt2 = Cerrado *sensu stricto* in top of the tablelands.

called "chapadas" or "morros testemunhos") (Ribeiro et al. 2009). These two geomorphological units are separated by steep arenitic cliffs. Arenosols, Leptsols and Ferralsols (Tocantins 2003) predominate in the region.

Selection of different environments

We performed landscape stratification on environments from the integrated evaluation of pedological and phytophysiognomy (Profiles Table in MS). Two toposequences distributed in eight environments were chosen from the Jalapão vegetation mosaic in the Brazilian Cerrado areas on the sandstone domains (Urucuia Formation) (Figure 1). The eight environments were selected according to their classification in the World Reference Base for Soil Resources (IUSS Working Group WRB 2015). Profiles for each environment were collected and described according to Santos et al. (2013).

The first toposequence is located in Serra do Espírito Santo and is divided into five areas: Cerrado *sensu stricto* (CeSS1) on the Hyperdystric Protic Arenosols and *Campo sujo* (grassland with some shrubs) (CaSu) on the Hyperdystric Rhodic Arenosols inserted in the Jalapão Environmental Protection Area; *Campo* Cerrado (grassland) (CaCe) on the Hyperdystric Rhodic Arenosols, Cerrado rupestrian fields in slopes (CeRu1) on the Hyperdystric Colluvic Akroskeletic Regosols (Arenic, Ochric) and Cerrado *sensu stricto* on top of the tablelands (CeSSt1) on the Lixic Rhodic Ferritic Ferrasols (Clayic, Hyperdystric, Ferric, Ochric) in the Jalapão State Park. The second toposequence is located in Serra da Sambaíba and it is divided in three areas: Cerrado *sensu stricto* (CeSS2) on the Hyperdystric Rhodic Arenosols, Cerrado rupestrian in slopes (CeRu2) on the Hyperdystric Leptic Regosols (Arenic, Ochric, Raptic) and Cerrado *sensu stricto* on top of the tablelands (CeSSt2) on the Rhodic Ferralic Lixisols (Arenic, Ochric, Profondic) inserted in the Serra Geral de Tocantins Ecological Station (Table I).

Vegetation sampling

We allocated ten plots of 20 × 50 m in each of the eight environments mentioned above, at least 50 m apart from each other. In these plots, all woody individuals presenting circumference at soil height (CSH) ≥ 10 cm were sampled (upper stratum) (Moro & Martins 2011). Within

Table I. General description of the environments sampled in the Savanic Formations of the Jalapão, state of Tocantins, Brazil.

ENVIRONMENTS	SOIL CLASS	RELIEF AND ALTITUDE
(CeSS1) Cerrado ***sensu stricto***	Hyperdystric Protic Arenosols	Sandy tablelands - 464 m
(CaSu) ***Campo sujo*** (grassland with some shrubs)	Hyperdystric Rhodic Arenosols	Sandy tablelands - 420 m
(CaCe) ***Campo*** Cerrado (grassland)	Hyperdystric Rhodic Arenosols	Sandy tablelands - 448 m
(CeRu1) Cerrado rupestrian fields in slopes	Hyperdystric Colluvic Akroskeletic Regosols (Arenic, Ochric)	Slope of tablelands (Serra do Espírito Santo) - 756 m
(CeSSt1) Cerrado ***sensu stricto*** in top of the tablelands	Lixic Rhodic Ferritic Ferrasols (Clayic, Hyperdystric, Ferric, Ochric)	Top of the tablelands (Serra do Espírito Santo) - 788 m
(CeSS2) Cerrado ***sensu stricto***	Hyperdystric Rhodic Arenosols	Sandy tablelands - 576 m
(CeRu2) Cerrado rupestrian in slopes	Hyperdystric Leptic Regosols (Arenic, Ochric, Raptic)	Slope of tablelands - 598 m
(CeSSt2) Cerrado ***sensu stricto*** in top of the tablelands	Rhodic Ferralic Lixisols (Arenic, Ochric, Profondic)	Top of the tablelands - 670 m

the larger plot (20 × 50 m), subplots of 5 × 15 m were demarcated, where woody individuals with a circumference at soil height (CSH) ≥ 5 and <10 cm were sampled (medium stratum). Subplots of 2 × 2 m were also demarcated to sample herbaceous individuals (lower stratum). In the latter case, the plant community structure was evaluated using the cover-abundance scale proposed by Braun-Blanquet (1979). The sampling occured in the dry and rainy seasons. In these plots, all individuals from each vascular plant species were counted (i.e. number of individuals and number of focal stoloniferous and rhizomatous clonal plants). The botanical specimen was deposited in the Tocantins Herbarium (HTO) at the Universidade Federal de Tocantins (Tocantins, Brazil). Identifications were made by consulting specialists and the literature. Taxonomic classification followed APG IV (Angiosperm Phylogeny Group 2016).

Soil sampling

The soil physical and chemical properties were specified for each plot (20 × 50 m). A composite sample of five surface soil subsamples (0–20 cm depth) was collected. Samples were air-dried and sifted through a 2 mm mesh sieve. Analyses were conducted at the Laboratory of Soil Analysis, Universidade Federal de Viçosa, following international standards (Embrapa 2017). The analyses included granulometry (clay, silt, coarse and fine sand contents); active acidity (pH) in water and KCl; exchangeable potassium (K+), sodium (Na+), calcium (Ca2+), magnesium (Mg2+), aluminium (Al3+); potential acidity (H+Al); available phosphorus (P); remaining phosphorus (P-rem); sum of bases (BS); base saturation (V); aluminium saturation (m); total cation exchange capacity (CEC); effective cation exchange capacity (ECEC); micronutrients (Zn, Fe, Mn and Cu); organic matter content (OM); and Sodium Saturation Index (ISNa).

Data analysis

The importance value (IV) of each species was calculated by the sum of its relative density, relative frequency, and relative dominance (Mueller-Dombois & Ellenberg 1974, Moro & Martins 2011). With these results, a diagram was constructed with the species that occurred in at least six environments with their respective importance values. Shannon's diversity index and Pielou's evenness were calculated for each environmental (Magurran 2004).

Soil variables were summarized with the use of principal component analysis (PCA) and proceeded (analyzed or processed) via by standardisation by logarithmic transformation, in order to equalise their contributions on the axis (Supplementary Material - Figure S1). Water pH (pH_H2O) values were not transformed because they are already expressed on a logarithmic scale. Spearman's correlation analysis was used to remove correlated soil variables (Figure S2). The PCA was performed using the "*FactoMineR*" package (Husson et al. 2017) in the software R 3.6.2 (R Core Team 2020).

To investigate possible relationships between soil and vegetation, we used canonical correspondence analysis (CCA; ter Braak 1987). A Monte Carlo permutation with 1000 randomisations was used to verify the significance of the generated eigenvalues and species-environment relationships (ter Braak & Prentice 1988). For this analysis, species with a number of individuals ≥ 20 were selected (Supplementary Material - Table SI). The CCA was performed using PC-ORD version 6.0 (McCune & Mefford 2011).

RESULTS

Community diversity and structure pattern

Overall, 20.000 individuals that belong to 338 species and 76 families were sampled across all eight environments in the Brazilian Cerrado of the Jalapão region. Most families occurred with one or two species (58%). The dominant family was Fabaceae (68 species), with 89.47 % of total richness; followed by Poaceae (23), Malpighiaceae (15), Myrtaceae and Euphorbiaceae (14 species each). The two environments of Slope Cerrado Rupestrian (CeRu1 and CeRu2) were those with the highest number of species (153 and 158, respectively). The lowest number of species was found in *Campo Sujo* (grassland with some shrubs) (CaSu) with 73 (Table II).

Shannon index (H') values between eight environments remained between 1.17 and 3.12 to upper stratum; 1.77 and 3.15 to medium stratum; 2.46 and 3.66 to lower stratum in the dry season; and 3.22 and 3.77 to lower stratum in the rainy season (Table II). Pielou evenness (J) values between environments remained between 0.50 and 0.82 to upper stratum; and 0.77 and 0.93 to medium stratum.

From all identified species, 27 species occurred in at least six environments. Six of these species did not occur in the CaSu and four did not occur in the CeSSt1. In the upper stratum, the species that occurred in all environments and with great representativeness were *Pouteria ramiflora* (Mart.) Radlk. and *Hirtella ciliata* Mart. & Zucc. The species *Connarus suberosus* Planch. had greater representativeness in CeSS2, absent in CaSu and scarce in the remaining environments. *Vellozia variabilis* Mart. ex Schult. f. occured in all areas but stood out in environments CaSu and CeRu1. The lower stratum presents two extremes: *Aristida longiseta* Steud. was present in all environments with the highest importance value (IV), except for CeSSt2; and *Erythroxyllum betulaceum* Mart. was present in all areas with low IV (Figure 2).

Physical and Chemical Properties of Soil

There were differences in soil variables among environments (Table III; Figure S1). All soils have a sandy to sandy-loam texture (clay percentage of 1-14%) and yellowish color, except for CeSSt1, on the top of the tableland, which has red soil with a clay content well above the others (35-43%), thus indicating a contribution of a mixture of pellet materials (siltstones), sandstones, and increased weathering. There is a general predominance of fine sand compared to coarse sand in all environments, reflecting the nature of the Urucuia Formation, which is naturally composed of fine-grained sandstone-quartz

Table II. Values related to number of individuals (Abundance), species richness (SR), Shannon diversity index (Diversity H'), Pielou evenness index (J), density (D) and dominance (Do) in the Savanic Formations of the Jalapão, state of Tocantins, Brazil. CeSS1 = Cerrado *sensu stricto*; CaSu = *Campo Sujo*; CaCe = *Campo* Cerrado; CeRu1 = Cerrado rupestrian fields in slopes; CeSSt1 = Cerrado *sensu stricto* in top of the tablelands; CeSS2 = Cerrado *sensu stricto*; CeRu2 = Cerrado rupestrian in slopes; CeSSt2 = Cerrado *sensu stricto* in top of the tablelands. S = Upper Stratum; M = Medium Stratum; IS = Lower stratum in the dry season; IC = Lower stratum in the rainy season. Different letters indicate statistical differences between the dry and rainy seasons (Tukey p > 0.05).

Environments	Abundance				Species Richness					Diversity H'				Pielou´s evenness (J)		Density (D)			Dominance (Do)		
	S	M	IS	IC	S	M	IS	IC	Total	S	M	IS	IC	S	M	S	M	IS	S	M	IS
A1	648	138	828	351	30	29	58	62	111	2,89	3,08	2,669	3,291	0,82	0,86	1,08	1,84	20,7	6,539	0,826	219
A2	219	91	933	719	8	9	41	50	73	1,17	1,77	2,696	3,262	0,53	0,77	365	1,213	136,5	0,685	0,709	23,325
A3	470	131	1220	499	33	32	52	63	118	2,61	2,96	2,644	3,420	0,73	0,85	783	1,746	224,5	4,019	0,669	30,5
A4	1089	88	844	514	38	32	74	91	153	1,86	3,15	3,667	3,775	0,50	0,90	1,815	1,173	21,1	6,78	0,501	193
A5	353	49	1079	423	28	22	52	60	108	2,78	2,92	2,777	3,314	0,82	0,93	588	653	158,75	6,657	0,192	26,975
A6	395	100	1466	1486	29	24	62	87	132	2,26	2,59	2,464	3,222	0,66	0,80	658	1,333	36,65	3,736	0,46	199,5
A7	537	97	527	640	47	29	66	96	158	3,12	2,89	3,649	3,637	0,80	0,85	895	1,32	13,175	9,429	0,429	202,25
A8	365	107	1833	753	28	17	68	79	126	2,77	2,24	2,533	3,628	0,80	0,77	608	1,426	45,825	3,147	0,427	291

materials. The silt contents are very low and reflect the absolute lack of primary minerals with chemical reserve, as well as the high degree of weathering of these soils (Table SII).

The predominantly acid character of the Jalapão soils is noteworthy (ranging from 4.5 to 5.6), with all values of aluminum saturation (m%) greater than 88%, except in CeSSt1 and CeSSt2; the degree of weathering is so high that the soil practically lacks a negative charge, and the organic matter is naturally low. In addition to the very acidic pH, the extremely low levels of available phosphorus (< 2.1 mg kg^{-1} in horizons A; < 0.3 mg kg^{-1} in B or C) are also noteworthy, they reveal a general phosphorus deficiency and severe nutrient limitation (base saturation less than 50%). On the other hand, due to the sandy nature, the remaining phosphorus values are high, considering that there is little amount of iron and aluminum oxides to promote phosphorus adsorption. The only exception was CeSSt1, which shows the value of remaining phosphorus typical of more oxidic soils, being also the only one with higher percentage of clay.

Vegetation-soil properties relationships

In the upper stratum, 29 species were chosen. The eigenvalue of axis 1 was 0.38 and for axis 2 was 0.32. The two axes explained 17.7% of the variability in the data (Figure 3a). The Monte Carlo test indicated high correlations between the edaphic variables and the species related

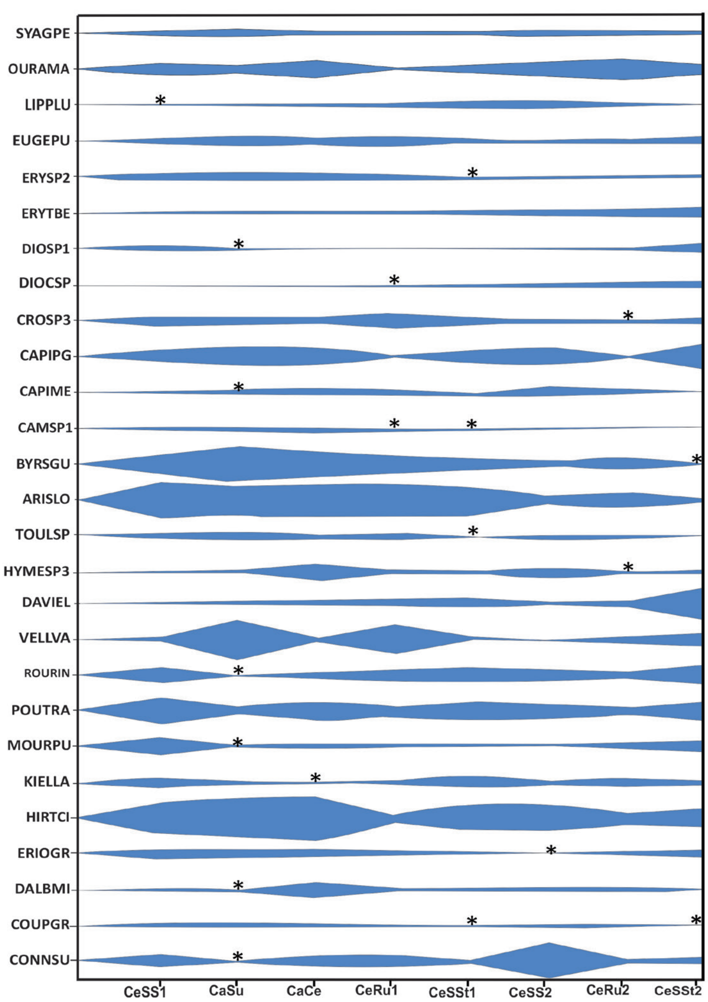

Figure 2. Values of importance of the species occurring in at least eight areas of the Savanic Formations of the Jalapão, state of Tocantins, Brazil. * = Not occurring in the area; CeSS1 = Cerrado *sensu stricto*; CaSu = *Campo Sujo*; CaCe = *Campo* Cerrado; CeRu1 = Cerrado rupestrian fields in slopes; CeSSt1 = Cerrado *sensu stricto* in top of the tablelands; CeSS2 = Cerrado *sensu stricto*; CeRu2 = Cerrado rupestrian in slopes; CeSSt2 = Cerrado *sensu stricto* in top of the tablelands. See full names of the species in Table SI.

to the first two axes of CCA (0.82, $p < 0.001$ for the first axis; and 0.78, $p < 0.001$ for the second). In the upper stratum, the variable presenting high correlation with the structural parameters in axis 1 was the clay content (0.26), and in axis 2, the content of coarse sand (0.38).

For the CCA, 8 species were utilized in the middle stratum (Figure 3b). Axis 1 had an eigenvalue of 0.46, and axis 2 had 0.37. The two axes explained 25.3% of the variability in the data. The Monte Carlo permutation test for the first two axes showed that correlations between species and edaphic variables were significant (Axis 1 = 0.81; Axis 2 = 0.79, $p < 0.001$). The variable with the highest correlation coefficient for the two axes was the content of Coarse sand with 0.38 for the first axis and 0.26 for the second axis.

For the CCA analysis, 68 species were utilized for the lower stratum (Figure 3c). The eigenvalue of axis 1 was 0.59, and axis 2 was 0.46. The two axes explained 8.7% of the variability in the data. In the Monte Carlo test, it presented a substantial result with 0.02 ($p < 0.05$). Regarding the species, the correlation with the soil properties was significant for the two axes ($p = 0.004$). The first axis explained 0.89, and the second one explained 0.84 of the variance. The variables with the highest correlation coefficient were organic matter (0.35) for the first axis, and fine sand (0.35) for the second axis.

To conduct the analysis of all strata, 94 species were chosen (Figure 3d). The eigenvalues for the first two axes were 0.50 (axis 1) and 0.36 (axis 2), with the first axis accounting for 5.4% and the second accounting for 3.9% of the data variability. The Monte Carlo test was significant ($p = 0.002$) for the correlation between soil properties (0.02) and species (0.005). The variables with the highest correlation coefficients for axis 1 were organic matter (0.34) and fine sand (0.29), and for the second axis, pH in water (0.51) and phosphorus (0.43).

DISCUSSION

We described relevant differences on communities composition and structural patterns linked to variation in soil along the environmental gradient in the Brazilian Cerrado of the Jalapão region. In general, soil conditions among the eight plant communities exhibited significant environmental heterogeneity, where the physical and chemical properties of the soil can lead to differences in the composition and structure of the vegetation. Our results reinforce the notion that abiotic filtering operates at a fine-scale as a crucial driver of plant communities in the Brazilian Cerrado. Soil attributes are considered key drivers for plant species distribution and community diversity in the Brazilian Cerrado (e.g., Amorim & Batalha 2007, Neri et al. 2013, Torres et al. 2017, Bueno et al. 2018, Amaral et al. 2022).

With regard to the most species-rich families our data are consistent with results of other surveys related to the Brazilian Cerrado (Campos et al. 2006, Amorim & Batalha 2007, Silva & Felfili 2012, Miguel et al. 2016). We can highlight Fabaceae as, in a general aspect, the most representative family in floristic inventories of the Domain (Campos et al. 2006, Neri & Camargos 2007, Neri et al. 2013, Miguel et al. 2016, Bueno et al. 2018, Silva et al. 2019, Filho et al. 2020). The family comprises 24% of the species listed for the vascular flora of the Brazilian Cerrado (Mendonça et al. 2008). The taxa of the Fabaceae family are important to the dynamics of ecosystems with poor nutrient levels due to their morphological adaptations, such as the presence of nodules in the roots (Oliveira et al. 2012).

Table III. Chemical and physical soil surface variables (0-20 cm) in the Savanic Formations of the Jalapão, state of Tocantins, Brazil. CeSS1 = Cerrado *sensu stricto*; CaSu = *Campo Sujo*; CaCe = *Campo* Cerrado; CeRu1 = Cerrado rupestrian fields in slopes; CeSSt1 = Cerrado *sensu stricto* in top of the tablelands; CeSS2 = Cerrado *sensu stricto*; CeRu2 = Cerrado rupestrian in slopes; CeSSt2 = Cerrado *sensu stricto* in top of the tablelands. Data are represented by the Mean, Maximum (max) and Minimum (Min) Value of each area with its respective Standard Deviation.

	CeSS1				CaSu				CaCe				CeRu1				CeSSt1				CeSS2				CeRu2				CeSSt2			
	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD
pH H2O	5,05	5,21	4,81	0,12	5,12	5,41	4,91	0,18	5,20	5,30	4,99	0,10	5,04	5,24	4,71	0,18	4,82	4,95	4,57	0,12	5,05	5,40	4,78	0,19	4,85	5,07	4,62	0,14	5,40	5,60	5,23	0,12
ph KCl	4,24	4,38	4,15	0,08	4,33	4,50	4,21	0,10	4,51	4,69	4,27	0,14	4,10	4,25	3,84	0,11	4,43	4,64	4,18	0,15	4,44	4,53	4,32	0,06	4,09	4,40	3,85	0,20	4,57	4,63	4,50	0,04
P (mg/dm³)	0,64	0,90	0,48	0,14	0,79	1,10	0,50	0,21	1,05	1,52	0,76	0,28	1,30	1,94	0,82	0,36	0,36	0,82	0,18	0,21	0,48	1,26	0,02	0,35	0,79	1,68	0,16	0,48	0,68	1,04	0,30	0,22
K+mg/dm³	4,08	7,00	2,60	1,68	1,96	3,00	0,80	0,80	1,72	4,00	0,40	1,05	6,48	8,40	3,60	1,37	5,00	8,80	1,60	2,65	2,40	3,80	1,40	0,74	5,34	10,20	1,20	2,64	1,20	2,40	0,00	0,88
Na+mg/dm³	0,68	1,60	0,00	0,63	0,00	0,00	0,00	0,00	0,17	0,70	0,00	0,24	2,87	3,60	2,40	0,41	3,20	6,78	1,20	1,81	0,45	1,10	0,24	0,28	2,10	3,74	0,30	0,96	1,74	2,10	1,30	0,35
Ca2+cmolc/dm³	0,07	0,08	0,05	0,01	0,07	0,10	0,03	0,03	0,11	0,19	0,09	0,03	0,18	0,25	0,15	0,03	0,16	0,17	0,15	0,01	0,19	0,21	0,16	0,02	0,20	0,28	0,16	0,03	0,18	0,20	0,17	0,01
Mg2+cmolc/dm³	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,00	0,01	0,00	0,02	0,00	0,01	0,00	0,01	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,00	0,01	0,00	0,00	0,00	0,00
Al3+cmolc/dm³	0,50	0,63	0,41	0,08	0,31	0,43	0,24	0,07	0,25	0,37	0,14	0,09	0,61	0,78	0,39	0,12	0,70	1,25	0,35	0,32	0,35	0,41	0,29	0,04	0,79	1,31	0,43	0,27	0,26	0,31	0,18	0,04
H+Al (cmolc/dm³)	2,88	3,88	2,28	0,53	1,69	2,38	1,26	0,40	1,77	2,78	1,00	0,57	3,46	4,56	2,26	0,83	5,28	8,82	2,58	2,22	1,93	2,20	1,68	0,17	4,74	8,32	2,94	1,66	1,75	2,02	1,36	0,17
SBcmolc/dm³	0,08	0,10	0,07	0,01	0,08	0,11	0,04	0,03	0,12	0,23	0,10	0,04	0,21	0,30	0,18	0,04	0,19	0,24	0,16	0,03	0,19	0,22	0,17	0,02	0,23	0,31	0,18	0,04	0,19	0,21	0,17	0,01
CTC efetiva cmolc/dm³	0,59	0,72	0,48	0,08	0,39	0,54	0,30	0,08	0,38	0,56	0,24	0,11	0,83	0,99	0,69	0,12	0,89	1,47	0,51	0,34	0,55	0,61	0,47	0,04	1,02	1,60	0,62	0,30	0,45	0,49	0,37	0,04
CTC pH 7 cmolc/dm³	2,96	3,96	2,35	0,53	1,77	2,48	1,33	0,41	1,89	2,88	1,11	0,58	3,67	4,78	2,44	0,83	5,46	9,04	2,74	2,25	2,12	2,40	1,90	0,17	4,97	8,61	3,15	1,69	1,95	2,20	1,57	0,17
V (%)	3,13	4,00	2,34	0,58	5,00	9,32	2,56	1,89	7,12	10,08	3,78	2,11	6,27	10,06	4,58	1,61	3,89	5,94	2,46	1,26	10,90	27,72	7,54	5,95	5,31	7,04	3,92	1,10	10,50	15,42	8,42	2,03
m (%)	84,84	87,88	81,18	2,33	78,39	88,44	70,58	6,03	63,37	76,08	50,22	9,15	73,11	78,84	58,20	5,75	76,65	84,90	68,12	5,98	64,10	68,96	57,66	3,60	75,59	80,70	68,28	3,86	56,37	62,54	48,28	4,40
ISNa (mg/dm³)	0,48	1,17	0,00	0,44	0,00	0,00	0,00	0,00	0,16	0,60	0,00	0,22	1,57	2,07	1,08	0,36	1,51	2,11	0,96	0,36	0,38	1,10	0,21	0,28	0,93	1,53	0,11	0,41	1,73	2,49	1,19	0,42
M.O. (dag/kg)	0,64	1,01	0,43	0,18	0,58	0,84	0,20	0,23	0,69	1,01	0,42	0,18	1,04	1,41	0,63	0,22	2,04	3,52	1,23	0,78	0,38	0,51	0,23	0,09	1,46	3,34	0,72	0,79	0,27	0,36	0,21	0,05
P-rem (mg/dm³)	50,60	54,18	46,78	2,14	54,48	56,90	50,12	1,99	50,25	54,18	46,18	2,70	48,45	51,48	43,96	2,43	26,93	31,30	22,54	2,32	51,31	54,90	46,38	2,56	46,55	50,38	39,26	3,35	51,75	53,14	50,24	0,97
Zn (mg/dm³)	0,39	0,50	0,32	0,05	0,42	0,49	0,34	0,05	0,47	0,54	0,32	0,08	0,54	0,95	0,29	0,27	0,38	0,43	0,32	0,04	0,71	0,75	0,66	0,03	0,81	0,96	0,68	0,08	0,87	1,04	0,78	0,08
Fe (mg/dm³)	72,23	104,20	25,42	27,81	51,72	69,50	36,06	8,77	94,07	236,62	28,74	67,45	54,11	89,84	25,66	16,89	62,23	105,22	40,70	19,66	76,09	123,54	55,56	20,30	62,42	95,30	34,16	17,28	70,71	88,76	56,62	10,54
Mn (mg/dm³)	0,20	0,40	0,14	0,09	0,10	0,42	0,00	0,14	0,00	0,02	0,00	0,01	0,25	0,48	0,12	0,11	0,52	1,02	0,16	0,31	0,21	0,34	0,10	0,08	0,33	1,02	0,06	0,28	0,10	0,26	0,02	0,07
Cu (mg/dm³)	0,36	0,49	0,26	0,09	0,70	1,70	0,28	0,39	0,76	1,00	0,61	0,15	0,38	0,49	0,23	0,09	0,30	0,47	0,18	0,10	0,66	0,79	0,60	0,06	0,61	0,81	0,38	0,14	0,47	0,59	0,39	0,06
Coarse sand	31,68	40,60	22,20	5,48	30,16	33,80	25,00	2,74	18,48	26,60	11,40	4,94	18,42	32,20	9,00	8,43	20,72	31,00	17,20	3,90	38,30	48,20	25,20	7,61	14,92	19,20	8,80	3,59	19,08	28,00	6,20	5,98
Fine sand	62,10	69,20	55,20	4,30	64,68	70,60	60,60	3,09	75,42	82,20	68,60	4,98	78,10	87,20	63,80	7,71	74,98	78,20	62,60	4,49	49,56	60,80	35,60	7,88	48,76	54,00	44,00	3,52	78,66	92,40	69,60	6,22
Silt	1,06	1,40	0,40	0,28	0,96	2,00	0,20	0,63	1,68	2,80	0,80	0,75	1,76	4,00	0,60	1,02	1,26	2,20	0,40	0,67	1,56	3,00	0,40	0,87	3,56	4,80	2,60	0,70	1,30	2,80	0,40	0,76
Clay	5,16	7,60	3,00	1,44	4,20	5,40	2,20	0,98	4,42	6,40	3,20	1,11	1,72	2,60	0,20	0,76	3,04	4,20	2,00	0,82	10,58	14,00	8,00	2,42	32,76	35,40	30,00	1,75	0,96	1,80	0,40	0,48

Our different environments sampled were floristically diverse. The plant species richness is elevated in comparison to other studies in the Brazilian Cerrado (Teixeira et al. 2004, Neri et al. 2013, Silva & Felfili 2012, Rodrigues et al. 2019). We presumed that these results might be associated with different phytophysiognomies sampled. Furthermore, the substantial number of species suggests a good state of conservation for the assessed environments, as no observed anthropic activities that could negatively impact species richness were noted (e.g., selective cutting of specific species, extractive activities, or grazing). Our findings emphasize the floristic importance of different Brazilian Cerrado phytophysiognomies of the Jalapão region for the conservation of its woody and herbaceous flora.

Compared to other environments, the CeRu1 and CeRu2 showed the greatest richness. Some phytosociological studies have found high richness per area unit in rupestrian ecosystems, due to a complex system of environmental gradients that operate on a small spatial scale (Abreu et al. 2012, Fernandes 2016, Campos et al. 2021). The geomorphological heterogeneity of the rock outcrops offers a vast spectrum of microhabitats, such as cracks, fractures, pools, rock fragments and soil islands, all of which create subtle differences in resource

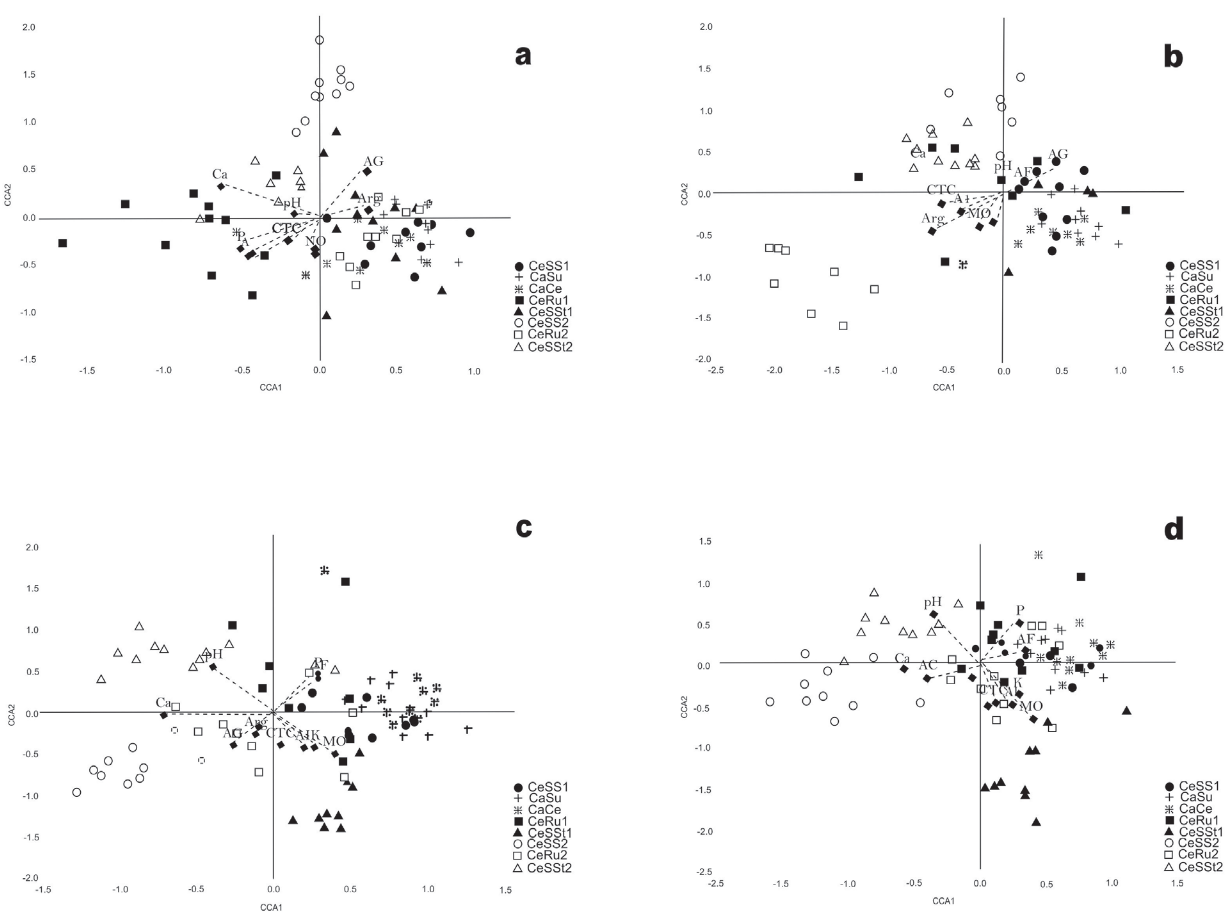

Figure 3. Ordination Diagram of the Upper Stratum (**a**), Medium Stratum (**b**), Lower Stratum (**c**) and all strata together (**d**) produced by the CCA. CeSS1 = Cerrado *sensu stricto*; CaSu = *Campo Sujo*; CaCe = *Campo* Cerrado; CeRu1 = Cerrado rupestrian fields in slopes; CeSSt1 = Cerrado *sensu stricto* in top of the tablelands; CeSS2 = Cerrado *sensu stricto*; CeRu2 = Cerrado rupestrian in slopes; CeSSt2 = Cerrado *sensu stricto* in top of the tablelands.

availability (Abreu et al. 2012, Carmo et al. 2016). The environments can vary from total absence of soils with exposure of rocks, where some plants are established, such as *Vellozia tubiflora* (A. Rich.) Kunth to others that present greater shading and humidity, thus allowing the establishment of Pteridophytes (*Adiantum* sp.). Likewise, the low floristic similarities between environments sampled may be associated with different conditions of substrate (Abreu et al. 2012, Lemos et al. 2013, Neri et al. 2013, Campos et al. 2021). According to Abreu et al. (2012), at a local scale, physical-chemical Properties of the soil may strongly influence the floristic and structural differentiation between numerous Brazilian Cerrado phytophysiognomies (e.g. Cerrado *sensu stricto* and rocky outcrop Cerrado).

Edaphic differences among the eight environments underscore the marked environmental heterogeneity in the Jalapão region. Within the Cerrado, soil nutrient availability and texture can account for a significant portion of the variation in species composition and distribution, influencing the various community types (Bueno et al. 2017). In chemical terms, the natural fertility of the soils is very low compared to other soils under Brazilian Cerrado, as reported in the literature (Ruggiero et al. 2006, Amorim & Batalha 2007, Silva & Batalha 2008, Abreu et al. 2012, Bueno et al. 2013, Torres et al. 2017). Although most of the Brazilian Cerrado is dominated by clayey Latosols (Lopes 1983), predominantly sandy Cerrado covers about 15% of the biome (Reatto et al. 1998), with the states of Tocantins and Mato Grosso do Sul having the highest occurrence of “sandy” Cerrados. The values of aluminum saturation are much higher than the average reported for the Brazilian Cerrado by Lopes (1983) (Campo Cerrado = 58%, Cerrado sensu stricto = 44%), thus representing one of the poorest (dystrophic) sets of soils within the Brazilian Cerrado. The organic matter contents are low, even in the superficial horizons. These results fall within the range found in other studies conducted in Brazilian Cerrado areas (Lopes 1983, Furley & Ratter 1988, Haridasan 2001, Lindoso et al. 2011).

In Brazilian Cerrado, as the soil clay content decreases, the organic matter content tends to be lower (Tognon et al. 1998). These low contents can be explained by the low amount of clay mineral-organic matter associations in soils (Dutartre et al. 1993). Sandy horizons create a barrier and affect the interactions with organic matter, impeding the formation of aggregates. (Edwards & Bremer 1967). Sandy soils have lower aggregate stability, as well as a smaller specific surface area and density of charges compared to soils with higher clay content, which diminishes the availability of nutrients intended for plants. Each species has different requirements for its own establishment, those are corroborated by the variations in the results of the CCA related to the analyzed environmental variables. According to Swaine (1996), the plant species require different resources and have diverse tolerances to environmental conditions depending on the stage of the species. In agreement with Carvalho et al. (2009), the differences in vegetation strata are mainly due to the distinct size of the plants, which causes the form of absorption (water and nutrients), and, consequently, the metabolic requirements to be differentiated.

The areas showed a tendency for separation according to the different soil types: Ferrasols, Lixisols, Regosols and Arenosols, presenting in this last class a proximity and/or an overlap of the three areas (CeSS1, CaSu and CaCe). In general, sandy savanic formations of the Jalapão are influenced primarily by soil texture. In the same soil type with distinct vegetation formations, such as the Arenosols, the amount of clay significantly decreased towards the *Campo* Cerrado. The texture is the physical property of the soil that least undergoes alteration over time (Gonçalves & Stape 2002), the differences found in the texture characteristics influenced the structure and distribution of the species, increasing substantially the density and dominance. For example, *Vellozia variabilis* that stood out in environments CaSu and CeRu1, with the highest importance value, due the high relative values of density and dominance. Velloziaceae often occur in sandy and nutrient-poor environments (Conceição & Pirani 2007). Some species of the family are characterized by having specific adaptation strategies such as desiccation tolerance, since sandy soils have lower water retention levels (Porembski 2007).

According to Donovan et al. (2011), species in environments with low availability of resources related to the strategy of acquisition and utilization are called conservative, since they are characterized by slow growth, protection of the tissues and storage organ, they have long-life leaves, low concentrations of nutrients and low photosynthetic and respiration rate. These characteristics are more important for plant performance in comparison to those that lead to a high capacity of resource capture (Aerts 1999). There is a trade-off between plants from nutrient-rich soils, where they have a higher ability to absorb rapidly, and plants from environments with poor soils, which have a greater capacity of nutrient retention (Tessier & Woodruff 2002). The plant species of the Jalapão establish themselves in a remarkable edaphic climax because the soil presents a severe restriction for their development. Some species have characteristics that allow high abundance in conditions of low availability of resources, in which only a few are able to establish themselves.

CONCLUSION

Our study has revealed differences on species richness, plant communities composition and structural patterns along the environmental gradient in the Brazilian Cerrado of the Jalapão region. The region, considered one of the largest extensions of Cerrado still preserved in the country, has chemically poor, sandy soils with low water availability. The vegetation composition and distribution of species in the Jalapão region was influenced by soils with an emphasis on particle size attributes, especially in the content of coarse sand and fine sand. Moreover, our results demonstrated, for the first time, the fine-scale effects of the physical-chemical aspects of the soil on the plant community in the Brazilian Cerrado of the Jalapão region.

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SUPPLEMENTARY MATERIAL

Figures S1, S2.
Tables SI, SII.

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RHOV and CEGRS conceived the idea and designed methodology. RHOV, GRC and PVC collected the samples. RHOV, AVN, SFL, PMSR, GRC and PVC analyzed the vegetation and soil data. RHOV wrote the manuscript with contributions from all co-authors.