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Original Article

Soil-vegetation relationships influence the regeneration after fire in the species composition and structural parameters of Cerrado-Amazonia ecotone

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ABSTRACT

In ecotonal Cerrado areas, the addition of Amazonian and Atlantic Forest species mainly occurs through connections between forest areas and forest physiognomies. In this context, the biome is a unique region for research on the influence of geographical and historical factors on its biota. In tropical ecotonal regions, integrated communities can exist on soils that present variations in fertility, physical properties and depth, which results in heterogeneity of physiognomies. It was tested the hypothesis that edaphic conditions related to calcium availability are significantly related to species composition and structural parameters in two physiognomies. The study was conducted in the Cerrado of the Chapada das Mesas National Park (CMNP) in the city of Carolina, Northeast Brazil, and the sample universe consisted of 18 areas in two physiognomies. The initial hypothesis was confirmed. The results and inferences about the vegetation structure and physical-chemical parameters of the soil, suggest that the management for conservation of the CMNP must consider the particularities of the Cerrado physiognomies and the vegetation responses to environmental filters, such as edaphic conditions and associations with other organisms.

Keywords: Cerrado, environmental filters, gallery forest, herbaceous, physiognomies, shrubs.

Introduction

Cerrado megadiversity has been associated with the proximity of species-rich vegetation such as the Amazon Rainforest and the Atlantic Forest (Simon *et al*. 2009). In ecotonal Cerrado areas, the addition of Amazonian and Atlantic Forest species mainly occurs through connections between forest areas and forest physiognomies (Oliveira-Filho & Ratter 1995). Indeed, in areas of the ecotonal Cerrado where there are no biogeographic barriers, species

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interpenetration and, consequently, the formation of subregional landscape complexes may occur (Ab'Saber 2003). In this context, the biome is a unique region for research on the influence of geographical and historical factors on its biota (Méio *et al.* 2003).

The Cerrado biome faces continuous exposure to forest fires, which directly lead to losses in biomass and a decline in the vigor of existing forest types (Strassburg *et al*. 2017; Barbieri *et al*. 2019). Despite its profound environmental significance, mounting pressures to open up new agricultural areas have threatened the integrity of its natural habitats. Within this context, fire plays a central role in generating a series of interactions and disturbances in vegetation dynamics. It is also a critical factor for certain species, as it directly impacts productivity, resilience, biodiversity, and the hydrological cycle of the area, while also serving as a substantial source of greenhouse gases (Silva *et al*. 2022).

In tropical ecotonal regions, integrated communities can exist on soils that present variations in fertility, physical properties and depth, which results in heterogeneity of physiognomies (Oliveras & Malhi 2016). The complexity of plant responses to soil conditions may be related to the physical and chemical parameters of the soil, since the availability of nutrients is an important environmental filter (Lortie *et al*. 2004; Laliberté *et al*. 2013; Demetrio & Coelho 2018).

The complexity of the Cerrado vegetation is more related to soil fertility (Veenendaal *et al*. 2014; Soares *et al*. 2015). However, more research is needed to understand this topic, as the structure of vegetation can be influenced by nutrient availability in combination with other factors such as water retention, geographic space and fire (Bond 2010; Pivello *et al*. 2010; Oliveras & Malhi 2016; Maracahipes-Santos *et al*. 2017).

The Cerrado is the biome that occupies most of the territory of the State of Maranhão, about 65% of the total area (Sano *et al*. 2008). The expansion of agricultural projects in Maranhão occurs predominantly in the Southwest and South regions, which coincides with distribution of part of the Cerrado in the State. Cerrado areas in these regions was identified as a conservation priority (MMA 2018) due to the extension of continuous vegetation areas, which may be relevant to the species distribution process and ecosystem dynamics (Barreto 2007). Thus, the Chapada das Mesas National Park, located in this region, holds significant value for the preservation of Brazilian biodiversity, as it is situated in this transitional zone (Cerrado - Amazon) and, therefore, has the potential to host high levels of species richness and abundance in both flora and fauna. Furthermore, it contributes to the ecological corridor known as the Araguaia-Bananal (Galinkin *et al*. 2004).

The understanding of the distribution patterns of biological species has been the subject of studies in different biomes (Eiten 1972; Felfili *et al*. 2011; Bueno *et al*. 2013; Pellegrini *et al*. 2016) because there is a perception that comprehending these patterns will enable better natural resource management and conservation, providing support for biodiversity preservation (Cox & Moore 2014).

Since species distribution and patterns of biological organization are related to environmental characteristics and structural complexity of the environment, such as environmental heterogeneity of vegetation, habitat quality, type and quantity, and contact zones between formations (Pires *et al*. 2014), understanding these differences is fundamental to comprehend how communities establish themselves. Each biome is differently affected by environmental factors, and these factors contribute to the diversity of the environment.

For Cerrado areas, factors such as soil depth, drainage, water table depth, soil fertility (Eiten 1972; Scariot *et al*. 2005), precipitation, occurrence of fire, and anthropogenic disturbances (Hoffmann *et al*. 2009) are the most relevant. In the Amazon Rainforest, precipitation, water availability, litter production, and nutrient cycling are the determining factors for the abundance and distribution of plant species, becoming selective factors in these environments where water and nutrient availability are low (Farquhar & Sharkey 1982; Hoffmann & Franco 2008). Therefore, studying the behavior of variables that are determinants for vegetation structure in a transitional environment can contribute to a better understanding of the impacts of climate change and support environmental monitoring policies.

In this context, the objective of this work was to evaluate the influence of chemical and granulometric properties of the soil on the occurrence and abundance of species of the herbaceous-shrub and regenerating tree strata in the cerrado *sensu stricto* and in gallery forest physiognomies, aiming to contribute to the characterization of vegetation structure and for understanding the soil-vegetation relationship in the ecotonal Cerrado-Amazonia of the Chapada das Mesas National Park (CMNP). It was tested the hypothesis that edaphic conditions related to calcium availability are significantly related to species composition and structural parameters in the two physiognomies.

Material and methods

Study area and experiment design

The study was conducted in the CMNP in the city of Carolina, Northeast Brazil (Fig. 1). The relief is predominantly flat-undulating, with altitudes ranging from 250 m in the valleys and up to 524 m in the hills. Hilltops are relatively flat, which explains the name "Chapada das Mesas". The regional climate is Tropical Aw (savannah with a drier season in winter), according to the Köppen classification (Belda *et al*. 2014). Average annual temperature is 26.1 ºC and average annual precipitation is 1250 to 1500 mm. The rainy season occurs between November and April while the dry season occurs between May and October, the most critical period in relation to fires. The soil of the study area

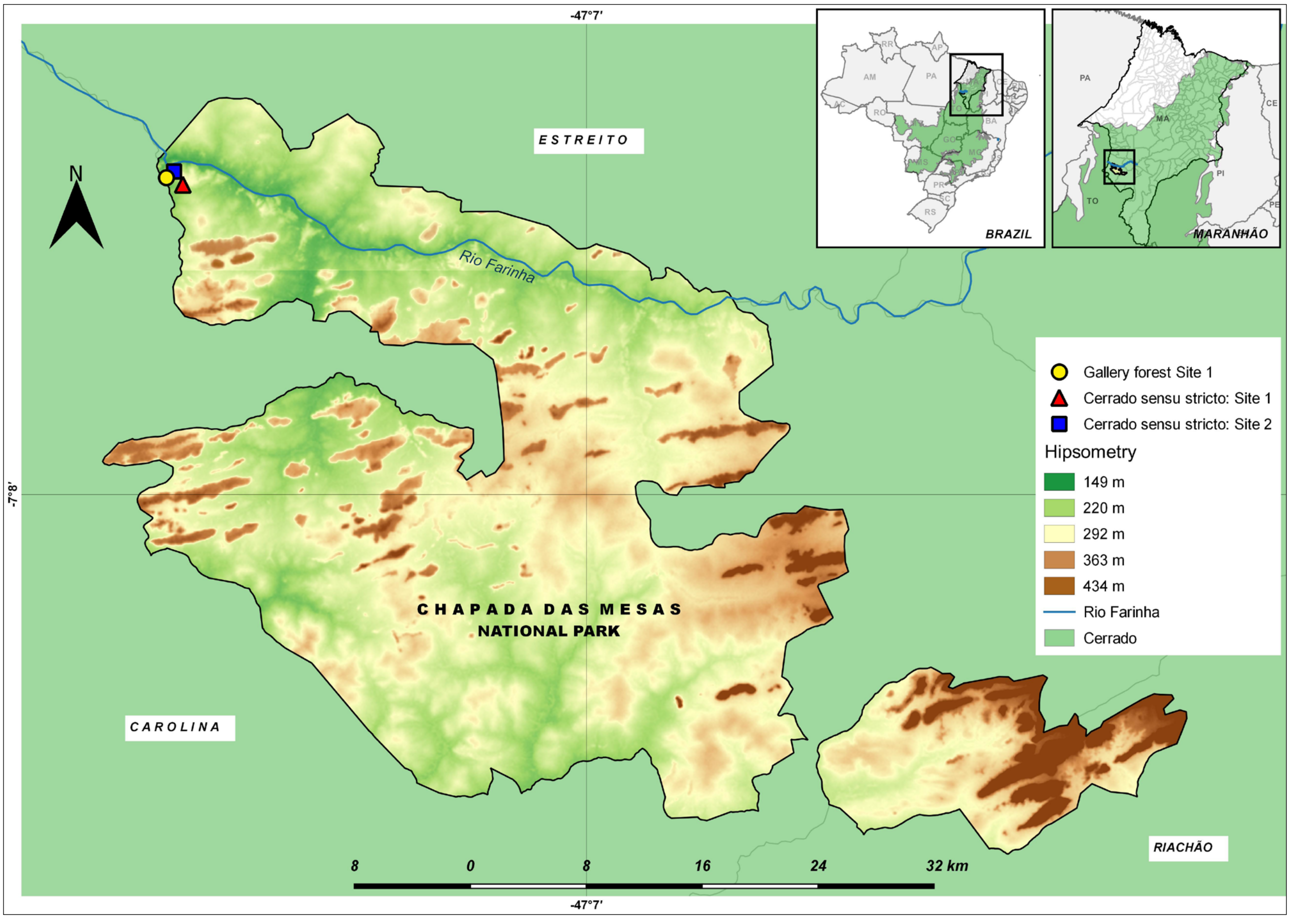

Figure 1. Location of the CMNP and areas of the typical cerrado and gallery forest areas consideres in this study.

is an Arenosols, Quartzipsamments (Soil Taxonomy and WBR Classification, IBAMA 2013), which corresponds to a Neossolos Quartzarênicos according to the Brazilian Soil Classification System (Santos *et al*. 2018).

The CMNP Cerrado has ecotone characteristics because of its geographical positioning in the Southwest portion of Maranhão's Cerrado where it borders the Amazon Forest. In addition, the presence of altitudes lower than that of the Cerrado in the Brazilian Central Plateau allows biogeographic barriers in species distribution to be overcome and thus there can be greater exchange between species of adjacent vegetation in this region. These characteristics contributed to the identification of the region as of high biological importance, through calculation in a study carried out by the organization WWF-Brasil and the Brazilian Ministry of the Environment (WWF 2015). The biological importance can be confirmed by recent discoveries of new species and occurrences in the CMNP (Guarçoni *et al*. 2020; Saraiva *et al*. 2020; Fernandes *et al*. 2022).

The general characterization of the Cerrado areas studied was made in accordance with Ribeiro and Walter (2008), considering: (i) typical cerrado is a savanna formation in which tree and shrub stratum predominates with irregular and twisted branches; it has tree cover of 20% to 50% and average height of the tree layer from 3 m to 6 m; (ii) gallery forest is a perennial forest vegetation that accompanies the small rivers and streams; it has tree coverage of 70% to 95% and the average height of the tree layer varies between 20 m and 30 m.

The sample universe consisted of 18 areas in Cerrado-Amazonia ecotone. Semi-annual phytosociological research was carried out on the cerrado *sensu stricto* physiognomy, typical cerrado subtype, in two areas of 300 × 300 m that were about 1.4 km apart. The two areas were subdivided into four plots measuring 150 × 150 m. In area 1 of the typical cerrado, a line was placed in each of the plots in the years 2017 and 2018. The same method was used in area 2 in 2018, totaling 12 sample units in the physiognomy. Minimum distance from one line to another was 60 m and total length of physiognomy sample was 480 m. In parallel, semi-annual phytosociological research was carried out on the gallery forest physiognomy in an area of 640 × 70 m along the course of a Farinha River tributary. During the rainy season, the stream level increases, but it does not even flood gallery forest physiognomy. In this single plot along the stream, six lines were placed with a minimum distance of 100 m between them and the total sample length was 240 m (Table 1).

Table 1. Physiognomies types for phytosociological and edaphic analysis at CMNP, Carolina, MA. TC1: Typical cerrado area 1; TC2: Typical cerrado area 2 and GF: Gallery Forest; * Not evaluated.

Code	Coordinates	Altitude (a.s.l.)	Collection date	Post-burn time
TC 1	6°56'47.68"S, 47°22'20.35"W	220	Oct/2017	Four months
TC 2	6°56'46.7"S, 47°22'23.65"W	216	Oct/2017	Four months
TC 3	6°56'51.92"S, 47°22'26.89"W	211	Oct/2017	Four months
TC 4	6°56'56.16"S, 47°22'20.21"W	219	Oct/2017	Four months
TC 5	6°56'48.49"S, 47°22'18.89"W	222	Apr/2018	Ten months
TC 6	6°56'52.17"S, 47°22'23.82"W	216	Apr/2018	Ten months
TC 7	6°56'48.49"S, 47°22'24.76"W	214	Nov/2018	Six months
TC 8	6°56'55"S, 47°22'22.30"W	216	Nov/2018	Six months
TC 9	6°56'32.6"S, 47°22'53.4"W	194	Apr/2018	Two years and six months
TC 10	6°56'33.64"S, 47°22'54.92"W	192	Apr/2018	Two years and six months
TC 11	6°56'28.97"S, 47°22'51.4"W	197	Nov/2018	Three years and one month
TC 12	6°56'26.1"S, 47°22'53.6"W	199	Nov/2018	Three years and one month
GF 1	6°56'39.39"S, 47°22'55.54"W	190	Oct/2017	*
GF 2	6°56'46.29"S, 47°22'54.34"W	191	Oct/2017	*
GF 3	6°56'43.15"S, 47°22'55.13"W	192	Apr/2018	*
GF 4	6°56'31.94"S, 47°22'57.24"W	192	Apr/2018	*
GF 5	6°56'36.22"S, 47°22'57.52"W	193	Nov/2018	*
GF 6	6°56'28.72"S, 47°22'57.44"W	193	Nov/2018	*

Fire events

To monitor and understand post-fire forest recovery (Roccaforte *et al*. 2018), as well as to identify changes in vegetation floristic composition (Wang *et al*. 2017), the occurrence of fires was verified. From Landsat satellite image analysis (with spatial resolution of 30 m) of TM, ETM + and OLI sensors, burn mark occurrence was verified in the two areas of typical cerrado from 2016 to 2018 (Table 1).

Vegetation sampling and community structure

The natural state of the sites plays a crucial role in preserving the soil fertility and floral diversity (Mishra *et al*. 2017). Thus, was the line intersection method (Canfield 1941), adapted by Munhoz and Araújo (2011), was used to determine composition, coverage and frequency of herbaceous, shrub and regenerating tree species in the community. The method consisted of installing 40-meter graduated lines, at a height of about 10 cm from the ground, in the vegetation areas of the cerrado *sensu stricto* and gallery forest physiognomies. Each line was considered a sample unit, subdivided into 1-meter segments, which represented sample subunits.

Occurrence, height and horizontal projection of each species intersected by the line or that occurred below it were recorded. The horizontal projection sum of each species in all sample subunit corresponded to its absolute coverage value in the area. Relative coverage was given by dividing the absolute coverage of each species by the sum of the absolute coverage of all species multiplied by 100. Registration of each species in the sample units was used to determine their frequency in the physiognomies. Plants with many branches were considered to be a single individual. The following phytosociological parameters were calculated: absolute (FA) and relative (FR), absolute (CA) and relative (CR) coverage, importance value index (VI), obtained by adding the relative frequency and coverage values, the Shannon-Weiner diversity index (H') (Krebs 1989), Pielou's equitability (J) (Krebs 1989; Pielou 1977).

Soil study

The physical and chemical quality is important in assessing the degree of soil degradation, which allows for characterizing, evaluating, and monitoring the changes that occur in a given ecosystem (Andrade & Stone 2009). For that soil samples (0-20 cm) were collected at all plots, each six months in 2017 and 2018 in both physiognomies, totaling five replicates per sample unit. Chemical and physical analyzes were conducted at the Soil Analysis Laboratory at the State University of Maranhão, in compliance with the Embrapa protocol (1997). Chemical analyses measured the following variables: soil pH ($CaCl_2$); P, Na and K by the Mehlich-1 extraction method; Ca, Mg and Al by extraction with 1 mol/L KCl; H+Al by extraction with KCl N; Al saturation index; C and organic matter (OM) after oxidation with 0.5 mol/L Na_2Cr_2O7, and 5 mol/L H_2SO_4; and remaining P (P-rem), using 0.01 mol/L $CaCl_2$. The granulometric analysis was performed using the pipette method (Embrapa 1997). For the interpretation of the results, we used the criteria defined by the Soil Global Information System, SoilGrids (Hengl *et al*. 2014).

Botanical identification

Botanical material was herborized and exsiccates were deposited in the SLUI herbarium, State University of Maranhao, UEMA, with duplicates in ALCB, FLOR, HUEFS, MAR and UB herbariums (acronyms follow Thiers 2020). Species were identified using specialized bibliography, taxonomist expertise, specimen comparison in the SLUI herbarium and virtual international herbariums through the worldwide network. The floristic list was compiled according to the classification system based on Chase *et al.* (2016) and spelling of species names were confirmed by consulting the Missouri Botanical Garden database contained in the "Tropical System" (tropicos.org) and the REFLORA Program (Flora do Brasil 2020 under construction). The species list in the "Brazilian Flora Group" (BFG 2018) database was used to obtain information on endemism (species that occur only in the Cerrado biome), geographic distribution and new species registered in Maranhão and in the Cerrado biome.

Budowski's proposal (1965) and Almeida's proposal (2016) were used for the ecophysiological group classification. The species were separated into ecological groups according to life strategies and lighting requirements: pioneer (P), early secondary (ES), late secondary (LS) and demanding climax of light (CL). Species classification according to habit followed the general descriptions of Souza *et al.* (2013) for tree, shrub, sub-shrub, grass and creeper. Species classification was determined according to the life form (Raunkiaer 1934).

Statistical analysis

To verify sample sufficiency the Bootstrap richness estimator (permutations N = 9999) was used. For floristic richness and diversity analysis, incidence and species abundance matrices in the sample units were used. With chemical matrices and physical parameters of the soil, it was possible to test the difference between the sample units for edaphic characteristics by the Kruskal-Wallis non-parametric test (at a significance level of 5%), as the data had not normal distribution. When significant, paired comparisons were conduced using the Mann-Whitney test (Hollander & Wolfe 1999).

In order to obtain direct inferences about species' relationships with environmental factors, Redundancy analysis (RDA) was used (Legendre & Legendre 2012). For these analyzes, composition and species abundance matrices were used, in which species that occurred in only one sample unit were removed, following the routine proposed by Eisenlohr *et al.* (2014) and that had an abundance ≤ 10. The Hellinger transformation was applied to species matrices (Legendre & Gallagher 2001). The chemical and physical parameter matrices of the soil were also used, which were transformed logarithmically and edaphic data was examined to eliminate variables with autocorrelation ≥ 0.7. After the RDA analysis, group significance was tested using a permuted ANOVA variance analysis (Legendre & Legendre 2012).

Analyses were carried out using the software R (version 3.6.1), packages "vegan", "ade4", "biodiversityR" (R Development Core Team 2016) and PAST 3 (Hammer *et al*. 2001).

Results

Typical cerrado structure

A total of 1.529 individuals, distributed in 59 species, 48 genera and 25 families were recorded in sample units of typical cerrado, where the number of species per sample unit ranged from 10 to 21. The families with the largest number of species were Fabaceae (n = 16), Euphorbiaceae (n = 4) and Poaceae (n = 4). Twelve families were represented by a single species. Fabaceae was the family with the largest number of species per sample unit. Of the total species collected, 46 belonged to the herbaceous-shrub stratum and 13 were arboreal in regeneration. As for distribution, eight species were new for Maranhão, six of them occurred exclusively in the Cerrado and seven occurring exclusively in the Cerrado and Caatinga biomes (Table S1, Fig. 2).

In total, 45.76% of the species were classified as pioneer, 28.81% secondary and 25.42% climax. There was a high abundance of herbaceous individuals from the hemicryptophyte and camephyte life forms, represented by the species with the highest cover, relative frequency and importance, *Trachypogon spicatus* (L.f.) Kuntze and *Croton agoensis* Baill., respectively (Table S1).

Gallery forest structure

A total of 440 individuals, distributed in 56 species, 51 genera and 33 families were registered in sample units of gallery forest, where the number of species per sample unit ranged from 15 to 26. The families with the largest number of species were Fabaceae (n = 8), Arecaceae (n = 5), Annonaceae and Myrtaceae (n = 4). 25 families were represented by a single species. Fabaceae was the family with the largest number of species per sample unit. 41 species belonged to the herbaceous-shrub stratum, eight were climbing plants and 15 were regenerating trees. As for distribution, 11 were new records for the State of Maranhão, five occurred exclusively in the Cerrado biome and ten of them occurred exclusively in the Cerrado and Amazon biomes (Table S2, Fig. 3).

In total, 30.36% of the species were classified as pioneer, 44.64% secondary and 25% climax. There was a high abundance of individuals from phanerophytic (39) and liana (8) forms of life. The species with the highest coverage, relative frequency and importance were *Protium heptaphyllum* (Aubl.) Marchand and *Bauhinia dubia* G. Don, respectively.

Physiognomy sample sufficiency and diversity

The analytical richness estimator (Bootstrap) showed a total of 68.67 and 66.44 species for the total sampling of typical cerrado and gallery forests, respectively. Thus, there was a good representation of common species and part of rare species in physiognomies. Considering the species of the herbaceous-shrub stratum of the typical cerrado, sample units 7 and 8 were the most diverse and most equitable. For gallery forests, sample units 3 and 6 were the most diverse and most equitable (Table 2).

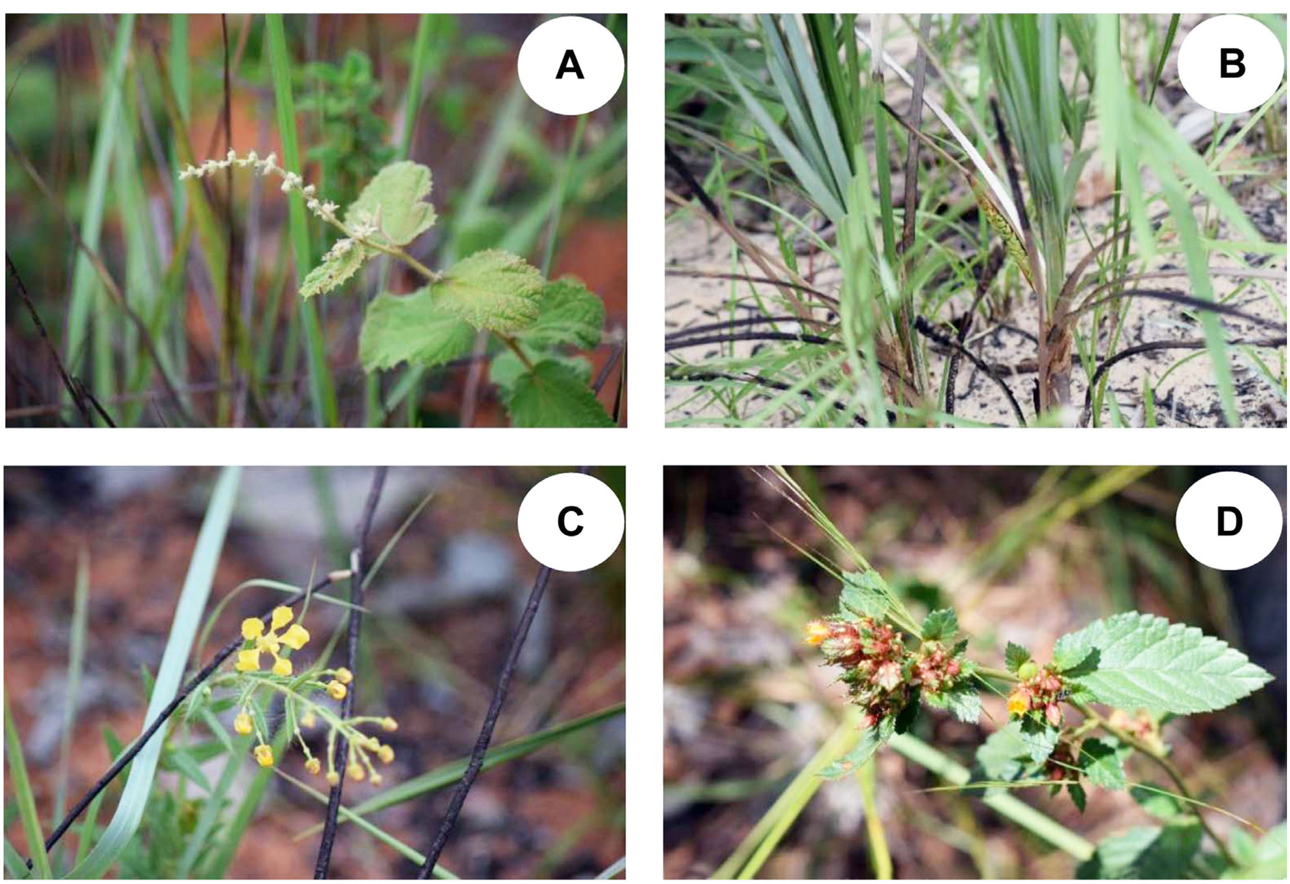

Figure 2. Species of the herbaceous-shrub and regenerating tree strata of typical cerrado in CMNP. (A) *Croton agoensis* Baill.; (B) *Syagrus allagopteroides* Noblick & Lorenzi; (C) *Camarea affinis* A.St.-Hil; (D) *Turnera melochioides* Cambess. (SARAIVA, R.V.C.).

Figure 3. Species of the herbaceous-shrub and regenerating tree strata of gallery forest in CMNP. (A) *Bauhinia dubia* G.Don.; (B) *Rhynchospora cephalotes* (L.) Vahl; (C) *Oenocarpus distichus* Mart.(em regeneração); (D) *Turnera stipularis* Urb. (SARAIVA, R.V.C.).

Table 2. Shannon-Weiner diversity index (H') and Pielou's equitability (J) for the herbaceous-shrub species of twelve sampling units of typical cerrado (TC) and six of gallery forest (GF). *Nonexistent

	1	2	3	4	5	6	7	8	9	10	11	12
TC N	92	94	113	114	145	160	171	159	90	103	132	107
TC S	10	12	9	8	18	13	18	18	9	10	10	8
TC H'	1.12	1.23	0.76	0.96	1.89	1.45	1.95	2.05	1.22	1.26	1.47	1.4
TC J	0.49	0.49	0.35	0.46	0.66	0.56	0.68	0.71	0.56	0.55	0.64	0.67
GF N	62	61	75	67	32	35	*	*	–	–	–	–
GF S	15	16	21	15	10	12	–	–	–	–	–	–
GF H'	2.28	2.14	2.69	1.63	2.06	2.38	–	–	*	*	–	–
GF J	0.84	0.77	0.88	0.6	0.89	0.96	–	–	–	–	*	*

Edaphic factors and vegetation

In typical cerrado, the soil showed a red color, sandy texture, good aeration, large pores and high permeability. The gallery forest soil showed similar physical characteristics, but was brownish. Regarding chemical variables, the soils of both physiognomies were characterized as strongly acidic, with low levels of organic matter, sodium (Na), phosphorus (P), potassium (K); medium to low Mg content and with exchangeable aluminum in high quantity. Calcium (Ca) concentration was considered low in typical cerrado and in sample unit 2 of the gallery forest (the other units had high levels). There was a difference between the physiognomies regarding concentrations of K, Ca, Mg, H + Al, Al, H and granulometric parameters (Fig. 4).

The Redundancy Analysis revealed that the typical cerrado and gallery forest sample units formed two distinct groups, based on composition and species abundance, and

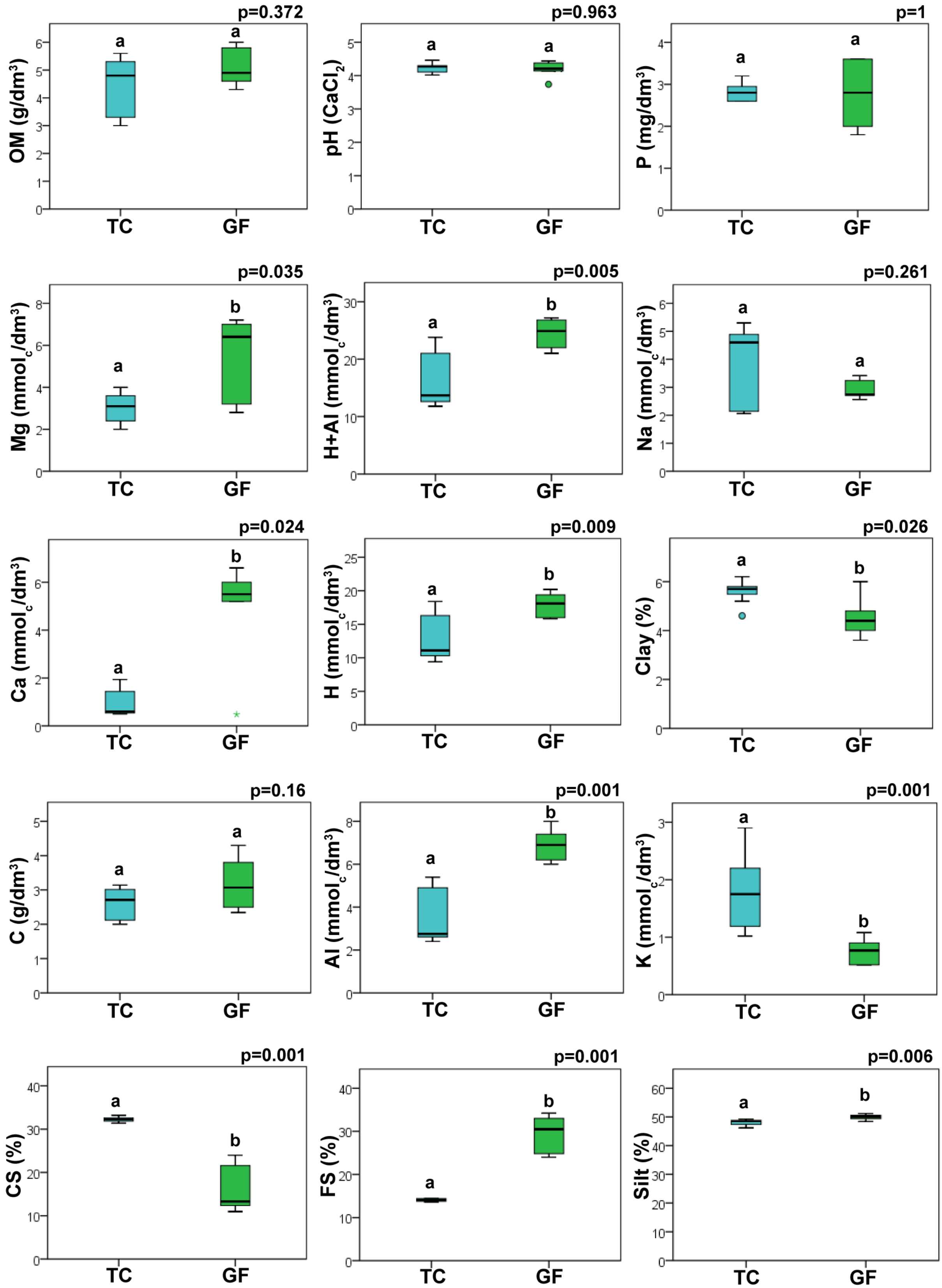

Figure 4. Boxplots graphs for 15 soil parameters analyzed for typical cerrado (TC) and gallery forest (GF) sampling units at CMNP. CS: coarse sand; FS: fine sand. The different letters indicate significant differences between the sampling units by the Kruskal-Wallis test (p<0,05).

their relationship with the chemical and granulometric soil properties. The first ordination axis explained 81.96% of structure and composition variation, which evidenced the clear separation of both physiognomies' sample units. The variable Al was more important for the first ordination axis. The predictor variables associated with each group presented pronounced differences. The second axis explained 6.49% of the variation in structure and species composition. The variable Ca was more important for the second ordination axis.The groups formed by the RDA were confirmed by the Variance Analysis ($F_{1,4}$ = 8.3; p = 0.001) (Fig. 5).

In typical cerrado, the RDA identified two groups of species. The first group made of species with higher coverage and importance values, with emphasis on *Trachypogon spicatus* (L.f.) Kuntze and *Croton agoensis* Baill. and associated species that tended to occur in clayish soils with high K content. The second group formed by *Lippia grata* Schauer, *Mimosa somnians* Humb. & Bonpl. Ex Willd., *Astrocaryum campestre* Mart., *Connarus suberosus* Planch., *Casearia sylvestris* Sw., *Desmodium barbatum* (L.) Benth., *Axonopus polydactylus* (Steud.) Dedecca, *Gomphrena virgata* Mart., *Combretum mellifluum* Eichler, *Byrsonima crassifolia* (L.) Kunth and *Diospyros lasiocalyx* (Mart.) B. Walln. is negatively associated with the parameters Ca and Mg (Fig. 5).

The RDA for gallery forest identified two groups of species. The first group suggested that species with higher coverage and importance values *Protium heptaphyllum* (Aubl.) Marchand e *Bauhinia dubia* G.Don and associated species tend to be more abundant in soils with high Al, Mg and Ca content.The second group suggested that *Attalea eichleri* (Drude) A.J.Hend., *Rhynchospora cephalotes* (L.) Vahl, *Siparuna guianensis* Aubl, *Myrcia splendens* (Sw.) DC. and *Schnella glabra* (Jacq.) Dugand had densities negatively associated to K and clay values (Fig. 5). The variation in the occurrence and abundance of the species among the two physiognomies can be explained by the purely edaphic fraction, adjusted R^2 = 68.22%, while 31.78% (residuals) remain unexplained.

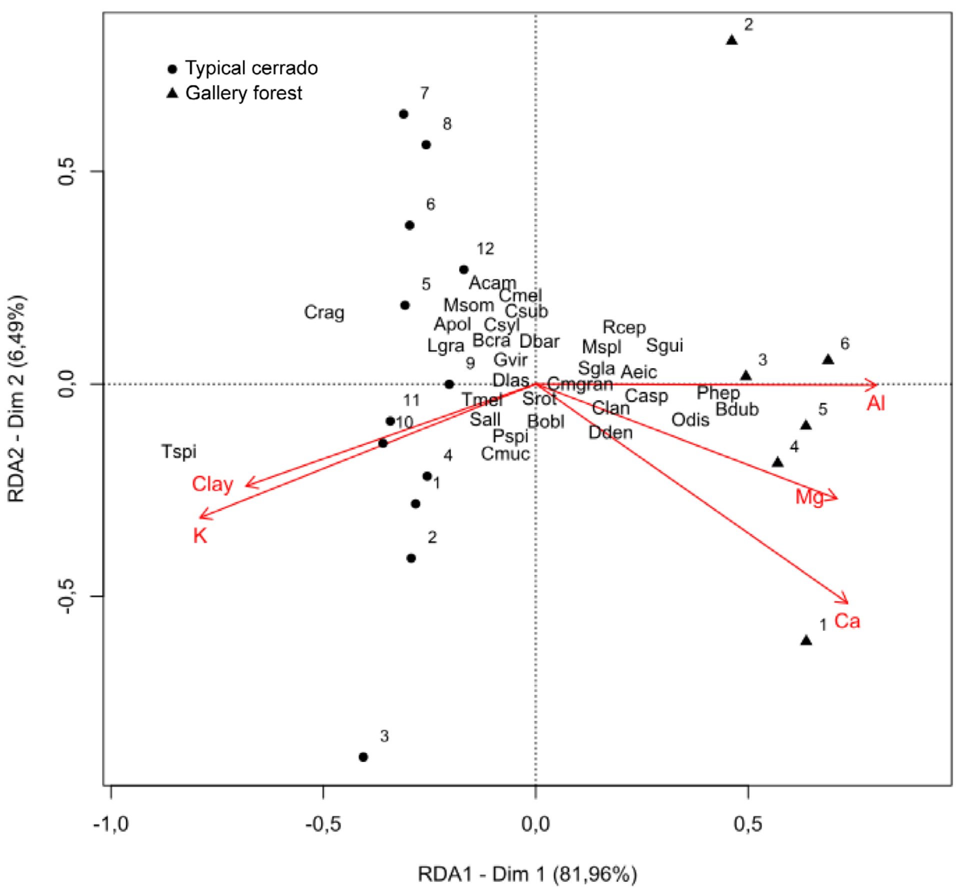

Figure 5. Redundancy Analysis of species of the herbaceous-shrub and regenerating tree strata, physical-chemical properties, in the two Cerrado phytophysiognomies sampled in the CMNP, Carolina, Maranhão, Brazil. OM: organic matery. Acam: *Astrocaryum campestre*; Aeic: *Attalea eichleri*;Apol: *Axonopus polydactylus*; Bcra: *Byrsonima crassifolia*; Bdub: *Bauhinia dubia;* Bobl: *Byrsonima oblongifolia*; Casp: *Campomanesia* sp.; Clan: *Copaifera langsdorffii*;Cmel: *Combretum mellifluum*; Cmgran: *Campomanesia grandiflora*; Crag: *Croton agoensis*; Csub: *Connarus suberosus*; Csyl: *Casearia sylvestris*; Cmuc: *Croton mucronifolius*; Dbar: *Desmodium barbatum*; Dden: *Doliocarpus dentatus*;Dlas: *Diospyros lasiocalyx*; Gvir: *Gomphrena virgata*; Lgra: *Lippia grata*; Msom: *Mimosa somnians*; Mspl: *Myrcia splendens;* Odis: *Oenocarpus distichus*; Phep: *Protium heptaphyllum*;Pspi: *Paspalum spissum*; Rcep: *Rhynchospora cephtalotes*; Sall*: Syagrus allagopteroides*; Sgla: *Schnella glabra*; Sgui: *Siparuna guianensis*; Srot: *Stryphnodendron rotundifolium*; Tmel: *Turnera melochioides*; Tspi: *Trachypogon spicatus*.

Discussion

The initial hypothesis was confirmed. The results and inferences about the vegetation structure and physical-chemical parameters of the soil, suggest that the management for conservation of the CMNP must consider the particularities of the Cerrado physiognomies and the vegetation responses to environmental filters, such as edaphic conditions and associations with other organisms.

Edaphic factors and vegetation

The existence of a significant positive association between structural parameters and soil properties emphasizes that edaphic factors are important environmental filters for the occurrence and distribution of strata species in the typical cerrado and gallery forest. The results of Redundancy analysis (RDA) for the typical cerrado showed that there is a tendency to gather sample units from the two areas analyzed, which means homogeneity in terms of composition and abundance of the most frequent species in the CMNP. The low beta diversity values in this physiognomy highlighted low variation in species composition between sample units.

Gallery forest RDA analysis recorded heterogeneity between sample units, despite sampling being carried out in the same area. In the sample units, the high beta diversity values and low association between species with higher importance values support the heterogeneous vegetation pattern established in gallery forest literature (Marimon *et al*. 2002; Marimon *et al*. 2010). This characteristic makes it difficult to choose species that are widely used in recovery programs and highlights the importance of local level physiognomy information (Oliveira & Paula 2001).

Physical properties and soil depth can be combined to determine water availability in the soil, which limits the establishment of regenerating herbaceous species and seedlings (Bond 2008). The interaction between soil fertility with the water availability and water retention ability can strongly influence forest and savanna physiognomy limits (Oliveras & Malhi 2016). According to Bond (2010), in savanna physiognomies, tree species obtain nutrients from deep layers in the soil (about 2 m), which there are adequate stocks of nutrients to sustain species with this habit. The edaphic conditions can also be influenced by the spreading of fires, as the ashes deposited on the surface tend to increase the pH and availability of cations in the soil (Pivello *et al*. 2010).

While we cannot definitively claim that fire directly impacts the ratio of sand and clay in the soil, it could exert an indirect influence by diminishing organic matter particles. These organic remnants become integrated into the soil, subsequently augmenting the quantity of clay soil particles (Fig. 4 and 5).

In the CMNP Cerrado, in typical cerrado physiognomy, P was considered a nutrient associated with the plant species abundance and composition. In this sense, the availability of P was one of the main nutrients that influenced the height and basal area of tree species in the Cerrado (Bond 2010). For gallery forest physiognomy, the importance of Ca for vegetation can be explained by the multiple effects that can favor plant development, contributing to a greater return of organic matter. Ca can be leached in large quantities by percolating water, replaced by H^+ ions, which results in acidic soils (Gama & Bezerra 2015). In Cerrado soils, M.O and Ca can be limiting factors, thus they can influence species occurrence in physiognomies (Bindraban *et al*. 2015).

Although not often researched, the relationship of gallery forest soils with vegetation has not been confirmed and the results were considered to be inconclusive in a Cerrado-Amazonia transition region (Maracahipes-Santos *et al*. 2017). In fact, species composition of gallery forests is the result of the influence of anthropic, edaphic and hydrogeomorphological factors (Correia *et al*. 2001; Marimon *et al*. 2010; Carvalho *et al*. 2013), with the last factor being considered the main one in arboreal communities (Sampaio *et al*. 2000). It is also suggested that the existence of plant communities can be mediated by biotic filters through direct interactions with other organisms (Macedo *et al*. 2020), such as mycorrhiza (Lortie *et al*. 2004).

It is important to emphasize that the fertility conditions of the fragments alone cannot be pointed out as the primary requirement for the establishment of one or another cerrado physiognomy. Most likely, it is the combination of various factors that govern this process, although the soil is undoubtedly one of the most important, whether due to its fertility or its physical or hydrological condition, or all of them.

Fire influencing diversity

The absence of a significant difference in the number of species and beta diversity with the distance in the typical cerrado and in the gallery forest may be associated with the size of the analyzed scale. There are greater distances where there could be an increase in the number of parameters, considering that species composition changes may be the result of limiting dispersion (Condit *et al*. 2002).

In this research, burning that occurred at the beginning of the dry season, in June 2017, probably contributed to stimulate *Byrsonima oblongifolia* A. Juss and *Gomphena virgata* Mart. flowering, both geophytes, found four months after the burning. It is known that the stimulus for geophyte species flowering with adaptive characteristics for the effect of fire can have origins in the occurrence of burning or isolated rains during the drought (Munhoz & Felfili 2005; Pausas & Keeley 2017).

The proximity of the H' values between sample units in different post-fire periods showed that the herbaceous-shrub stratum vegetation in the typical cerrado recovered in a short period after the burning at the beginning of the dry season. The importance of evaluating the burning regimes, which can interfere with the ability to recompose species in this stratum, is emphasized (Keeley *et al*. 2011).

In the area without fire for at least two years (area 2), there was no significant increase in herbaceous-shrub layer diversity in the seven-month period, which may be related to the negative effect of fire suppression, which causes invasion of forest vegetation (Oliveras & Malhi 2016). In addition to structural changes, fire suppression results in species composition changes, mainly in the herbaceous-shrub layer since many of them depend on light to germinate (positive photoblastic species) (Kolb *et al*. 2016). Species diversity reduction in this stratum was verified by Pinheiro and Durigan (2009), when part of the Cerrado vegetation (field formation) at the Ecological Station of Assis, state of São Paulo, was protected from fire for 22 years and over that period to present forest characteristics in terms of structure and composition.

Research at CMNP contributed to filling the gap on the association between vegetation structural parameters and soil physical-chemical properties, which is a challenging topic in tropical ecotonal regions, such as in the Cerrado-Amazon transition zone. The significant association between the aforementioned parameters emphasizes that Al and Ca are important environmental filters for the distribution and diversity of species in the herbaceous-shrub and regenerating arboreal stratum in the ecotonal Cerrado in homogeneous (typical cerrado) and heterogeneous (gallery forest) physiognomy. Management of ecotonal Cerrado conservation must consider diversity and edaphic condition maintenance that can influence the restoration of herbaceous-shrub and regenerating tree vegetation.

As limitations of the work, which may be suggestions for future studies, we can mention research in more than one gallery forest area for the purpose of comparing the parameters in these areas. We also emphasize that in this physiognomy, in addition to edaphic parameters, studies are needed that consider how the vegetation structure can be influenced by water retention. In the physiognomy of a typical cerrado, it is important to evaluate how burning regimes can interfere with the species' ability to regenerate in the long term. In both physiognomies it is also necessary to consider biotic filters through direct interactions with other organisms, such as mycorrhiza.

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Supplementary Materials

The following online material is available for this article:

Table S1. Species of the herbaceous-shrub and regenerating tree strata that occurred in twelve sampling units of typical cerrado in CMNP, Carolina, MA.

Table S2. Species of the herbaceous-shrub and regenerating tree strata that occurred in six sampling units of gallery forest in CMNP, Carolina, MA.

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