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Influence of edaphic variables on the floristic composition and structure of the tree-shrub vegetation in typical and rocky outcrop *cerrado* areas in Serra Negra, Goiás State, Brazil¹

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ABSTRACT – (Influence of edaphic variables on the floristic composition and structure of the tree-shrub vegetation in typical and rocky outcrop *cerrado* areas in Serra Negra, Goiás State, Brazil). The present study analyzed the influence of edaphic variables on the floristic compositions and structures of the arboreal and shrub vegetation of typical cerrado (TC) and rocky outcrop cerrado (RC) communities in the Serra Negra mountain range in Piranhas Municipality, Goiás State, Brazil. Ten 20×50 m plots were established in each community, and all individuals with minimum diameters ≥ 5 cm measured at 30 cm above soil level were sampled. Composite soil samples were collected at 0-20 cm depths in each plot for physical and chemical analyses. The proportions of above-ground rock cover work also estimated in each RC plot. A total of 2,009 individuals (83 species, 69 genera, and 34 families) were recorded. *Qualea parviflora* was the only species consistently among the 10 most structurally important taxa in both communities, and was considered a generalist species. The observed and estimated species richnesses were greater in RC than in TC, although plant basal areas and heights did not differ between them. There were positive correlations between rock cover \times plant density and rock cover \times basal areas. TWINSPAN and PCA analysis separated the TC and RC plots, and three RC habitat specialist species (Wunderlichia mirabilis, Norantea guianensis, and Tibouchina papyrus) were identified. Soil variables were found to have greater effects on the species compositions of the TC and RC sites than the geographic distances between sampling plots. According to CCA analysis, the exclusive (or more abundant species) of each community were correlated with soil variables, and these variables therefore determined the selection of some species and influenced the differentiation of the vegetation structures of the communities studied.

Key words - conservation, rocky outcrops, savanna, soils

INTRODUCTION

The occurrence of a plant species in a given environment is dependent on distinct factors acting at different spatial scales. The floristic composition and structure of the vegetation on local scales may be related to local topography and geomorphology (Motta et al. 2002), physicochemical properties of the soil (Reatto et al. 2008, Ribeiro & Walter 2008), local fire history (Moreira 2000, Miranda et al. 2007), and/or anthropogenic disturbances (Ribeiro & Walter 2008). The wide distribution of the *Cerrado* biome (approximately 2,000,000 km²) and its contact with the Amazon Forest, Atlantic Forest, *Caatinga* (dryland), and *Pantanal* (seasonally inundated) (Ribeiro & Walter 2008) allow for ample floristic mixing at regional scales (Castro & Martins 1999, Méio et al. 2003). Therefore, regional variations in climatic conditions (Silva et al. 2008) and altitudes (Motta et al. 2002), as well as the floristic influences of the biomes in direct contact with the Cerrado (Castro & Martins 1999, Pinto & Oliveira Filho 1999, Méio et al. 2003, Ratter et al. 2003, Bridgewater et al. 2004) act as determinates of regional species composition, favoring high richness.

According to Ribeiro & Walter (2008), the Cerrado biome comprises forest, savanna, and *campestre* (open field) formations, with cerrado sensu stricto being characterized as a savanna formation composed of dense, typical, thin, and rocky outcrop cerrado physiognomies that are distinguishable based on their densities, heights, and tree-shrub covers. The principal

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determinants of these vegetation types are largely related to edaphic factors – especially the depth of the water table, drainage, the effective depth of the soil profile, the presence of concretions (Haridasan 2000), soil texture (Marimon Junior & Haridasan 2005), and the percentage of exposed rock. Other environmental factors such as fire frequency also have a role in determining cerrado savanna typologies (Ribeiro & Walter 2008).

Rocky outcrop cerrado is distinguishable from the other three cerrado physiognomies by the presence of many endemic habitat-specialist species (Romero & Nakajima 1999, Simon & Proença 2000, Pinto et al. 2009, Lima et al. 2010) that grow in areas of accentuated topography with many rock outcrops and shallow soils, where individual trees establish themselves in clefts in the rocks so that their densities will vary as a function of the specific conditions of each site (Ribeiro & Walter 2008).

Comparative studies of the woody vegetation of rocky outcrop and typical cerrado sites can aid in evaluating the effects of edaphic conditions on their floristic compositions and structures. Floristic and phytosociological surveys are important vehicles for increasing our knowledge and understanding of the woody flora of rocky outcrop cerrado vegetation, especially in light of the fact that this phytophysiognomy has been well described (Ribeiro & Walter 2008) but its community structure, spatial distribution, and interactions with the abiotic environment are not yet well understood. Rocky outcrop cerrado physiognomies have apparently been less impacted by anthropogenic activities as its stony nature makes crop cultivation nearly impossible (Machado et al. 2004). This situation increases the importance of floristic and structural analyses of the vegetation structure of rocky outcrop cerrado sites in elucidating interactions between vegetation formations and edaphic factors as well the role of this vegetation in maintaining the floral diversity of the Cerrado biome as a whole.

As such, the present study describes and compares the floristic compositions and structures of the tree-shrub vegetation of neighboring areas of typical cerrado and rocky outcrop cerrado vegetation, and evaluates the effects of distance and soil properties on the floristic composition at a local geographical scale in the Serra Negra Mountain Range, Goiás State, Brazil, in order to address the following hypotheses: 1. That the floristic compositions and vegetation structures of typical cerrado and rocky outcrop cerrado are different; 2. That soil characteristics influence the unique floristic compositions and vegetation structures of rocky outcrop cerrado and typical cerrado; 3. That the densities and basal areas of tree-shrub individuals in rocky outcrop cerrado sites are inferior to those of typical cerrado.

MATERIAL AND METHODS

The present study was undertaken in the Serra Negra Mountain Range, in Piranhas Municipality, in the western mesoregion of Goiás State, Brazil (16°25'37" S and 51°49'20" W). The regional climate is predominately type Aw according to the Köppen classification system, with two well-defined seasons: one dry and cold, and the other hot and humid; with an annual average precipitation rate of 1700 mm, an annual average temperature of 25 °C, maximum and minimal annual average temperature of 32 °C, and 18 °C, respectively (Silva et al. 2008).

The Serra Negra Range varies in altitude between 650 and 1000 m a.s.l. (Oliveira 2000) and extends between the cities of Piranhas and Baliza in Goiás State. It has a strongly contrasting topography of elevated peaks composed of rocks belonging to the Goiás Volcanic-Sedimentary Bom Jardim Complex of the Cuiabá and Granito Piranhas Group – part of the Goiás Magmatic Arc that formed during the Neoproterozoic era; the rocky outcrops are composed of approximately 500,000,000 year-old granites (Oliveira 2000).

The vegetation of the Serra Negra is composed of a mosaic of different cerrado physiognomies (sensu Ribeiro & Walter 2008) with deciduous forests dominating on the steep slopes of the mountains, with high abundance of *Attalea speciosa* Mart. ex Spreng. (Arecaceae), and small natural areas of rocky outcrop cerrado. Narrow strands of non-flooding gallery forests are found in the valleys at the bases of the mountains. The tops of the mountains tend to be flat to undulating, and the typical cerrado there has largely been converted to pasture – leaving only small fragments of this original vegetation.

The study area was located 15 km from the town of Piranhas. We inventoried the trees and shrubs of the woody plant communities of typical cerrado (TC) ("cerrado típico" sensu Ribeiro & Walter 2008) ($16^{\circ}27^{2}3^{\circ}$ S and $51^{\circ}53^{\circ}46^{\circ}$ W; altitudes between 740 and 790 m) and rocky outcrop cerrado (RC) ("cerrado rupestre" sensu Ribeiro & Walter 2008) ($16^{\circ}26^{\circ}55^{\circ}$ S and $51^{\circ}53^{\circ}58^{\circ}$ W; altitudes between 760 and 810 m); the two inventory sites were separated by 300 m. We established ten 20×50 m (0.1 hectare) plots separated by minimum distances of 50 m in both communities, totaling 2 ha, following the methodology described by Felfili et al. (2005)

Floristic and phytosociological surveys were undertaken in all plots, identifying to the species level all of trees, shrubs and monocotyledons individuals with minimum stem diameters ≥ 5 cm at 30 cm above soil level (DB₃₀). The circumferences of all living individuals (including monocotyledons) were measured at 30 cm above soil level, as well as their total heights. Plant identifications were made in the field whenever possible, or by subsequent consultation of the published literature and herbarium specimens held at the Nova Xavantina (NX) and Brasília University (UB) herbaria. The botanical classification followed APG III (2009) and the current nomenclature was confirmed using the Flora do Brasil electronic databank (Forzza et al. 2010). Reference samples of fertile individuals of all of the species collected were incorporated into the NX herbarium.

Soil samples were collected at depths of 0-20 cm, using a soil auger (Van Raij 1991), at three points (beginning, middle, and end) in each of the 10 plots in the TC and RC sites surveyed, totaling 20 samples. The soil samples were chemically analyzed by a commercial laboratory to determine their pH, organic material content (OM), cationic exchange capacity (CEC), texture, and the concentrations of P, K, Ca, Mg, S, Na, Al, Fe, Zn, Mn, Cu, and B, following Embrapa (1997) protocols. Total N concentrations were estimated by calculating N = OM/40, according to Bezerra (2006). The percentage coverage of rock outcrops (or stones) in the rocky outcrop cerrado sites were visually estimated in each plot and classified into four categories: class 1 – from 0 to 25% rock cover; class 2 – from 26 to 50%; class 3 – from 51 to 75%; class 4 – from 76 to 100%.

The EstimateS 8.0 software was used to estimate the accumulated species richnesses of the two communities using 10,000 randomizations and eight different estimators (ICE, Chao 1, Chao 2, Jack 1, Jack 2, Boostrap, MMRuns, and MMMeans) (Gotelli & Colwell 2001, Colwell 2008). The best estimator was chosen based on analyses of the Spearman Correlations between the observed and estimated values of each area based on the maximum correlation value (Brose et al. 2003).

In order to characterize the phytosociological parameters of the plant communities examined we calculated the relative and absolute values of density, frequency, and dominance, which together yield the importance value (IV) (Mueller-Dombois & Ellenberg 1974), using the Mata Nativa 2 software package (Cientec 2005).

Vegetation classification in the two study areas was undertaken using TWINSPAN (Two-Way Indicator Species Analysis) (Hill 1979) including all of the species sampled, with cutoff levels of 10, 15, 20, 25, and 30. Principal Component Analysis (PCA) was used to reduce the edaphic variables, using the PC-Ord program (McCune & Mefford 1997). The principal matrix included all of the 20 chemical and physical soil variables (Ca, Mg, Al, H+Al, K, P, organic material – OM, S, Na, Zn, B, Cu, Fe, Mn, cation exchange capacity – CEC, base saturation, aluminum saturation, clay, sand, and silt) while the secondary matrix considered the TC and RC plots. This procedure helped eliminate variables with low correlations and significance, resulting in the selection of nine principal edaphic variables (CEC, OM, Mg, Ca, base saturation, aluminum saturation, sand, clay, and silt).

After selection, a second PCA was performed to correlate these edaphic variables with the plots of the

communities sampled. Canonic Correspondence Analysis (CCA) was used to ordinate the edaphic variables with the vegetations of the TC and RC communities, with the principal matrix being composed of species with 10 or more individuals in at least one community (totaling 39 species), the secondary matrix used the nine edaphic variables selected by PCA.

The Mantel Partial test was used to examine the effects of the edaphic variables and the distances between the sites on species composition, using species abundance as the principal matrix and the edaphic variables and the distances between the plots as secondary matrices, using NTSYS 2.1 software (Rohlf 2000). Environmental data expressed in varying units were standardized to comparable equivalences and weights, and the positions of the plots were expressed in metric units (UTM coordinates).

Spearman Correlation analyses were performed only for the rocky outcrop cerrado sites, in terms of their different estimated exposed rock covers per plot, considering the densities of the individuals, their basal areas, and median heights. The median diameters (DB₃₀), heights, and densities between the two communities were compared using the Mann-Whitney test (U). This same test was also used to evaluate the differences between the edaphic variables of the two sites. These analyses were undertaken using BioStat 5.0 software (Ayres et al. 2007). A 5% level of significance was adopted in all of the statistical analyses.

RESULTS

A total of 2009 individuals were encountered in the two vegetation communities, representing 83 species, 69 genera, and 34 families (table 1). Twenty-two species occurred only in typical cerrado (TC) and 23 only in rocky outcrop cerrado (RC); 38 species were common to both communities. Fifty-eight species, 51 genera, and 31 families were encountered in the TC, while 61 species, 51 genera, and 27 families were encountered in the RC. The estimated species richness of the TC using the Mao Tau method, when compared to the abundance of 931 individuals in the RC, was 56.33 ± 1.85 , which was less than the number of species recorded in the RC. The correlation analyses indicated that Bootstrap was the best species estimator as it estimated 63.24 species in the TC site and 67.34 species in the RC, with a correlation value of r = 0.999 with the numbers of species observed in the two communities.

Three species were most highly represented in the TC in terms of numbers of individuals: *Byrsonima pachyphylla* (174 ind ha⁻¹), *Qualea parviflora* (121 ind ha⁻¹), and *Davilla elliptica* (91 ind ha⁻¹), which represented approximately 16%, 11% and 8% of the community respectively. The three most abundant species in the

ocky outcrop cerrado (RC) sites sampled in the Serra Negra	D = absolute density; RD = relative density; AF = absolute	ce value).
Phytosociological parameters of tree-shrub vegetation (DB ₃₀ \ge 5 cm) of typical cerrado (TC) and rocky of	n range in Piranhas Municipality, Goiás State, Brazil. Species in decreasing order of IV of TC. (AD = abs	y; RF = relative frequency; ADo = absolute dominance; RDo = relative dominance; IV = importance val
Table 1.	mountai	frequent

Chariae	Equily	AD		RD		A	AF	RF		ADo		RDo		N
species	raumy	TC	RC	TC	RC	TC	RC	TC RC	TC	RC	TC	RC	TC	RC
Qualea parviflora Mart.	Vochysiaceae	121	186	11.22	19.98	100	100	3.56 4.27	2.37	7 3.17	18.15	5 26.66	32.93	50.90
Byrsonima pachyphylla A.Juss.	Malpighiaceae	174	Ι	16.14	Ι	100	I	3.56 -	1.06	5	8.15		27.84	Ι
Byrsonima coccolobifolia Kunth	Malpighiaceae	60	8	5.57	0.86	100	70	3.56 2.99	0.73	3 0.07	5.62	0.59	14.74	4.43
Davilla elliptica A.StHil.	Dilleniaceae	91	33	8.44	3.54	100	40	3.56 1.71	0.34		2.62		14.62	6.31
Terminalia argentea Mart.	Combretaceae	32	8	2.97	0.86	80	60	2.85 2.56		_		2 1.29	12.73	4.71
Pouteria ramiflora (Mart.) Radlk.	Sapotaceae	35	1	3.25	0.11	100	10	3.56 0.43				_	12.40	0.73
Curatella americana L.	Dilleniaceae	36	7	3.34	0.75	100	30	3.56 1.28	0.71			1.20	12.33	3.23
Eriotheca gracilipes (K.Schum.)	Malvaceae	19	12	1.76	1.29	90	60	3.2 2.56	0.96	5 0.30	7.34	1 2.51	12.30	6.36
A.Robyns														
Bowdichia virgilioides Kunth	Fabaceae	21	5	1.95	0.54	90	40	3.2 1.71					11.44	
Ouratea spectabilis (Mart. ex Engl.) Fnol	Ochnaceae	31	4	2.88	0.43	100	30	3.56 1.28	0.56	5 0.10	4.33	0.85	10.76	2.56
	,					0					i			
Qualea grandiflora Mart.	Vochysiaceae	37	4	3.43	0.43	90	20				3.56		10.20	
Qualea multiflora Mart.	Vochysiaceae	43	16	3.99	1.72	100	60	3.56 2.56		5 0.19	1.92	2 1.61	9.46	5.89
Vernonia sp.	Asteraceae	50	I	4.64	I	70	I	2.49 –	0.22	-	1.69		8.82	I
<i>Roupala montana</i> Aubl.	Proteaceae	39	I	3.62	Ι	100	I	3.56 -	0.17	- 2	1.31	I	8.48	Ι
Erythroxylum tortuosum Mart.	Erythroxylaceae	40	Ι	3.71	Ι	100	Ι	3.56 -	0.14		1.04	۱ ـــ	8.31	I
Tabebuia aurea (Silva Manso) Benth.	Bignoniaceae	12	9	1.11	0.64	70	40	2.49 1.71	0.29	90.0 6	2.19	0.73	5.79	3.08
& Hook.f. ex S.Moore	1													
Leptolobium dasycarpum (Vogel) Yakovlev	Fabaceae	17	4	1.58	0.43	70	30	2.49 1.28	0.22	2 0.03	1.68	8 0.22	5.74	1.93
Licania humilis Cham. & Schltdl.	Chrysobalanaceae	16	Ι	1.48	Ι	70	Ι	2.49 –	0.23	-	1.75		5.72	Ι
Lafoensia pacari A.StHil.	Lythraceae	18	58	1.67	6.23	70	100	2.49 4.27	0.12	2 0.51	0.91	4.29	5.06	14.79
Stryphnodendron rotundifolium Mart.	Fabaceae	15	1	1.39	0.11	80	10	2.85 0.43	0.08	8 0.00	0.60		4.83	0.56
Hymenaea stigonocarpa Mart. ex	Fabaceae	16	26	1.48	2.79	09	80	2.14 3.42	0.15	5 0.44	1.15	3.72	4.77	9.92
Hayne														
Connarus suberosus Planch.	Connaraceae	15	1	1.39	0.11	70	10				0.39		4.27	0.61
Erythroxylum engleri O.E.Schulz	Erythroxylaceae	15	1	1.00	0.11	60	10				0.42		3.94	0.57
Mouriri elliptica Mart.	Melastomataceae	6	4	1.02	0.43	60	20	2.14 0.85	0.09	9 0.04	0.72	0.33	3.87	1.61
Psidium salutare (Kunth) O.Berg	Myrtaceae	8	7	0.74	0.75	60	30	2.14 1.28	0.11	1 0.08	0.83	9.0.68	3.71	2.71
Salvertia convallaeriodora A.StHil.	Vochysiaceae	5	Ι	0.46	Ι	30	Ι	1.07 -	0.27		2.07		3.59	Ι
Diospyros hispida A.DC.	Ebenaceae	11	I	1.21	Ι	50	I	1.78 –	0.08		0.58	1	3.56	Ι
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Species	Family	TC	RC	TC	RC	TC	RC	TC RC	TC	RC	TC	RC	TC	RC
Annona crassiflora Matt. Psendohombar tomentosum (Mart &	Annonaceae Malvaceae	9	<u>ب</u> ا	0.56	0.64	50 30	- 08	1.78 – 1.07 1.28	0.10	- 0.06	0.80	- 050	3.13 2.04	- 7 43
Zucc.) A.Robyns		D	þ		F 0.0	2	2		01.0	0.00	C1.1	00.0	F 2.4	CF4
Astronium fraxinifolium Schott	Anacardiaceae	S	13	0.46	1.40	50	80	1.78 3.42	0.05	0.16	0.41	1.37	2.65	6.18
Buchenavia tomentosa Eichler	Combretaceae	9	0	0.56	0.21	50	10		0.04	0.01	0.29	0.12	2.62	0.76
Syagrus flexuosa (Mart.) Becc.	Arecaceae	8	45	0.74	4.83	40	80		0.02	0.18	0.18	1.55	2.34	9.80
Caryocar brasiliense Cambess.	Caryocaraceae	4	4	0.37	0.43	40	20		0.03	0.42	0.26	3.56	2.05	4.84
Butia sp.	Arecaceae	ŝ	4	0.28	0.43	30	30		0.04	0.05	0.29	0.40	1.63	2.10
Andira cujabensis Benth.	Fabaceae	4	Ι	0.37	Ι	30	Ι		0.02	Ι	0.19	Ι	1.62	I
<i>Mezilaurus crassiramea</i> (Meisn.) Taub. ex Mez	Lauraceae	4	1	0.37	0.11	20	10	0.71 0.43	0.05	0.08	0.42	0.64	1.5	1.17
Piptocarpha rotundifolia (Less.) Baker	Asteraceae	5	I	0.46	I	10	I		0.07	I	0.55	I	1.37	I
Cordiera sessilis (Vell.) Kuntze	Rubiaceae	0	0	0.21	0.21	20	20	0.85 0.85	0.02	0.02	0.14	0.14	1.20	1.20
Vochysia rufa Mart.	Vochysiaceae	0	Ι	0.19	Ι	20	Ι		0.03	Ι	0.25	I	1.15	I
Luehea grandiflora Mart. & Zucc.	Malvaceae	С	I	0.28	I	20	I		0.02	I	0.14	Ι	1.12	Ι
Vatairea macrocarpa (Benth.) Ducke	Fabaceae	С	7	0.28	0.21	20	10		0.02	0.02	0.12	0.20	1.10	0.84
Tachigali aurea Tul.	Fabaceae	0	I	0.19	I	20	I		0.02	I	0.13	I	1.02	I
Guapira noxia (Netto) Lundell	Nyctaginaceae	0	I	0.19	I	20	I		0.02	I	0.12	I	1.01	I
<i>Chamaecrista orbiculata</i> (Benth.) H.S.Irwin & Barneby	Fabaceae	7	I	0.19	I	20	Ι		0.01	I	0.11	I	1.00	I
Aspidosperma tomentosum Mart.	Apocynaceae	0	44	0.19	4.73	20	70		0.01	0.27	0.05	2.23	0.95	9.94
Magonia pubescens A.StHil.	Sapindaceae	4	55	0.37	5.91	10	80	0.36 3.42	0.03	0.69	0.21	5.78	0.94	15.10
Agonandra brasiliensis Miers ex Benth. & Hook. f.	Opiliaceae	7	I	0.19	I	20	I		0.01	I	0.04	ı.	0.93	ı
Kielmeyera rubriflora Cambess.	Clusiaceae	0	48	0.19	5.16	10	80		0.02	0.49	0.17	4.15	0.70	12.72
Dipteryx alata Vogel	Fabaceae	1	7	0.09	0.21	10	20	0.36 0.85	0.03	0.08	0.20	0.68	0.64	1.74
Hancornia speciosa Gomes	Apocynaceae	1	1	0.09	0.11	10	10		0.02	0.02	0.14	0.15	0.59	0.68
Copaifera langsdorffii Desf.	Fabaceae	1	1	0.11	0.11	10	10		0.01	0.01	0.05	0.05	0.58	0.58
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae	-	I	0.09	I	10	I	0.36 –	0.01	I	0.10	ı	0.55	ı
Strychnos pseudoquina A.StHil.	Loganiaceae	1	I	0.09	I	10	I		0.01	I	0.09	I	0.53	ı
Erythroxylum daphnites Mart.	Erythroxylaceae	1	1	0.09	0.11	10	10	0.36 0.43	0.01	0.00	0.09	0.02	0.53	0.55
Olacaceae NI 1	Olacaceae	1	I	0.09	I	10	I		0.01	I	0.09	ı	0.53	ı

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obecies	r'amuy	TC	RC	TC	RC	TC	RC	TC RC	TC	RC	TC	RC	TC	RC
Myrtacae NI 1	Myrtaceae	-	13	0.09	1.40	10	70	0.36 2.99		1 0.18	0.04	1.53	0.48	5.91
Andira vermifuga (Mart.) Benth.	Fabaceae	1	Ι	0.09	Ι	10	Ι	0.36 -	0.00		0.03	ı	0.48	ı
Enterolobium gummiferum (Mart.) J.F.Macbr.	Fabaceae	1	I	0.09	I	10	I	0.36 -	0.0	-	0.03	ı	0.48	ı
Machaerium acutifolium Vogel	Fabaceae	1	1	0.09	0.11	10	10	0.36 0.43		0.00	0.02	0.04	0.47	0.57
Rudgea viburnoides (Cham.) Benth.	Rubiaceae	1	Ι	0.09	I	10	I	0.36 -	00.00		0.02	ı	0.47	ı
<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Arecaceae	I	7	I	0.21	Ι	20	- 0.85		0.04	Ι	0.35	I	1.41
Aspidosperma macrocarpon Mart.	Apocynaceae	Ι	11	Ι	1.18	I	70	- 2.99	- (0.21	I	1.78	ı	5.95
Aspidosperma subincanum Mart.	Apocynaceae	Ι	4	Ι	0.43	I	20	- 0.85		0.02	I	0.15	ı	1.43
Banisteriopsis latifolia (A.Juss.) B Gates	Malpighiaceae	I	1	I	0.11	I	10	- 0.43	-	0.00	Ι	0.02	I	0.55
Callisthene fasciculata Mart	Vochvsiaceae	I	6	I	0 97	I	30	- 1 25	 ~	0.22	I	1 83	ı	4 08
Ervthroxvlum suberosum A.StHil.	Ervthroxvlaceae	I	ŝ	Ι	0.32	Ι	30	- 1.28		0.05	Ι	0.40	ı	2.00
Eugenia aurata O.Berg	Myrtaceae	Ι	14	I	1.50	I	60	- 2.5(0.18	I	1.48	I	5.54
Eugenia punicifolia (Kunth) DC.	Myrtaceae	Ι	14	Ι	1.50	Ι	40	- 1.71		0.12	Ι	0.98	ı	4.19
Sapium argutum (Müll. Arg.) Huber	Euphorbiaceae	I	6	Ι	0.97	Ι	60	- 2.50		0.04	Ι	0.37	ı	3.90
Heisteria ovata Benth.	Olacaceae	Ι	0	Ι	0.21	Ι	20	- 0.85		0.01	Ι	0.06	ı	1.134
Kielmeyera coriacea Mart. & Zucc.	Clusiaceae	Ι	116	Ι	12.46	Ι	100	- 4.27		0.91	Ι	7.69	ı	24.42
Luehea candicans Mart. & Zucc.	Malvaceae	I	1	Ι	0.11	I	10	- 0.43		0.01	Ι	0.07	ı	0.60
Luetzelburgia praecox (Harms) Harms	Fabaceae	Ι	17	Ι	1.83	I	60	- 2.56		0.19	I	1.59	ı	5.98
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	Ι	ω	Ι	0.32	Ι	20	- 0.85		0.02	Ι	0.19	ı	1.36
Norantea guianensis Aubl.	Marcgraviaceae	I	17	Ι	1.83	I	50	- 2.14		0.23	I	1.90	ı	5.85
Peltogyne confertiflora (Mart. ex Hayne) Benth.	Fabaceae	Ι	2	I	0.54	I	20	- 0.85		0.06	I	0.50	I	1.89
Plathymenia reticulata Benth.	Fabaceae	Ι	1	Ι	0.11	Ι	10	- 0.43		0.00	Ι	0.03	ı	0.56
Platypodium elegans Vogel	Fabaceae	I	0	Ι	0.21	Ι	20	- 0.85		0.02	Ι	0.20	ı	1.27
<i>Plenckia populnea</i> Reissek	Celastraceae	I	8	Ι	0.86	Ι	50	- 2.14		0.04	Ι	0.32	ı	3.31
Pseudobombax longiflorum (Mart. & Zucc.) A.Robvns	Malvaceae	I	39	I	4.19	I	100	- 4.2	-	0.65	I	5.50	I	13.96
Syagrus comosa (Mart.) Mart.	Arecaceae	1	1	0.09	0.11	Ι	10	- 0.43		0.01	Ι	0.04	ı	0.57
Tibouchina papyrus (Pohl) Toledo	Melastomataceae	I	1	Ι	0.11	Ι	10	- 0.43		0.00	Ι	0.02	ı	0.55
<i>Wunderlichia mirabilis</i> Riedel ex Baker	Asteraceae	I	14	I	1.5	I	20	- 0.85	1	0.39	I	3.30	ı	5.66
Total		1.078	931	100	100	2.810	2.340	100 100	13.04	4 11.87	100	100	300	300

RC were: *Qualea parviflora* (186 ind ha⁻¹), *Kielmeyera coriacea* (116 ind ha⁻¹), and *Lafoensia pacari* (58 ind ha⁻¹), which represented approximately 20%, 12%, and 6% of the community respectively (table 1).

The densities of live individuals in the 10 TC and RC plots were 1078 ind ha⁻¹ and 931 ind ha⁻¹ respectively, while the total basal areas of live individuals were 13.04 m² ha⁻¹ in TC, and 11.7 m² ha⁻¹ in RC. The densities of live individuals per plot were significantly higher in the TC (U = 5.27; P = 0.0001), although there were no differences between the basal areas per plot between TC and RC sites (U = 1.436; P = 0.9069). The greatest concentrations of live individuals in the TC and RC sites were between the height classes of 2.1 and 4.0 m, reinforcing the tree-shrub characters of these two woody communities. The average heights in the TC and RC sites (3.7 and 3.8 m respectively) were similar (U = 1.52; P = 0.1278), while the average diameter of the individuals in the TC sites (9.2 cm) was lesser than that found in the RC (10.1 cm) (U = 4.60; P = 0.0001). The percentage rock exposition in the RC was positively related to plant density ($r^2 = 0.2991$; P = 0.0025) and basal area ($r^2 = 0.3127$; P = 0.0015), but no relationship was identified between percentage rock exposition and the heights of individuals per plot ($r^2 = 0.0547$; P = 0.5887).

The 10 species with the greatest Importance Value (IV) in the TC accounted for approximately 54% of the total IV, 70% of the total basal area, and 57% of the total density, while the 10 species with the greatest IV in the RC contributed to 56% of the IV, 64% of the total basal area, and 67% of the density (table 1). Of the 10 most important species in the two areas, *Qualea parviflora* demonstrated the largest relative values of density, dominance, and frequency – which guaranteed it the greatest IV in the two areas. Species such as *Wunderlichia mirabilis*, *Tibouchina papyrus*, *Norantea guianensis*, *Kielmeyera coriacea*, and *Pseudobombax longiflorum* were recorded only in RC, while *Byrsonima pachyphylla*, *Roupala montana*, *Erythroxylum tortuosum* and *Vernonia* sp. occurred only in TC.

TWINSPAN classification consistently separated the TC and RC plots in the first division (eigenvalue of 0.56), with only two RC plots (RC2 and RC7) being grouped with those of TC (figure 1). *Byrsonima pachyphylla* was considered as the indicator species of TC, as it only occurred in that community. *Davilla elliptica, Qualea grandiflora,* and *Vernonia* sp. demonstrated consistently higher numbers of individuals in TC. *Kielmeyera coriacea* was considered as the indicator species of RC, while *Aspidosperma*

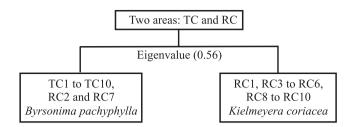


Figure 1. TWINSPAN classifications of 20 sampling plots of the typical cerrado (TC1 to TC10) and rocky outcrop cerrado (RC1 to RC10) in the Serra Negra mountain range in Piranhas Municipality, Goiás State, Brazil.

tomentosum, Qualea parviflora, Magonia pubescens, Syagrus flexuosa, and Kielmeyera rubriflora were considered as the preferential.

Based on field observations and on the physical analyses of the soils (table 2), the TC site was found to have well-drained Red-Yellow Latosols with large quantities of clay and silt. The soils at the RC site were identified as Sandy Shallow Neosols on granitic outcrops. The superficial layer of the RC soil was dark, indicating the presence of organic material in the substrates occurring in the rock fissures. The soils of both communities had loam-clay-sandy textures (sensu Embrapa 2006), were dystrophic, acidic, and allic, had low CECs and base saturations and high concentrations of exchangeable potassium (table 2). There were significant differences between the two areas in terms of their concentrations of H+Al, K, P, OM, N, and Na, and in terms of soil texture, with the greatest mineral concentrations found in the RC site (table 2).

Phosphorus availability was considered low in both areas, with values between 0.1 and 1.8 mg dm⁻³; K values were 93 mg dm⁻³ in the TC and 115 mg dm⁻³ in the RC. All of the soil samples demonstrated elevated acidity, with pH values between 3.8 and 4.3 (Malavolta 1992). The RC site had high OM contents, especially in plots 5, 7 and 8 (with values of 54 g dm⁻³) (Bezerra 2006). In general, Ca and Mg varied from low to moderate in the TC and RC sites respectively. High Al saturation values were observed in both TC (38.2%) and RC (48.7%) sites, with low base saturations in both communities (table 2). In relation to the micronutrients, B, Zn and Cu showed low concentrations, while Fe and Mn concentrations were very high in both areas (Malavolta 1992).

The concentrations of the macronutrients N, P and K were always greater in RC. No significant differences were noted between the micronutrient concentrations in the two phytophysiognomies examined, or differences between their CECs and base saturations. The clay

Table 2. Comparisons of the physical and chemical characteristics of the soils (0-20 cm depth) of typical cerrado (TC) and
rocky outcrop cerrado (RC) areas in the Serra Negra mountain range in Piranhas Municipality, Goiás State, Brazil. Results
of <i>P</i> in bold type represent significant differences (< 0.05) between the areas by the Mann-Whitney test (U). (OM = organic
material; CEC = cation exchange capacity).

Drace artica		TC			RC		U	Р
Properties	Maximum	Minimum	Average	Maximum	Minimum	Average	U	P
Ca (cmol _c dm ⁻³)	1.50	0.40	0.65	1.00	0.10	0.45	1.81	0.06
Mg (cmol _c dm ⁻³)	0.90	0.30	0.35	0.60	0.10	0.30	1.47	0.14
Al (cmol _c dm ⁻³)	1.00	0.50	0.80	1.20	0.80	0.90	1.47	0.14
H+Al(cmol _c dm ⁻³)	8.90	5.30	6.70	10.10	7.20	8.15	2.45	0.01
$K (mg dm^{-3})$	115.00	81.00	93.00	128.00	95.00	115.00	3.02	<<0.01
$P(mg dm^{-3})$	0.30	0.10	0.20	4.00	0.10	0.50	2.04	0.04
OM (g dm ⁻³)	54.00	31.00	38.00	54.00	35.00	48.00	2.34	0.01
N (40%) (g dm-3)	1.35	0.77	0.95	1.35	0.87	1.20	2.34	0.01
S (mg dm ⁻³)	7.10	3.40	5.60	8.7	2.80	4.20	1.22	0.22
Na (mg dm ⁻³)	6.00	4.00	5.00	7.00	5.00	6.00	2.34	0.01
Zn (mg dm ⁻³)	1.80	0.40	0.50	0.80	0.40	0.70	1.36	0.17
$B (mg dm^{-3})$	0.17	0.12	0.15	0.17	0.12	0.15	0.49	0.62
Cu (mg dm ⁻³)	0.70	0.40	0.50	0.60	0.30	0.50	1.28	0.19
Fe (mg dm ⁻³)	125.90	81.90	90.15	116.20	72.10	91.55	0.03	0.96
Mn (mg dm ⁻³)	56.40	31.70	42.80	52.20	20.10	36.70	1.28	0.19
CEC	9.94	6.86	8.32	11.51	8.10	9.03	1.81	0.06
Base Sat. (V%)	31.88	10.48	13.99	19.87	6.41	11.40	1.73	0.08
Al Sat. (m%)	52.08	15.67	38.20	67.07	28.23	48.70	1.51	0.13
pH/CaCl ₂	4.30	3.80	3.90	4.00	3.80	3.90	0.64	0.52
Clay (g kg ⁻¹)	370.00	300.00	345.00	320.00	300.00	300.00	3.17	<<0.01
Silt (g kg ⁻¹)	100.00	80.00	90.00	90.00	80.00	80.00	2.38	0.01
Sand (g kg ⁻¹)	620.00	540.00	560.00	620.00	590.00	620.00	3.17	0.00

content of the TC soil was greater than that of the RC substrate (table 2).

The TC and RC plots were separated by Principal Component Analysis (PCA), with the variance percentage of axis 1 being 44.33% and axis 2 being 28.34%; both axes together explained 72.68% of the accumulated variance (figure 2). In general, axis 1 was associated with soil chemical variables, while axis 2 reflected their physical variables. The TC plots, located in the lower left of the diagram, were related to larger concentrations of the micronutrients Ca and Mg, greater base saturations, and higher concentrations of clay and silt. The RC plots, located in the upper right of the diagram, were related to sites with higher aluminum saturation, and higher concentrations of organic material, CEC, and sand.

Soil properties had greater influence on species composition of the TC and RC sites (r = 0.27886; P = 0.0016) than did the distances between the plots (r = 0.14510; P = 0.0463) as determined by Mantel Partial Analysis. Canonic Correspondence Analysis (CCA) demonstrated a separation of the plant species of the TC and RC communities, corroborating the previous analyses (figures 1, 2 and 3). The variance percentages explained by the CCA axes (figure 3) were 33 and 5.8% for axis 1 and 2 respectively. The Pearson Correlations were significant for both axis 1 (r = 0.932) and axis 2 (r = 0.875). In general, edaphic variables were better correlated with axis 1, while only the variables OM and Al were better correlated with axis 2. The Monte Carlo permutation test yielded a value of P = 0.005, indicating that the species-variables relationships of the two axes were significant.

Species that demonstrated positive and significant correlations with the right side of axis 1 in the CCA (figure 3), such as *Norantea guianensis* and *Wunderlichia mirabilis*, were exclusive to or most abundant in RC and were associated with greater values of sand, aluminum saturation, OM, and CEC. The species on the left side of axis 1 of the CCA were exclusive to or most abundant in TC, such as *Byrsonima pachyphylla*, *Roupala montana*, and *Davilla elliptica*, and were associated with greater values of clay, silt, base saturations, Ca, and Mg.

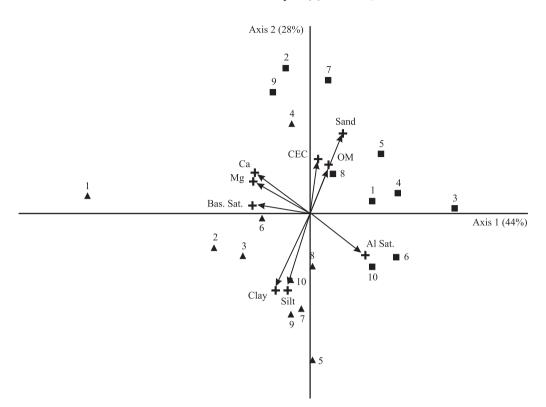


Figure 2. Principal Components Analysis (PCA) of the attributes of the 10 plots $(20 \times 50 \text{ m})$ established in typical cerrado (**A**) and 10 plots in rocky outcrop cerrado (**B**) and their physicochemical soil variables (+) in the Serra Negra mountain range in Piranhas Municipality, Goiás State, Brazil.

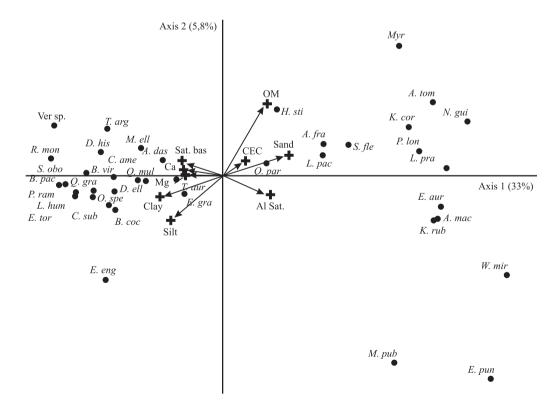


Figure 3. Ordination diagram of Canonical Correspondence Analysis (CCA) of the densities of 39 (\bullet) common species ($n \ge 10$ individuals) of typical cerrado (TC) and rocky outcrop cerrado (RC) and (+) edaphic variables in the Serra Negra Mountain Range in Piranhas Municipality, Goiás State, Brazil.

DISCUSSION

Tree-shrub cerrado savanna formations growing on rocky substrates might be expected to have reduced plant densities (Ribeiro & Walter 2008) - which could limit species richness. However, both the recorded and estimated (Bootstrap) species richnesses of RC were greater than those of TC in the present study, and similar studies undertaken in rocky outcrop cerrado areas in central Brazil corroborate this similarity in species richness between the two formations (Pinto et al. 2009, Lima et al. 2010, Moura et al. 2010, Maracahipes et al. 2011, Gomes et al. 2011). Hypothesis 1, that RC areas should be more restrictive to the establishment of plant species because of their rock outcrops and shallow soils, was not corroborated in the present study or by other studies undertaken in the Cerrado biome (Pinto et al. 2009, Lima et al. 2010, Gomes et al. 2011). As such, it can be concluded that the shallow substrate and uneven topography of rocky outcrop cerrado sites are not determinate factors of local richness or alpha-diversity (Felfili & Felfili 2001, Moura et al. 2010).

The fact that the densities of live individuals in TC were observed to be greater than those of RC indicates that the inclined topography and the rocky and shallow RC substrate are determinate factors limiting the establishment of individuals (Ribeiro & Walter 2008). In spite of the lower densities of plants in the RC, the basal area values and average heights of those individuals did not differ between TC and RC sites. Additionally, the diameter values in the RC areas were greater than those seen in TC sites, indicating that in spite of the lower densities of individuals in the RC studied here their development and biomass accumulations were significant greater. As such, species established in areas with rock outcrops appear to possess appropriate colonization strategies and are adapted to surviving in rocky crevices, those successfully occupying the few sites available to them (Ribeiro & Walter 2008). Other authors have likewise noted the capacity of certain species to develop in shallow rocky soils, resulting in woody communities that are structurally similar to those observed on deep soils (Silva et al. 2002, Pinto et al. 2009, Moura et al. 2010, Lima et al. 2010, Gomes et al. 2011). Individuals of some woody cerrado species that occur in rocky outcrop cerrado areas demonstrate more premature, intense, and prolonged deciduousness during the dry season than individuals of the same species growing in typical cerrado sites on deep soils (Silvério & Lenza 2010). As such, we can infer that one of the strategies of plants growing on soils with reduced capacities for water retention (as in the case of rocky outcrop cerrado) is the plasticity of their phenological events – which serve to reduce water losses and maximize water use during the dry season.

Other indications of the success of individuals growing on rocky RC soils included significant positive relationships between the percentages of rock cover (rock cover classes) and plant density, and between rock cover and basal area; no significant relation was detected between rock cover and plant height. These results contradicted hypothesis 3 - that the densities and basal areas of tree-shrub individuals in rocky outcrop cerrado areas would be inferior to those values in typical cerrado sites. As such, the micro-sites available in RC areas studied apparently offer adequate conditions for the establishment and successful development of woody individuals. It also appears that the rocky substrate of the rocky outcrop cerrado promotes greater micro-habitat heterogeneity and therefore provides greater varieties of sites adequate to the establishment of different species - explaining the elevated richness values observed.

The high representivity of just a few species in terms of their numbers of individuals and their importance values, as seen in the present study, is often observed in woody savanna communities of typical cerrado (Felfili & Silva Júnior 1993, Cardoso et al. 2002, Campos et al. 2006) and rocky outcrop cerrado (Amaral et al. 2006, Viana & Lombardi 2007, Lima et al. 2010). There were, however, marked differences between the 10 most important species in the two cerrado communities, with only Qualea parviflora being of marked structural importance in both TC and RC sites. Other studies have likewise demonstrated significant differences between the most important species (in terms of vegetation structure) in typical cerrado and rocky outcrop cerrado areas (Pinto et al. 2009, Lima et al. 2010, Lenza et al. 2011, Gomes et al. 2011). Thus, although the TC and RC areas shared considerable numbers of species (n = 38species, 34.48% of the species of TC and 37.70% of the species of RC), they were still significantly different in terms of the species that dominated each community.

The high numbers of species and individuals of the genus *Qualea* and their high representivity suggests that the taxa of this genus are well-adapted to different substrates and are therefore widely distributed in the Cerrado biome (Ratter et al. 2003). *Qualea parviflora* demonstrated the largest IV in the RC, confirming a pattern observed in previous phytosociological studies of cerrado savanna formations (Nogueira et al. 2001, Felfili et al. 2002, Balduino et al. 2005, Amaral et al. 2006, Felfili & Fagg 2007, Miranda et al. 2007, Pinto et al. 2009). This taxon was considered a generalist species by Ratter et al. (2000), and has been reported in many areas throughout the Cerrado biome.

Rocky outcrop cerrado areas have generally been described as having high numbers of habitat-specialist species among herbaceous-subshrub plants (Pirani et al. 1994, Harley 1995, Romero & Martins 2002, Conceição & Pirani 2007) as well as in the tree-shrub layer (Simon & Proença 2000). The edaphic characteristics and climatic conditions of rupestral environments appear to favor the occurrence of rare, endemic, and habitat-specialist species (Pirani et al. 1994, Romero & Nakajima 1999, Simon & Proença 2000). Only three habitat-specialist species were encountered in the rocky outcrop cerrado (Tibouchina papyrus, Wunderlichia mirabilis and Norantea guianensis) in the present study, as was also reported by Amaral (2006), Pinto et al. (2009), and Ribeiro & Walter (2008), suggesting that the RC areas studied have peculiar flora.

The floristic and structural peculiarities of the TC and RC were confirmed by classification (TWINSPAN) and ordination (PCA) analyses that separated the two areas in consistent and significant manners according to their edaphic variables - corroborating our hypothesis that soil properties significantly influence the floristic and structural differences between rocky outcrop cerrado and typical cerrado sites. A study undertaken by Gomes et al. (2011) that compared adjacent areas of typical cerrado and rocky outcrop cerrado near Nova Xavantina, MT, demonstrated the formation of groups of plots from TC and RC areas using DCA - Detrended Correspondence Analysis. As such, certain soil properties must be acting at local scales in differential manners in the two communities. The floristic and structural results presented here reinforce the classification system of Cerrado physiognomies proposed by Ribeiro & Walter (2008) that is principally based on edaphic properties.

The chemical properties of RC soils may facilitate or maintain species growth as they contain significant quantities of the macronutrients N, P, K and S as well as organic material. It is known that rock crevices can accumulate organic material and, consequently, nutrients needed for plant growth and development (Benites et al. 2007).

It therefore appears that distinct physical-chemical soil properties, with greater proportions of clay and micronutrients in TC areas and sandier RC soils with higher levels of OM and macronutrients are responsible for the floristic and structural differences of these two vegetation communities. A number of studies have shown that edaphic factors, such as soil fertility and its physical composition, can influence local floristic compositions and species distributions (Ratter & Dargie 1992, Haridasan 2000, Oliveira Filho & Ratter 2002, Moura et al. 2010). Marimon Junior & Haridasan (2005), for example, reported large differences in the floristic compositions of two areas of typical cerrado and cerradão (arboreal cerrado) that were more closely related to soil texture than to any other factor. The thin soils of rocky outcrop cerrado areas and their highly sandy texture may limit the establishment and development of certain arboreal species, and these physical impediments to rooting may represent (together with the chemical attributes of the soils) a strong factor in species selection.

The results of the Mantel Partial Test consolidated the observation that the physical-chemical properties of the soils better explained the structural differences in the vegetation of the TC and RC areas than the distances between them – thus reinforcing hypothesis 2 (that the soil strongly influences floristic and structural differences between TC and RC). This hypothesis was also supported by the PCA analyses that demonstrated a relationship between RC plots and sandy soils with high levels of organic material and high aluminum saturation, while TC plots were more associated with finer soil textures (more clay and silt), greater base saturation, and higher concentrations of Ca and Mg. In specific terms, the CCA and TWINSPAN analyses indicated the separation of the vegetations of RC and TC sites. Among the species associated with RC by CCA were Wunderlichia mirabilis and Norantea guianensis – which are either habitat-specialists or endemic to rupestral environments (Paxisto 1985, Riberio & Walter 2008, Oliveira Filho & Fluminhan Filho 1999).

Species such as *Byrsonima pachyphylla*, *Roupala montana*, and *Davilla elliptica* were associated with TC soils, indicating their preferences for deeper substrates. These species have been cited as being abundant in areas of typical cerrado (Balduino et al. 2005, Marimon Junior & Haridasan 2005, Gomes et al. 2011) but generally do not occur (or are only found at very low densities) in rocky outcrop cerrado sites (Pinto et al. 2009, Lima et al. 2010, Moura et al. 2010, Lenza et al. 2011, Gomes et al. 2011). Thus, while generalist species such as *Qualea parviflora* can be found in both areas, there appears to be a selection for species more highly adapted to thin soils (such as *W. mirabilis* and *N. guianensis*) in RC sites and for species less tolerant to shallow soils (such as *R. montana* and *B. pachyphylla*) in TC sites.

Our results indicate that the rocky soils of RC areas do not restrict species richness or the establishment and development of woody individuals, but rather act to select for habitat-specialist species that prefer rocky soil and will dominate the community structure. Local factors, however, such as soils that have higher clay contents and higher concentrations of micronutrients in TC areas or sandy soils with high levels of OM and macronutrients in RC areas, may strongly influence the structural differentiation observed between rocky outcrop cerrado and typical cerrado areas.

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