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RESEARCH ARTICLE

Ferruginous Rupestrian Savannah: a floristic and structural analysis of these rare environments

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Abstract

The flora of the Rupestrian Savannah (Cerrado Rupestre) is composed of widely distributed species and endemic species from high altitude rocky outcrops. The aim of this study was to characterise the floristic composition, structure and diversity of fragments of Rupestrian Savannah in south-eastern Brazil and to examine the similarity with other rupestrian cerrado vegetations and with cerrado *sensu stricto* on profound soils. For this, phytosociological parameters, evenness and diversity were calculated and compared with other studies. The survey exhibited 72 species, 45 genera, 30 families and high floristic similarity with cerrado on profound soils. There were no indicator species of the Rupestrian Savannah, but there were typical species of rocky environments. The basal area was significantly larger in the profound soil cerrado in relationship to the Rupestrian Savannah and evenness was lower in the Rupestrian Savannah of this study compared to others. These variables reflect the lower exploration capacity of the root of rocky environments. The highest similarity between the Rupestrian Savannah and cerrado on profound soils refers to the canga ferruginous nature, which represents the limit of the tableland of cerrado on the edge of the plateaus, allowing greater sharing of flora.

Keywords
Brazilian flora, cerrado *sensu stricto*, floristic similarity, ironstone outcrop, species distribution

Introduction

The Cerrado constitutes the second largest Brazilian plant domain and the richest savannah in the world (Bueno et al. 2018). This domain is characterised by vegetation with a proper structure and flora (Lehmann et al. 2014), submitted to high aluminium content, low availability of nutrients and pronounced climatic seasonality (Arruda et al. 2017; Stevens et al. 2017). Nevertheless, it is estimated that the Cerrado flora comprises more than 12,000 vascular species (Mendonça et al. 2008), with communities that vary in different physiognomies (Bueno et al. 2018). However, although widely studied in terms of its flora and fauna, some of its formations have been only recently examined, such as the Ferruginous Rupestrian Savannah (or Ironstone Rupestrian Savannah) and many issues still remain unanswered.

The *core* area of the Cerrado *sensu lato* is clearly a *continuum*, with physiognomies that vary from grassland to forest (Ratter et al. 2003), whose variation is mainly based on edaphic, climatic and spatial factors. Ratter and collaborators (2003) have observed a strong phytogeographic pattern in the species distribution, indicating the prevalence of seven groups: Meridional, central south-east, central south-west, widely dispersed areas with a strong mesotrophic character, mesotrophic areas of the far west, isolated areas of the Amazon Rainforest and north-northeast.

The Cerrado vegetations occurs in various types of soil, but most of them are well drained, profound, acidic, nutrient poor and present high aluminium saturation (Arruda et al. 2017; Lenza et al. 2017). The Rupestrian Savannah is distinguished from cerrado *sensu stricto* (*s.s.*) because it occurs in shallow soils with rocky outcrops and its structure diverges from the Campo Rupestre by presenting arboreal covering of 5 to 20%, average height of 2 to 4 meters and scarce herbaceous stratum (Ribeiro and Walter 2008). The occurrence of the Rupestrian Savannah is restricted to the border of the plateaus of Central Brazil, where the formation of lateritic cangas (petroplintitas) predominates. This rock is similar to those of the Quadrilatero Ferrífero in Minas Gerais and Carajás in Pará (Schaefer et al. 2015). Already, the cerrado on profound soil presents lowest fertility, being related to chemically leached sediments on old and stable land surfaces. Their leached (low base contents, with a predominance of Al^{3+} in the exchange complex) and well drained (high sand content) soils reflect the high degree of evolution of these environments, when the desilicification process was facilitated (Arruda et al. 2015).

Studies conducted in areas of the Rupestrian Savannah reveal differences in density, basal area and richness in relation to cerrado *s.s.* on profound soils (Amaral et al. 2006; Jacobi et al. 2007; Moura et al. 2007; Pinto et al. 2009). The flora of the Rupestrian Savannah, on the other hand, is composed by species of large distribution in the Cerrado, considered as generalist and marked by the presence of endemic species of high-altitude rupestrian areas (Amaral et al. 2006; Miranda et al. 2007; Moura et al. 2007; Pinto et al. 2009; Carmo and Jacobi 2013; Carmo et al. 2018). However, studies that directly compare the floristic composition of these two formations are scarce.

Aiming for a better understanding of this plant formation, the objective of this study is to characterise the floristic composition, structure and diversity of a fragment of the Rupestrian Savannah and to examine the similarity amongst other Rupestrian Savannah areas and cerrado *s.s.* on profound soils to answer the following questions: i) Is this remnant more similar to other Rupestrian Savannah vegetations or to cerrado *s.s.*? ii) Are there species indicators of the Rupestrian Savannah? iii) Does the structure of the vegetation differ between the Rupestrian Savannah and those found on profound soils? iv) Do the richness and diversity from Rupestrian Savannah differ from those observed on profound soils?

Material and methods

Study area

Five fragments of Rupestrian Savannah located in Rio Paranaíba, state of Minas Gerais, south-eastern Brazil (19°11'38"S, 46°14'49"W) have been evaluated (Fig. 1). The evaluated fragments are predominantly composed of a continuous crust of canga, also known as "canga couraçada" (Rizzini 1979; Jacobi and Carmo 2008). The canga types observed in these areas form a rigid layer on the ground, the roots accessing the soil through cracks or settle down in rock pockets. This municipality is located in the mesoregion of Alto Paranaíba, with an average altitude of 922 m a.s.l. and area of approximately 1352.71 km^2. The regional climate is tropical savannah (Aw *sensu* Köppen – Alvares et al. 2014), with marked dry and wet seasons. The average annual temperature is 21 °C and the average rainfall is 1474 mm (Instituto Nacional de Meteorologia 2018). The region corresponds to the Plateaus of Central Brazil, with predominance of profound soils (Latosols). However, the study area corresponds to the plateau border, where there is a predominance of shallow soils (Cambisol and Litholic Neosol) and rock outcrop. These outcrops correspond to the ferruginous concretions (canga) and are observed in the form of a continuous crust or individualised bodies of different sizes (Motta et al. 2004).

Sampling

For the survey of woody species, 10 plots of 10 × 10 m were allocated at random on each of the five fragments, totalling 0.5 ha. All individuals with basal stem diameters (BSD) equal to or larger than 3.0 cm were evaluated in each of the plots (Moro and Martins 2011). Dead individuals were not included in our sampling. The identification of these species was conducted by comparison with herbarium specimens, the list of species of the Brazilian Flora (2018) and with the aid of specialists. For comparison

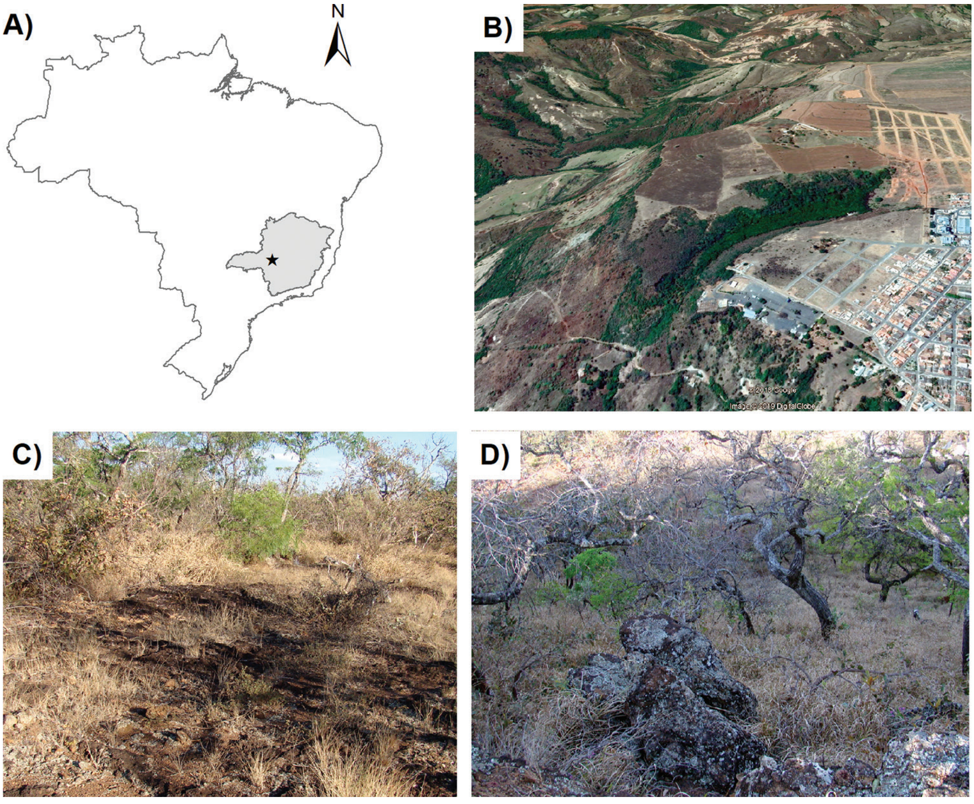

Figure 1. Geographic location (**A**) and aerial image of the border of the Rio Paranaíba plateau (**B**), Minas Gerais, south-eastern Brazil (image: Google Earth, 2019). The Rupestrian Savannah fragments have soils with ferruginous concretions (canga) and can be found in the form of continuous crust (**C**) or in blocks (**D**). The grey outline on the map represents the state of Minas Gerais and the star is the location of the municipality of Rio Paranaíba.

with other studies, we compiled twelve studies on the Rupestrian Savannah and eight studies on profound soils conducted in Minas Gerais and Goiás states (Table 1), both belonging to the same phytogeographic group, according to Ratter et al. (2003).

Data analysis

The phytosociological parameters (density, basal area), equitability and diversity (Shannon's diversity index – H') were calculated using the FITOPAC software (Shepherd 2010). The richness, structure and diversity of the present study were compared with the above-mentioned studies (Table 1) using the Student's t-test at a 5% significance level. To evaluate the floristic similarity of these areas, the divisional cluster analysis TWINSPAN (Two-Way Indicator Species Analysis) has been adopted using the PC-ORD software (McCune and Mefford 2006). For this, a matrix was prepared with data on the presence and absence of species that occurred in the twenty areas used for comparison, as well as in the present study (Table 1).

Table 1. Characteristics of Rupestrian Savannah and deep soil cerrado surveys conducted in Minas Gerais and Goiás states, Brazil, for the comparison of the present study. BSC = basal stem circumference; BSD = basal stem diameter.

Municipality/ Vegetation (Abbreviation)	Substrate	Area sampled (ha)	Inclusion criteria (cm)	Method	Richness	Diversity (H')	Equability (J')	Basal area (m^2/ha)	Density (ind/ha)	Source
Paraopeba-MG/ deep soil cerrado (PAS)	Dark-Red Latosol, Red-Yellow Latosol and Yellow Latosol	1	BSD ≥ 5	Plots	73	3.57	0.83	18.13	1990	Balduino et al. (2005)
Caldas Novas –GO/ deep soil cerrado (CNS)	Dark-Red Latosol, Red-Yellow Latosol	6	BSC ≥ 13	Square points	67	–	0.72	16.25 Area 1, 19.46 Area 2	1907 Area1, 2124 Area 2	Silva et al. (2002)
Abaeté- MG/ deep soil cerrado (ABS)	Dystrophic Red Latosol	0.3	BSC ≥ 10	Plots	85	3.5	0.8	29.97	4463.3	Saporetti et al. (2003)
Cocalzinho de Goiás/ Rupestrian Savannah (COC)	Quartzite and Quartzite-derived rock outcrops	1	BSD ≥ 5	Plots	65	3.45	0.83	5.67	674	Pinto et al. (2009)
Pirenópolis-GO/ Rupestrian Savannah (APR)	Litholic, Cambisol	1	BSD ≥ 5	Plots	65	3.65	0.87	11.03	1105	Moura et al. (2010)
Caldas Novas –GO/ Rupestrian Savannah (CNR)	Cambisols and Litholic Neosols	1	BSD ≥ 5	Plots	66	3.33	0.79	12.39	1357	Lima et al. (2010)
Alto Paraíso-GO/ Rupestrian Savannah (PLR)	Litholic Neosols, Cambisols and Quartz Sands associated with quartzite outcrops	1	BSD ≥ 5	Plots	71	2.81	0.66	11.25	1977	Lenza et al. (2011)
Cerrado-Amazonian Forest transition-MT/ Rupestrian Savannah (CFL)	Dystrophic Red-Yellow Latosol	1	BSD ≥ 3	Plots	85	3.45	0.77	15.72	376	Maracahipes et al. (2011)
Serra Negra-GO/ Rupestrian Savannah (SENrup)	Quartzite and Quartzite-derived rock outcrops	1	BSD ≥ 5	Plots	61	–	–	11.7	931	Abreu et al. (2012)
Serra Negra-GO/ cerrado *s.s.* (SENss)	Red-Yellow Latosol	1	BSD ≥ 5	Plots	60	–	–	13.04	1078	Abreu et al. (2012)
FLONA de Paraopeba-MG/ cerrado *s.s.* (PARyl)	Yellow Latosol	0.5	BSD ≥ 10	Plots	61	3.35	0.81	19.27	3365	Neri et al. (2012)
FLONA de Paraopeba-MG/ cerrado *s.s.* (PARhc)	Haplic cambisol	0.5	BSD ≥ 10	Plots	53	2.85	0.72	19.32	3910	Neri et al. (2012)
Bacaba Municipal Park-GO/ Rupestrian Savannah (BACrup)	Dystrophic, alic and acidic cambisols	1	BSD ≥ 3	Plots	78	–	–	13.00	2171	Gomes et al. (2016)
Bacaba Municipal Park-GO/ cerrado *s.s.* (BACss)	Quartzic lithic neosol	1	BSD ≥ 3	Plots	89	–	–	8.70	1523	Gomes et al. (2016)
Salto de São Domingos-GO/ Rupestrian Savannah (SSD)	–	1	BSD ≥ 5	Plots	58	1.51	0.37	4.6	543	Leles and Diniz (2017)
Sul de Minas gerais/ Rupestrian Savannah (SMGrup)	Litholic Neosol	1	BSD ≥ 5	Plots	47	3.10	0.79	10.91	769.16	Torres et al. (2017)
Sul de Minas gerais/ cerrado *s.s.* (SMGss)	Red Argisol	1	BSD ≥ 5	Plots	46	3.19	0.83	5.20	717.78	Torres et al. (2017)
Rio Paranaíba-MG/ Rupestrian Savannah (RPR)	Litholic Neosol with ferruginous concretions	0.1	BSD ≥ 3	Plots	72	2.89	0.67	9.19	2574	Present study

Results

In the Rupestrian Savannah of Rio Paranaíba, 1,287 individuals were sampled, corresponding to 72 species, 44 genera and 29 families. Six species, represented by only one individual each, remained undetermined, because they did not provide leaves or reproductive material during the development of the experiment. This vegetation exhibited a density of 2574 ind/ha and a basal area of 9.19 m^2/ha (Table 1). The richest families were Myrtaceae, Fabaceae, Malpighiaceae and Erythroxylaceae (Fig. 2A), corresponding to 58.66% of the observed richness. Sixteen families were composed of only one species and accounted for 55.17% of the richness. The most abundant families were Fabaceae, Erythroxylaceae, Vochysiaceae and Apocynaceae (Fig. 2B), representing 67.4% of the total individuals. The Pielou evenness (J) was 0.67 and the Shannon's diversity index (H') was 2.89.

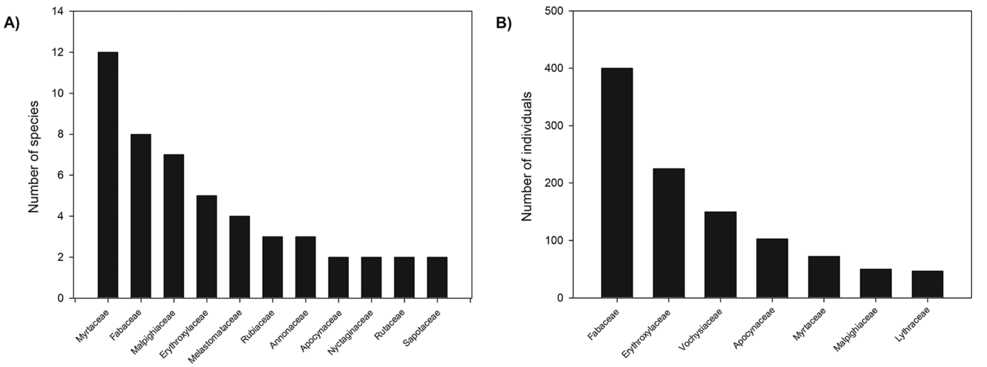

Figure 2. Distribution of species in the richest families (**A**) and individuals of the most abundant families (**B**) of the Rupestrian Savannah of Rio Paranaíba, Minas Gerais, south-eastern Brazil.

Table 2. Phytosociological parameters of species sampled in canga at Rio Paranaíba, Minas Gerais, south-eastern Brazil. AD = absolute density; ADo = absolute dominance; AF = absolute frequency; IV = importance value; N = number of individuals; RD = relative density; RDo = relative dominance; RF = relative frequency.

Species	N	AD	RD	AF	RF	ADo	RDo	IV
Dalbergia miscolobium Benth.	363	726.0	28.21	86.00	10.14	8.42	45.81	84.15
Erythroxylum daphnites Mart.	191	382.0	14.84	84.00	9.91	1.43	7.79	32.54
Qualea multiflora Mart.	128	256.0	9.95	68.00	8.02	1.23	6.71	24.68
Aspidosperma tomentosum Mart.	79	158.0	6.14	72.00	8.49	1.53	8.34	22.97
Erythroxylum tortuosum Mart.	34	68.0	2.64	40.00	4.72	0.25	1.37	8.73
Lafoensia pacari A.St.-Hil.	47	94.0	3.65	20.00	2.36	0.41	2.24	8.25
Heteropterys byrsonimifolia A.Juss.	20	40.0	1.55	22.00	2.59	0.54	2.92	7.07
Plenckia populnea Reissek	35	70.0	2.72	24.00	2.83	0.27	1.47	7.02
Kielmeyera petiolaris Mart.	18	36.0	1.40	16.00	1.89	0.66	3.57	6.85
Virola sebifera Aubl.	30	60.0	2.33	22.00	2.59	0.18	1.00	5.92
Hancornia speciosa Gomes	18	36.0	1.40	18.00	2.12	0.28	1.53	5.05
Palicourea rigida Kunth	21	42.0	1.63	24.00	2.83	0.10	0.54	5.01
Miconia albicans (Sw.) Triana	15	30.0	1.17	22.00	2.59	0.17	0.93	4.69

Species	N	AD	RD	AF	RF	ADo	RDo	IV
Stryphnodendron adstringens (Mart.) Coville	18	36.0	1.40	22.00	2.59	0.12	0.64	4.63
Eugenia sp. 2	19	38.0	1.48	20.00	2.36	0.10	0.52	4.36
Myrcia splendens (Sw.) DC.	18	36.0	1.40	18.00	2.12	0.07	0.38	3.91
Banisteriopsis malifolia (Ness & Mart.) B.Gates	14	28.0	1.09	20.00	2.36	0.07	0.35	3.80
Annona coriacea Mart.	10	20.0	0.78	18.00	2.12	0.13	0.69	3.59
Guapira noxia (Netto) Lundell	12	24.0	0.93	16.00	1.89	0.10	0.53	3.35
Styrax ferrugineus Nees & Mart.	15	30.0	1.17	12.00	1.42	0.13	0.73	3.31
Xylopia sericia A.St.-Hil.	21	42.0	1.63	8.00	0.94	0.13	0.70	3.28
Caryocar brasiliense Cambess.	5	10.0	0.39	6.00	0.71	0.30	1.60	2.70
Byrsonima verbascifolia (L.) DC.	9	18.0	0.70	12.00	1.42	0.07	0.40	2.51
Pouteria torta (Mart.) Radlk.	12	24.0	0.93	8.00	0.94	0.10	0.53	2.41
Vochysia thyrsoidea Pohl	7	14.0	0.54	4.00	0.47	0.22	1.20	2.22
Miconia sp. 1	9	18.0	0.70	6.00	0.71	0.15	0.80	2.21
Undetermined 1	7	14.0	0.54	10.00	1.18	0.02	0.12	1.84
Myrtaceae sp. 1	8	16.0	0.62	6.00	0.71	0.07	0.37	1.70
Myrtaceae sp. 2	5	10.0	0.39	6.00	0.71	0.10	0.53	1.63
Psidium pohlianum O. Berg	3	6.0	0.23	6.00	0.71	0.13	0.69	1.63
Machaerium sp. 2	10	20.0	0.78	4.00	0.47	0.06	0.35	1.60
Undetermined 2	5	10.0	0.39	8.00	0.94	0.03	0.17	1.50
Connarus suberosus Planch.	5	10.0	0.39	6.00	0.71	0.04	0.20	1.30
Eugenia sp. 1	5	10.0	0.39	6.00	0.71	0.03	0.17	1.27
Qualea parviflora Mart.	3	6.0	0.23	4.00	0.47	0.10	0.54	1.25
Tocoyena formosa (Cham. & Schltdl.) Schum.	4	8.0	0.31	6.00	0.71	0.03	0.15	1.17
Byrsonima crassifolia (L.) Kunth	4	8.0	0.31	4.00	0.47	0.04	0.23	1.01
Myrcia variabilis DC.	3	6.0	0.23	6.00	0.71	0.01	0.04	0.98
Undetermined 5	2	4.0	0.16	4.00	0.47	0.05	0.28	0.90
Machaerium sp. 1	4	8.0	0.31	4.00	0.47	0.01	0.06	0.84
Qualea grandiflora Mart.	2	4.0	0.16	4.00	0.47	0.04	0.20	0.83
Banisteriopsis sp.	3	6.0	0.23	4.00	0.47	0.02	0.09	0.79
Byrsonima coccolobifolia Kunth	2	4.0	0.16	4.00	0.47	0.03	0.17	0.79
Machaerium villosum Vogel	2	4.0	0.16	4.00	0.47	0.03	0.14	0.77
Enterolobium gummiferum (Mart.) J.F.Macbr.	2	4.0	0.16	4.00	0.47	0.03	0.14	0.77
Roupala montana Aubl.	2	4.0	0.16	4.00	0.47	0.02	0.12	0.75
Erythroxylum campestre A.St.-Hil.	2	4.0	0.16	4.00	0.47	0.02	0.11	0.73
Aegiphila lhotzkiana Cham.	2	4.0	0.16	4.00	0.47	0.02	0.10	0.73
Piptocarpha rotundifolia (Less.) Baker	2	4.0	0.16	2.00	0.24	0.06	0.33	0.73
Fabaceae sp.	3	6.0	0.23	2.00	0.24	0.04	0.23	0.70
Solanum lycocarpum A.St.-Hil.	3	6.0	0.23	2.00	0.24	0.02	0.10	0.57
Pouteria ramiflora (Mart.) Radlk.	2	4.0	0.16	2.00	0.24	0.02	0.10	0.49
Rudgea viburnoides (Cham.) Benth.	2	4.0	0.16	2.00	0.24	0.01	0.06	0.46
Ouratea castaneifolia (DC.) Engl.	1	2.0	0.08	2.00	0.24	0.03	0.14	0.45
Terminalia argentea Mart.	1	2.0	0.08	2.00	0.24	0.03	0.14	0.45
Undetermined. 4	2	4.0	0.16	2.00	0.24	0.01	0.05	0.44
Erythroxylum sp.	2	4.0	0.16	2.00	0.24	0.01	0.03	0.42
Undetermined 6	2	4.0	0.16	2.00	0.24	0.00	0.02	0.41
Tabebuia ochracea (Cham.) Standl.	1	2.0	0.08	2.00	0.24	0.02	0.09	0.40
Zanthoxylum sp.	1	2.0	0.08	2.00	0.24	0.01	0.07	0.38
Miconia sp. 2	1	2.0	0.08	2.00	0.24	0.01	0.06	0.38
Myrcia sp.	1	2.0	0.08	2.00	0.24	0.01	0.06	0.37
Blepharocalyx salicifolius (Kunth) O.Berg	1	2.0	0.08	2.00	0.24	0.01	0.05	0.36
Malpighiaceae sp.	1	2.0	0.08	2.00	0.24	0.01	0.05	0.36
Myrtaceae sp. 3	1	2.0	0.08	2.00	0.24	0.01	0.03	0.35
Pera glabrata (Schott) Poepp. Ex Baill.	1	2.0	0.08	2.00	0.24	0.00	0.02	0.33
Spiranthera odoratissima A.St.-Hil.	1	2.0	0.08	2.00	0.24	0.00	0.02	0.33
Myrcia língua (O.Berg) Mattos	1	2.0	0.08	2.00	0.24	0.00	0.01	0.33
Cabralea canjerana (Vell.) Mart.	1	2.0	0.08	2.00	0.24	0.00	0.01	0.32
Neea theifera Oerst.	1	2.0	0.08	2.00	0.24	0.00	0.01	0.32
Undetermined 3	1	2.0	0.08	2.00	0.24	0.00	0.01	0.32
Couepia grandiflora (Mart. & Zucc.) Benth.	1	2.0	0.08	2.00	0.24	0.00	0.01	0.32

Table 3. List of indicator species of the groups formed by TWINSPAN analysis. The meaning of community acronyms are in Fig. 3.

Family/species	Groups	Communities
Anacardiaceae R.Br.		
Anacardium occidentale L.	E	BACrup, BACss, CFL
Tapirira guianensis Aubl.	C	ABS, PARhc, PARyl, PAS
Annonaceae Juss.		
Annona coriacea Mart.	E	BACrup, BACss, CFL
Annona crassiflora Mart.	C	ABS, PARhc, PARyl, PAS
Xylopia aromatica (Lam.) Mart.	Not preferred, C	ABS, PARhc, PARyl, PAS
Xylopia sericea A.St.-Hil.	B	RPR
Apocynaceae Juss.		
Hancornia speciosa Gomes	B	RPR
Himatanthus obovatus (Müll. Arg.) Woodson	E	BACrup, BACss, CFL
Araliaceae Juss.		
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	Not preferred, C, F	ABS, CNR, CNS, PARhc, PARyl, PAS, SSD
Asteraceae Bercht. & J.Presl		
Baccharis dracunculifolia DC.	A	SMGrup, SMGss
Eremanthus elaeagnus (Mart. ex DC.) Sch.Bip.	A	SMGrup, SMGss
Eremanthus glomerulatus Less.	A	SMGrup, SMGss
Moquiniastrum polymorphum (Less.) G. Sancho	A	SMGrup, SMGss
Bignoniaceae Juss.		
Cybistax antisyphilitica (Mart.) Mart.	E	BACrup, BACss, CFL
Fridericia cinnamomea (DC.) L.G.Lohmann	E	BACrup, BACss, CFL
Handroanthus serratifolius (Vahl) S.Grose	A	SMGrup, SMGss
Zeyheria montana Mart.	C	ABS, PARhc, PARyl, PAS
Boraginaceae Juss.		
Cordia trichotoma (Vell.) Arráb. ex Steud.	A	SMGrup, SMGss
Burseraceae Kunth		
Protium heptaphyllum (Aubl.) Marchand	E	BACrup, BACss, CFL
Calophyllaceae J.Agardh		
Kielmeyera petiolaris Mart. & Zucc.	B	RPR
Caryocaraceae Szyszył.		
Caryocar brasiliense Cambess.	Not preferred	–
Celastraceae R.Br.		
Peritassa campestris (Cambess.) A.C. Sm.	E	BACrup, BACss, CFL
Clethraceae Klotzsch		
Clethra scabra Pers.	A	SMGrup, SMGss
Connaraceae R.Br.		
Rourea induta Planch.	E	BACrup, BACss, CFL
Dilleniaceae Salisb.		
Curatella americana L.	C	ABS, PARhc, PARyl, PAS
Erythroxylaceae Kunth		
Erythroxylum campestre A.St.-Hil.	B	RPR
Erythroxylum suberosum A.St.-Hil.	Not preferred, C	ABS, PARhc, PARyl, PAS
Erythroxylum tortuosum Mart.	Not preferred	–
Fabaceae Lindl.		
Bowdichia virgilioides Kunth	Not preferred, C	ABS, PARhc, PARyl, PAS
Dalbergia miscolobium Benth.	E	BACrup, BACss, CFL
Dalbergia villosa (Benth.) Benth.	A	SMGrup, SMGss
Dimorphandra mollis Benth.	C, E	ABS, BACrup, BACss, CFL, PARhc, PARyl, PAS
Hymenaea stigonocarpa Mart. ex Hayne	Not preferred	–
Leptolobium dasycarpum Vogel	Not preferred, C	ABS, PARhc, PARyl, PAS

Family/species	Groups	Communities
Machaerium hirtum (Vell.) Stellfeld	A	SMGrup, SMGss
Machaerium opacum Vogel	C	ABS, PARhc, PARyl, PAS
Machaerium villosum Vogel	B	RPR
Mimosa laticifera Rizzini & A.Mattos	E	BACrup, BACss, CFL
Pterodon pubescens (Benth.) Benth.	E	BACrup, BACss, CFL
Stryphnodendron rotundifolium Mart.	D	SENrup, SENss
Tachigali aurea Tul.	C	ABS, PARhc, PARyl, PAS
Tachigali subvelutina (Benth.) Oliveira-Filho	F	CNR, CNS, SSD
Lamiaceae Martinov		
Vitex megapotamica (Spreng.) Moldenke	A	SMGrup, SMGss
Lauraceae Juss.		
Ocotea pomaderroides (Meisn.) Mez	G	APR, COC, PLR
Loganiaceae R.Br. ex Mart.		
Antonia ovata Pohl	E	BACrup, BACss, CFL
Malpighiaceae Juss.		
Banisteriopsis malifolia (Nees & Mart.) B.Gates	B	RPR
Byrsonima coccolobifolia Kunth	Not preferred	–
Diplopterys pubipetala (A.Juss.) W.R.Anderson & C.C.Davis	E	BACrup, BACss, CFL
Heteropterys byrsonimifolia A.Juss.	E	BACrup, BACss, CFL
Melastomataceae A. Juss.		
Miconia tristis Spring	A	SMGrup, SMGss
Myrtaceae Juss.		
Blepharocalyx salicifolius (Kunth) O.Berg	B	RPR
Eugenia dysenterica (Mart.) DC.	C	ABS, PARhc, PARyl, PAS
Eugenia gemmiflora O.Berg	E	BACrup, BACss, CFL
Myrcia lanuginosa O.Berg	E	BACrup, BACss, CFL
Myrcia tomentosa (Aubl.) DC.	C	ABS, PARhc, PARyl, PAS
Myrcia variabilis DC.	B	RPR
Psidium pohlianum O.Berg	B	RPR
Psidium salutare (Kunth) O.Berg	D	SENrup, SENss
Siphoneugena densiflora O.Berg	A	SMGrup, SMGss
Nyctaginaceae Juss.		
Guapira graciliflora (Mart. ex Schmidt) Lundell	E	BACrup, BACss, CFL
Ochnaceae DC.		
Ouratea hexasperma (A.St.-Hil.) Baill.	E	BACrup, BACss, CFL
Proteaceae Juss.		
Roupala montana Aubl.	Not preferred	-
Rubiaceae Juss.		
Palicourea rigida Kunth	F	CNR, CNS, SSD
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Not preferred, E	BACrup, BACss, CFL
Rutaceae A.Juss.		
Spiranthera odoratissima A.St.-Hil.	B	RPR
Salicaceae Mirb.		
Casearia sylvestris Sw.	E	BACrup, BACss, CFL
Sapotaceae Juss.		
Pouteria torta (Mart.) Radlk.	B	RPR
Styracaceae DC. & Spreng.		
Styrax camporum Pohl	C	ABS, PARhc, PARyl, PAS
Vochysiaceae A.St.-Hil.		
Qualea dichotoma (Mart.) Warm.	A	SMGrup, SMGss
Qualea grandiflora Mart.	Not preferred	–
Qualea multiflora Mart.	Not preferred	–
Qualea parviflora Mart.	Not preferred	–

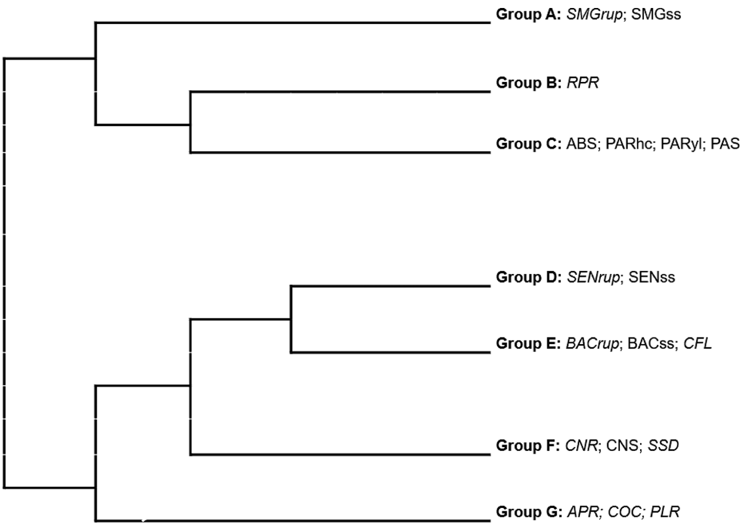

Figure 3. Dendrogram formed from the divisional cluster analysis (TWINSPAN) showing the relationship of floristic similarity amongst cerrado communities. ABS = Abaeté-MG; APR = Pirenópolis-GO; BAC = Bacaba Municipal Park-GO; CFL= Rupestrian Savannah in the transition Cerrado-Amazonian Forest; CNR = Caldas Novas-GO; CNS = Caldas Novas-GO; COC = Cocalzinho de Goiás-GO; PARhc = FLONA de Paraopeba-MG with haplic cambissol; PARyl = FLONA de Paraopeba-MG with yellow latossol; PAS = Paraopeba-MG; PLR = Alto Paraíso-GO; RPR = Rio Paranaíba-MG; SEN = Serra Negra-GO; SMG = Sul de Minas Gerais; SSD = Salto de São Domingos-GO. Italic = Rupestrian Savannah.

The 10 most important species in terms of importance value (IV) (Table 2) are 73.42% of the absolute density and 68.03% of the total IV of the community, indicating a high dominance in this environment. For most species, such as *Aspidosperma tomentosum* Mart. & Zucc., *Erythroxylum tortuosum* Mart., *Plenckia populnea* Reissek and *Virola sebifera* Aubl., relative frequency was the parameter that most contributed to the IV (Table 2). However, relative dominance was sometimes the most important parameter for other species, e.g. *Dalbergia miscolobium* Benth., *Heteropterys byrsonimifolia* A.Juss. and *Kielmeyera petiolaris* Mart. & Zucc. For the species *Erythroxylum daphnites* Mart., *Qualea multiflora* Mart. and *Lafoensia pacari* A.St.-Hil., relative density was the most important parameter to establish the IV.

As for the floristic similarity amongst communities, the TWINSPAN analysis indicated weak differentiation of two groups in the first division (autovalue of 0.399) (Fig. 3). The indicator species of each group are listed in Table 3. In both groups formed, there was the indissociable presence of communities on shallow soils (rupestrian enclosures) on profound soils (cerrado *s.s.*).

The basal area was significantly larger in cerrado on profound soil comparatively to the Rupestrian Savannah areas (t = 3.17, P = 0.02), whereas density (t = 1.24, P 0.26), richness (t = 1.33, P = 0.24) and diversity (t = 1.23, P = 0.28) did not differ amongst them. The evenness of distribution amongst species, represented by the Pielou evenness (J = 0.37), was lower in the Rupestrian Savannah.

Discussion

The Ferruginous Rupestrian Savannah of the present study proved to be similar to other cerrado *s.s.* of the domain. Thus, the presence of shallow soils seems to be an effective environmental filter only for the basal area, restricting the species to greater biomass gain.

Similarly to other studies areas of Rupestrian Savannah (Silva et al. 1996; Amaral et al. 2006; Miranda et al. 2007, 2010; Moura et al. 2007, 2010; Oliveira and Martins 2007; Pinto et al. 2009; Abreu et al. 2012; Santos et al. 2012; Gomes et al. 2016; Torres et al. 2017), the families Myrtaceae, Fabaceae, Malpighiaceae and Erythroxylaceae were the richest families observed in the present study. These families were referred by Goodland and Ferri (1979) as "overrepresented" in the Cerrado. Fabaceae was cited by Mendonça et al. (1998) as the most diversified phanerogamous family in the Cerrado Domain. The concentration of many species in few families and the presence of many families with few species observed in the present study is a common characteristic in surveys conducted in cerrado *s.s.* areas (Felfili et al. 2004). Additionally, the most abundant families in the present study, namely Fabaceae, Erythroxylaceae, Vochysiaceae and Apocynaceae, were the most abundant in other Rupestrian Savannah areas (Amaral et al. 2006; Miranda et al. 2007; Moura et al. 2007).

The highest similarity between Rupestrian Savannah of Rio Paranaíba and areas of cerrado on profound soil can also be related to the wide occurrence of the species found in this studied environment. Most of the species found in the studied area are common to other phytogeographical domains and also occur in forests. According to Brazilian Flora (2018), 82.4% of the species sampled in the present study occur in other domains besides the Cerrado and 56.9% of them occur in forest formations, presenting great adaptation to different types of vegetation.

The Rupestrian Savannah of Rio Paranaíba showed a small number of species (the first 10 in IV) that comprise more than 50% of the density. This fact was considered common by Felfili and Silva-Júnior (2001) in tropical environments, where a small group of species dominates the area with the majority of individuals and basal area and a large number of species contribute with few individuals, as observed in areas of cerrado *sensu stricto* on rocky outcrops (Amaral et al. 2006; Miranda et al. 2007; Moura et al. 2007).

Despite the fact that richness and density of the Rupestrian Savannah of Rio Paranaíba were statistically similar when compared to the other areas, the basal area was one of the smallest amongst the comparative studies (Felfili and Fagg 2007, Moura et al. 2010, Lenza et al. 2011, Gomes et al. 2016). According to Ribeiro and Walter (2008), the woody individuals of the Rupestrian Savannah settle in the cracks between rocks and their density varies according to the availability of soil. The studied area has many sites with a predominance of canga, so there is a significant soil coverage consisting of rocks and, despite the high density of individuals, the amount of soil seems not to be sufficient for the existence of large individuals, corroborating observations in other Rupestrian Savannah areas (Amaral et al. 2006; Miranda et al. 2007; Moura et al. 2007; Pinto et al. 2009; Abreu et al. 2012). Thus, larger plants occur in sites with canga, where there is more soil and cracks between rocks. The same idea can be used to explain the lower evenness, once the thin layer of soil has restricted the development of plants, leading to the dominance of some species adapted to rocky environments.

Although *Mimosa setosissima* Taub., *Tibouchina papyrus* (Pohl) Toledo, *Wunderlichia mirabilis* Riedel ex Baker and *Hyptis pachyphylla* Epling have been considered typical species of Rupestrian Savannah (Ratter et al. 2000; Ribeiro and Walter 2008; Pinto et al. 2009), we cannot find them. This fact indicates that the species that constitute the community in the Rio Paranaíba are widely distributed, being shared with cerrado *sensu stricto* communities, not typical of Rupestrian Savannah.

The broad occurrence of generalist species in Rupestrian Savannah was also recorded in other regions of Brazil (e.g. Moura et al. 2010, Santos et al. 2012), indicating that the flora of this formation is in fact shared by other Cerrado physiognomies. Its floristic composition is characterised by tree-shrub species of the other savannah formations, particularly of the profound soil (e.g. *Byrsonima coccolobifolia* Kunth, *Caryocar brasiliense* Cambess., *Connarus suberosus* Planch., *Erythroxylum tortuosum* Mart., *Kielmeyera petiolaris* Mart. & Zucc., *Pouteria ramiflora* (Mart.) Radlk and *Pouteria torta* (Mart.) Radlk, *Qualea parviflora* Mart. and *Qualea grandiflora* Mart., *Roupala montana* Aubl. and *Stryphnodendron adstringens* (Mart.) Coville). Therefore, the Rupestrian Savannah of Rio Paranaíba has a floristic influence of the cerrado *s.s.* from the surrounding region. Felfili et al. (2007) related a similar fact as an indication of a geographic gradient influencing the floristic composition of the cerrado *s.s.* According to Ribeiro and Tabarelli (2002), in addition to the influence of the surrounding biota (Fernandes and Bezerra 1990; Fernandes 1998), the mass effect can also influence this pattern (Shmida and Wilson 1985).

It is probable that the differentiation of the Ferruginous Rupestrian Savannah can be captured in non-arboreal stratum. An explanation for that is the fact that the high endemism cited for rupestrian environments seems to be more strongly associated with the herbaceous stratum represented by the families Asteraceae, Celastraceae, Cyperaceae, Eriocaulaceae, Lamiaceae, Melastomataceae, Poaceae, Velloziaceae, Verbenaceae and Xyridaceae (Eiten 1994; Pirani et al. 1994; Harley 1995; Silva et al. 1996; Ribeiro and Walter 1998; Romero and Martins 2002) and such stratum was not sampled in the present study. Thus, the sampling effort and the different sampling criterion used in the studies may also have contributed to these results, since the sample criterion used in Rio Paranaíba was more similar to that used in studies of profound soil, which may have increased the similarity between these areas.

Lastly, the woody flora of the Rupestrian Savannah of Rio Paranaíba is a combination of species widely distributed in the Cerrado *sensu lato*. The greater similarity between the Rupestrian Savannah of Rio Paranaíba and the profound soil cerrado can be explained by the ferruginous nature of the canga, which is more similar to the Latosols than the rocky outcrops of quartzite or arenite nature, evidencing the influence of the substrate on the species occurring in one area. This study provides important information on the flora associated with these phytophysiognomies and contributes to a better understanding of these rare environments, potentially aiding to subsidise the determination of priority areas for conservation.

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