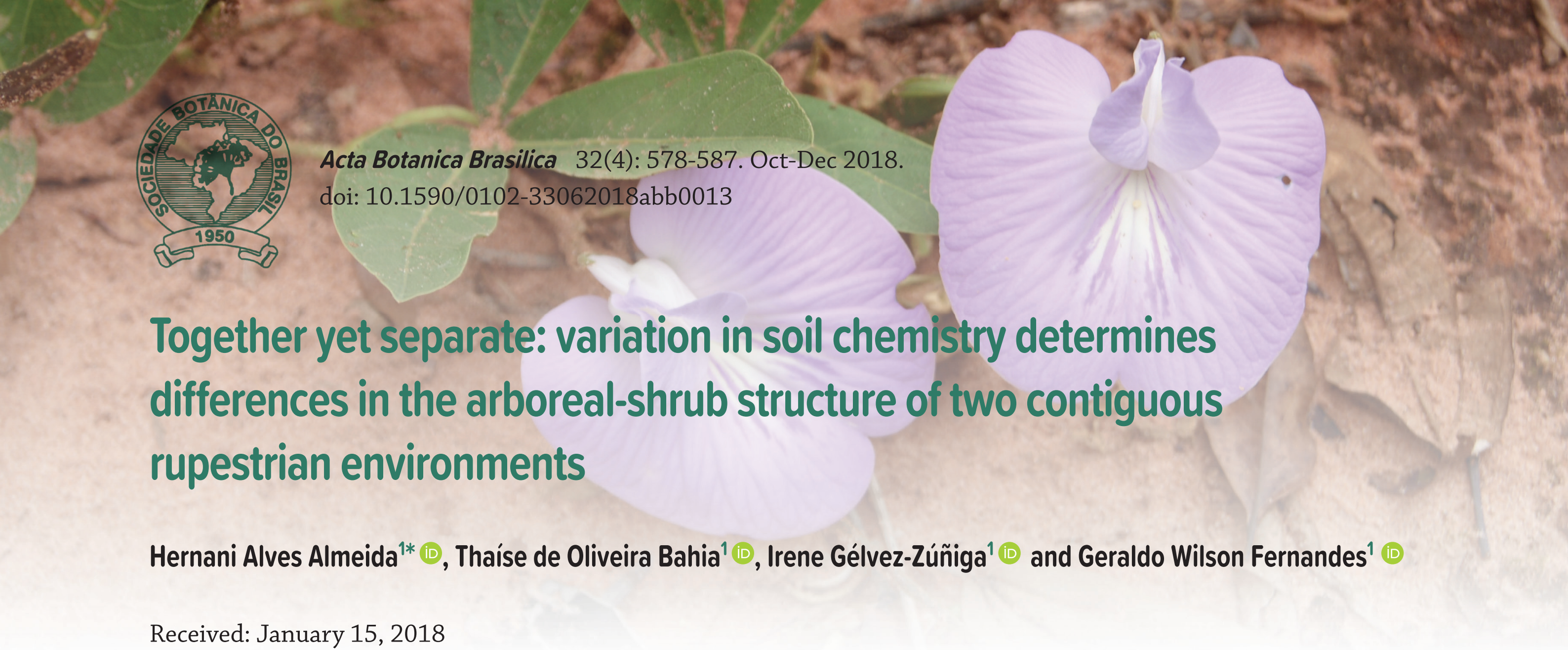

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Together yet separate: variation in soil chemistry determines differences in the arboreal-shrub structure of two contiguous rupestrian environments

Hernani Alves Almeida[1*], **Thaíse de Oliveira Bahia**[1], **Irene Gélvez-Zúñiga**[1] and **Geraldo Wilson Fernandes**[1]

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ABSTRACT

Rupestrian landscapes are characterized by vegetation mosaics comprised of different plant communities and strongly linked to environmental filters. These environments are nutrient-impoverished, and possess water retention deficits and high solar exposure. This study aimed to determine whether chemical properties of the soil shape the arboreal-shrub vegetation structure in two neighboring habitats; a rupestrian cerrado and a rupestrian grassland. We hypothesized that the habitat with higher soil chemical properties would have higher parameters for vegetation structure, and different species composition. We expected higher chemical properties of the soil to favor a greater variety of plant life-forms. A total of 1349 individuals of 85 species belonging to 24 families were recorded; 1141 individuals (65 species) in the rupestrian cerrado, and 208 individuals (20 species) in the rupestrian grassland. Overall, Asteraceae, Fabaceae and Melastomataceae had greater species richness in both areas. Both habitats floristic composition was strongly influenced by differences in soil chemistry. In the cerrado, species richness, composition, soil nutrient availability and acidity were greater than in the grassland. We demonstrated that variation in soil chemistry influences plant species richness and composition, and structural complexity of vegetation, in both contiguous rupestrian environments, and that soil chemistry heterogeneity yields different plant life-form strategies.

Keywords: arboreal-shrub, Asteraceae, *campo rupestre*, Cerrado, edaphic characteristics, environmental filters, Myrtaceae, phytosociology

Introduction

In Brazil, rupestrian grassland ecosystems, known as *campos rupestres*, are well known for their high plant biodiversity and endemism, comprising a mosaic of habitats that are shaped by, and strongly linked to, environmental filters (Fernandes 2016). These environments possess characteristics of old climatically-buffered infertile landscapes (OCBILs), including infertile soils, climatic stability and species with low capacity for dispersion and adaptations for resource acquisition (Hopper 2009; Silveira *et al*. 2016). Distinct habitats have been recognized within campos rupestres, including: rocky outcrops, peat bogs, gallery forests, stony grasslands, sandy grasslands, natural islands or pockets of cerrado vegetation, islands of Atlantic Forest, and *Candeal* (the latter characterized by the dominance of *Eremanthus erythropappus*), among others (*e.g*. Carvalho *et al*. 2012; 2014; Negreiros *et al*. 2014; Coutinho *et al*. 2015; Coelho *et al*. 2016; Kuster *et al*. 2016).

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1 Ecologia Evolutiva e Biodiversidade, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, 30161-970, Belo Horizonte, MG, Brazil

* Corresponding author: hernanifh@gmail.com

The major filters in rupestrian environments are climate, soil, fire, and water availability (e.g. Negreiros *et al*. 2014; Barbosa & Fernandes 2016; Figueira *et al*. 2016), among which the physico-chemical properties of the soil are considered one of the most important (Coutinho *et al*. 2015; Schaefer *et al*. 2016). In rupestrian environments, the distribution of various soils in the landscape has resulted in numerous habitats that are inhabited by different plant communities (e.g., Negreiros *et al*. 2014; Stradic *et al*. 2015; Mota *et al*. 2018). The origin of rupestrian habitats is largely due to the influence of topography, slope, soil type, texture, nutrient quantity, lithology and geomorphology, which together contribute to species composition and establishment (Messias *et al*. 2013; Schaefer *et al*. 2016).

Rupestrian grassland environments are nutrient-impoverished, and experience seasonal water deficit, high solar exposure, strong winds and characteristics influenced by rocks of chemically poor origin (Oliveira *et al*. 2015; see also Schaefer *et al*. 2016; Silveira *et al*. 2016). Such soils are located among quartzite or sandstone outcrops, and are derived from parent rocks of low nutritional value and with low macronutrient content (Schaefer *et al*. 2016). In general, rupestrian soils are acidic, shallow and possess high aluminum saturation, plus low levels of potassium (K), calcium (Ca), magnesium (Mg) and available phosphorus (P) (Negreiros *et al*. 2008). Features like soil texture, acidity, and Al, Ca and Mg ion concentrations are related to the arrangement of the soil mosaic, which is reinforced by levels of C, P, K and cation-exchange capacity (Schaefer *et al*. 2016).

In spite of the variety of habitats in the rupestrian landscape, sclerophylly is a common feature of its flora (Fernandes & Price 1991), particularly among the scattered shrubs within its herbaceous community (Messias *et al*. 2013; Barbosa *et al*. 2015; Stradic *et al*. 2015; Mota *et al*. 2016; 2018). Nutrient availability, along with soil depth, drainage, marked seasonality and heavy metal content have resulted in the establishment of species that are highly adapted to the various types of habitat (Benites *et al*. 2007; Vincent & Meguro 2008; Messias *et al*. 2011; Mews *et al*. 2016; Arruda *et al*. 2017). Different plant life forms are generally a response to changes in the landscape (Pausas & Austin 2001; Neves *et al*. 2016; Mota *et al*. 2018), while variation in plant phenotypes may also alter soil communities, thereby affecting the expression of plant traits (Nuland *et al*. 2016). Woody and/or herbaceous species are favored in deeper soils, while shallow and more impoverished soils harbor species with annual life cycles that have greater underground biomass to support environmental limitations (Mota *et al*. 2018). Likewise, Neves *et al*. (2016) reported that the most typical life forms of species of the Cerrado possess strategies that increase survivorship during hostile seasonal conditions. Plant species in P-impoverished soils of rupestrian grasslands experience less microorganism colonization and high root specialization, and possess several strategies for acquisition of mineral nutrition (Oliveira *et al*. 2015). The primarily source of organic matter in soils associated with rocky outcrops is from decomposition and microbial activity (Benites *et al*. 2007), hence favoring the establishment of vegetation due better nutrient levels and water retention.

In rupestrian areas, micro-environmental variation can result in functional and morphological differences among plants (Negreiros *et al*. 2014). Since the rupestrian landscapes of Serra do Cipó are mosaics with micro-environmental variation, we aimed to determine if variation in soil chemistry is shaping the structure and composition of arboreal-shrub vegetation of two contiguous habitats: a rupestrian cerrado and a quartzitic rupestrian grassland. We tested whether the habitat with higher soil chemical properties also had higher parameters for vegetation structure, as well as different species composition. Furthermore, since sizeable variation in soil properties can yield several strategies for acquiring nutritional resources (Araújo *et al*. 2011; Negreiros *et al*. 2014; Mota *et al*. 2018), we also tested whether higher soil chemical properties favor plants with a greater variety of life forms.

Materials and methods

Study area and habitat characterization

The study was conducted in Reserva Vellozia (19°16’45.7”S 43°35’27.8”W) in Serra do Cipó, Minas Gerais, Brazil. The region has a humid subtropical climate, “Cwb” according to Köppen classification, with a hot rainy season from November to March; a transition post-rainy period between April and May; a dry cold season from June to August; and a post-dry period between September and October (Rocha *et al*. 2016). The mean annual temperature at the study site is 18.5 °C, and the mean annual precipitation is 900 mm (Fernandes *et al*. 2016). The months with the lowest mean monthly precipitation and temperature are June, July and August. December has the highest mean monthly precipitation with 1000 mm, while January and February have the highest mean temperatures with 21.5 °C (Fernandes *et al*. 2016). The study area possesses patchy vegetation in the form of a mosaic of substrates, plant communities and micro-environments. Two contiguous habitats were chosen for test our hypothesis: a rupestrian cerrado island (Giulietti *et al*. 1987) (Fig. 1A) and a rupestrian grassland (Fig. 1B). Both areas are at 1250 m.a.s.l, and are 250 m from each other. The rupestrian cerrado island encompasses only 8000 m^2, and thus no more than 10 plots were set to assure sampling independence since both sampling areas were contiguous. Despite the fact that fire is a strong environmental filter in rupestrian environments (Figueira *et al*. 2016), some studies have reported no floristic differences after fires (Lenza *et al*. 2017), and so we disregard the effect of fire on the mosaic formation since no fires had been recorded for at least ten years in the study area.

Figure 1. Habitats of rupestrian cerrado (**A**) and rupestrian Grassland (**B**) in Serra do Cipó, Minas Gerais, Brazil.

The rupestrian grassland (hereafter grassland) is characterized by a quartzitic peat bog substrate (Carvalho *et al*. 2014), commonly with acidic soils, high aluminum saturation, low nutrient concentration, low water-retention capacity and moderate levels of organic matter (Silva 2005). The rupestrian cerrado island (hereafter cerrado) occurs in patches with a dominance of shrub-tree species on a rocky outcrop substrate (Carvalho *et al*. 2014). Its soils are generally poorly drained oxisols with reduced effective depth and fertility (Amorim & Batalha 2006). The cerrado soils in the region are also nutrient impoverished with high aluminum saturation and a low development profile, and are abruptly becoming rupestrian grasslands (Carvalho *et al*. 2014).

Vegetation sampling

A circular area with a radius of 50 m was delimited in each habitat for choosing 10 randomized 10x10 m plots (N=20). Each plot was marked with PVC pickets and the soil coverage percentage was estimated using a 1 m2frame, in which all plants with a diameter at soil height (DSH) greater than ≥ 1 cm being measured with a caliper (mm). Plant height was measured with a tape (cm). Classic vegetation structure parameters were calculated for both habitats using species DSH and abundance following Mueller-Dombois & Ellenberg (1974). The parameters estimated were: relative frequency (RF), relative density (RD), relative dominance (RDo), and Importance Value Index (IVI). The IVI indicates the importance of a given species to the community structure by adding its relative frequency, density and dominance. Mean plant height (AH) and stem diameter (AD) were also determined for each species. Collected plant material was processed and identified in consultation with specialists and specialized literature, and through comparisons with the botanical material deposited in the Universidade Federal de Minas Gerais Herbarium (BHCB). Plant species were grouped into families following the Angiosperm Phylogeny Group (APG IV 2016). All the sampled species were identified and their life form characterized according to the virtual herbarium REFLORA (Flora do Brasil 2020).

Soil analysis

A sample of superficial soil (0-20 cm in depth) was collected to analyze the chemical properties of the soil in each plot per habitat (N= 10, total =20). Each sample was a composite of five sub-samples (plot center and vertices). The properties measured were: pH in water (pH), potassium (K), phosphorus (P), remaining phosphorus (P-rem), calcium (Ca^2+), magnesium (Mg^2+), aluminum (Al^3+), hydrogen + aluminum (H+Al), exchangeable bases $cmol_c/dm^3$ (EB), base-saturation % (V), effective cation-exchange capacity $cmol_c/dm^3$ (t), aluminum saturation index % (m), pH 7.0 cation-exchange capacity $cmol_c/dm^3$ (T), organic matter (OM), copper (Cu), manganese (Mn), iron (Fe), and zinc (Zn).

Statistical analysis

To test if differences in plant community structure between the two rupestrian habitats are explained by micro-environmental variation in soil chemistry, a general-linear model was performed (Crawley 2007). The structural parameters set as response variables were: species abundance and richness, relative density, mean plant height, mean stem diameter, and soil coverage; while habitats represented the explanatory variable. For each model, the appropriate error distribution for each response variable was used, according to Crawley (2007).

To determine if species composition is influenced by micro-environmental soil chemical properties NMDS (non-metric multidimensional scaling) was performed using the Bray-Curtis similarity index, according to Hammer *et al*. (2001). After a second NMDS, the variables P-rem, Ca^2+, Mg^2+, H+Al, SB, V, T and Zn were removed. To test the differences in composition indicated by the NMDS, an ANOSIM (Similarity ANOVA – 5 % of significance) was performed (Clarke & Green 1988). To test whether the occurrence of life forms are explained by micro-environmental soil chemical variation between the two rupestrian habitats we performed another NMDS using the Bray-Curtis similarity index. After the differences in composition indicated by the NMDS were tested, an ANOSIM was performed (at 5 % of significance). Composition analyses were performed in PAST software (Hammer *et al*. 2001). To assess chemical soil variation between the two habitats, a Generalized Linear Model (GLM) was performed (Sólymos 2009). We used pH, K, P, P-rem, Ca^2+, Mg^2+, Al^3+, H+Al, SB, V, t, m, T, OM, Cu, Mn, Fe and Zn as response variables and habitats as the explanatory variable. For each model, the appropriate error distribution for each response variable was used, according to Crawley (2007). The data were analyzed using R software (R Core Team 2014).

To analyze whether variation in soil chemistry explains species abundance, the "model selection" approach was used. The strength of candidate models was analyzed using Akaike's Information Criterion (AICc), adjusted for small sample sizes, by determining relative difference of AICc between models (ΔAICc) and associated model weights (AICc weighted) (Burnham & Anderson 2002). The effect of micro-environmental variation of soil chemistry on species abundance (response variable) was performed by comparing each model with a subset of models. After determining the best models, the soil properties with greater interaction with species abundance (equal to or greater than 0.5) were identified and used to rank which soil parameters best correlated with the patterns of composition in each habitat. The best models were considered those that were equal to or less than two AICc from the initial model. To select soil chemical variables, a Pearson correlation test was performed, and the variables with correlations greater than 0.8 were excluded from the models. The model selection analysis was performed according to Burnham & Anderson (2002) and were carried out in the software R version 3.2.2 (R Core Team 2014), using the MuMIn package (Bartón 2012).

Results

Differences in floristic composition between the rupestrian habitats were strongly influenced by micro-environmental soil chemical variation (R2= 0.89 and p<0.001), as hypothesized. In the contiguous habitats, cerrado and grassland, variation in soil chemistry was strongly aggregated, with some homogeneity within habitat (Fig. 2). Axis 1 explained 90 % of the segregation with a stress value of 0.11. As expected, soil chemistry properties varied considerably in each habitat. Furthermore, each habitat also exhibited differences in plant life forms (R2= 0.82, P= <0.001). Axis 1 explained 83 % of the variation with a stress value of 0.07 (Fig. 3). Additionally, a predominance of arboreal, shrub and palm shrub species were found for the cerrado, while shrubby species dominated the grassland.

The studied habitats varied in soil pH, K, P, Ca^2+, Al^3+, SB, V, t, m, T, MO, Cu, Mn, Fe, and Zn concentrations (Tab. 1). The cerrado habitat had higher mean values than the grassland habitat for K, Ca^2+, Al^3+, SB, t, T, V, Cu, Mn, and Zn. (Tab. 1, Fig. 4). The levels of Al, Cu, K, Mn and effective cation-exchange capacity (t) were significantly higher in the cerrado habitat (Fig. 4 A, C, E, G, I); while soils of the grassland habitat had greater Fe, R, organic matter, pH levels and aluminum saturation (m) (Fig. 4 B, D, F, H, J).

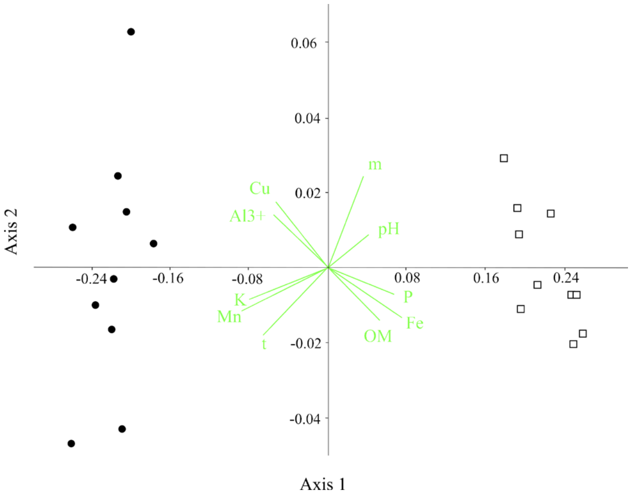

Figure 2. Soil chemical properties ordination in rupestrian cerrado (circle) and Grassland (square) habitat plots (N=20), in Serra do Cipó, Brazil. OM: organic matter, m: Aluminium saturation index, t: effective cation-exchange capacity.

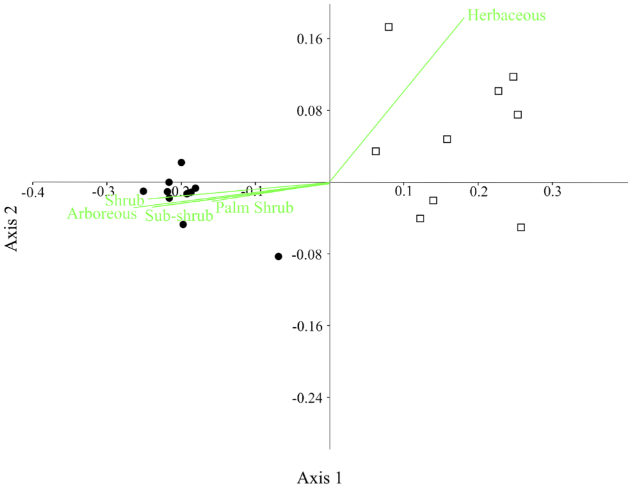

Figure 3. Life-form strategies ordination in rupestrian cerrado (circles) and Grassland (square) habitat plots (N=20), in Serra do Cipó, Brazil.

The most abundant plant species were influenced differently by micro-environmental variation in soil chemistry (Tab. 2). The most abundant and frequent species in the cerrado habitat were: *H. ochraceus*, *Mimosa radula* Benth., *M. guianensis*, *Erythroxylum campestre*, *Eugenia* sp., *Ruellia villosa*, *M. maguirei*, *C. papillata*, *Vernonanthura polyanthes*, *Diospyros hispida*, *Roupala Montana*, *Byrsonima variabilis*, *Eugenia punicifolia*, *Kielmeyera petiolaris*, and *Psidium firmum*. These species were more likely to occur with higher K, T and Al levels; and were negatively related with P, OM, m, and Zn levels. In the grassland habitat, *C. hilariana*, *R. polymorpha*, *A. bongardii*, and *P. argenteus* were

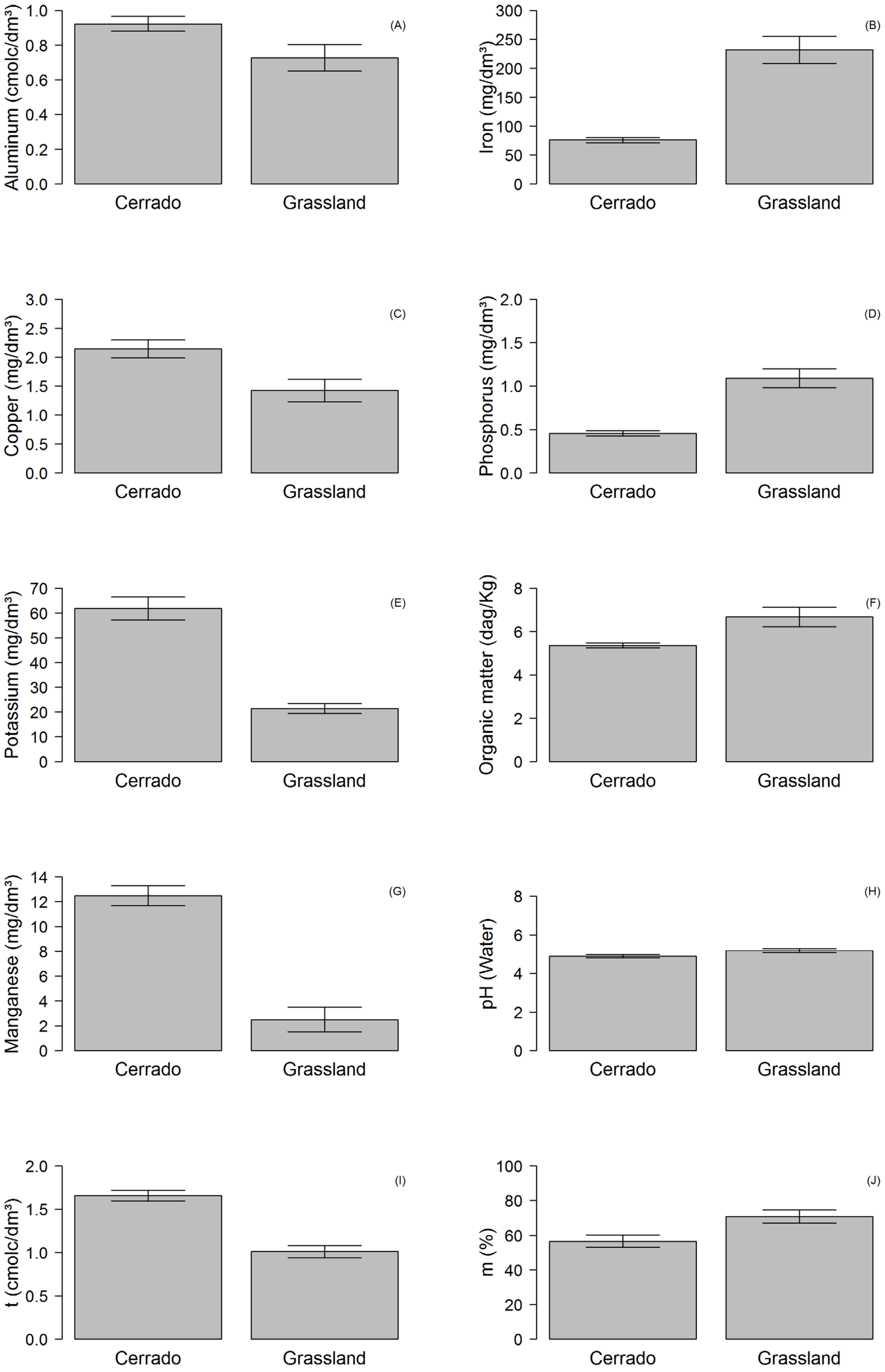

Figure 4. Soil physical properties in rupestrian cerrado and Grassland habitats in Serra do Cipó, Brazil. Aluminum (**A**), Iron (**B**), Copper (**C**), Phosphorus (**D**), Potassium (**E**), Organic Matter (**F**), Manganese (**G**), pH (**H**), t: effective cation-exchange capacity (**I**) and m: Aluminium saturation index (**J**).

the most abundant and frequent species. The species *P. argenteus*, *C. hilariana* and *A. bongardii* were less represented in the cerrado habitat, and were positively influenced by higher levels of organic matter, P, and Zn; and negatively related to Al and K concentrations.

Table 1. Soil chemical properties variations (Mean ± SD) between two rupestrian habitats (rupestrian cerrado and Grassland) in Serra do Cipó, Brazil. H+Al: hydrogen + aluminum cmol$_c$/dm^3, EB: exchangeable bases cmol$_c$/dm^3, t: effective cation-exchange capacity cmol$_c$/dm^3, T: cation-exchange capacity at pH 7.0 cmol$_c$/dm^3, V: base-saturation %, m: aluminum saturation index %, OM: organic matter dag/Kg, P-Rem: remaining phosphorus ml/L. * indicates significant values (P<0.05).

Attribute	"Cerrado"		Grassland	
	μ		μ	
pH*	4.85	± 0.09	5.25	± 0.08
P*	0.46	± 0.02	1.15	± 0.10
K*	59.4	± 4.80	19.8	± 1.28
Ca^{2}*	0.36	± 0.07	0.17	± 0.03
Mg^{2}	1.76	± 1.58	0.05	± 0.01
Al^{3}*	0.94	± 0.04	0.69	± 0.07
H+Al	8.04	± 0.24	7.79	± 0.13
EB*	0.69	± 0.08	0.28	± 0.04
t*	1.63	± 0.06	0.97	± 0.06
T*	8.74	± 0.27	8.07	± 0.09
V*	7.90	± 0.88	3.47	± 0.54
m*	58.35	± 3.57	70.40	± 4.12
MO*	5.23	± 0.16	6.93	± 0.40
P-Rem	11.74	± 0.69	12.21	± 0.72
Cu*	2.22	± 0.16	1.27	± 0.13
Mn*	12.46	± 0.72	1.53	± 0.26
Fe*	76.09	± 3.85	247.28	± 19.07
Zn*	2.65	± 0.34	1.49	± 0.21

The cerrado habitat had higher species richness and abundance, and individuals were taller and possessed greater diameters when compared to individuals of the grassland habitat (Tab. 3, Tab. S1 in supplementary material). Mean plant abundance in the cerrado habitat (106±9) was greater than that of the grassland (26±6) (Tab. 3). Mean plant height was higher in the cerrado (118.29±6.03cm) than in the grassland habitat (59.97±9.83cm) (Tab. 3). Relative density and soil coverage were the only vegetation structural parameters that did not differ between habitats (Tab. 3). In the cerrado habitat,78% of all the species were exclusive (51 out of 65), while in the grassland only30% of the species were exclusive (6 out of 20).

A total of 1349 individuals of 85 species, distributed among 24 families, were recorded; 1141 individuals of 65 species in the cerrado habitat, and 208 individuals of20 species in the grassland habitat. Three species could not be identified. The families with greatest species richness in the cerrado habitat were Myrtaceae (11 species), Asteraceae (nine), Fabaceae and Malpighiaceae (seven), and Melastomataceae (six), which together represented 61% (40 out of 65 species) of all the species in this habitat. In the grassland habitat, the families with greatest species richness were Asteraceae (four species), Fabaceae (four), Melastomataceae (four), and Eriocaulaceae (two), accounting for 70% (14 out of 20) of all the species recorded (detailed in Tab. S1 in supplementary material).

In the cerrado habitat, *Chamaecrista papillata* (80.36), *Myrsine* (29.30), *Mimosa maguirei* (14.37), *Handroanthus ochraceus* (14.09) and *Eugenia* sp. (13.55) had the highest IVIs. The most abundant species was *M. guianensis* (197 individuals), followed by *Chamaecrista papillata* (102) and

Table 2. Soil properties effect in the indicator species abundance between two rupestrian habitats (rupestrian cerrado and Grassland) in Serra do Cipó. OM: organic matter, T: pH 7.0 cation-exchange capacity cmol$_c$/dm^3, m: Aluminum saturation index %.

Habitat	Species	Soil variables								
		OM	pH	k	T	Al	P	m	Zn	Cu
"Cerrado"	*Handroanthus ochraceus*	-	-	+	+	+				
	Mimosa radula						-			
	Myrsine guianensis				+	+		-		
	Erythroxylum campestre		-			+	-			
	Eugenia sp.	-	-	+	+				-	
	Ruellia villosa	-	-	+		+	-			-
	Mimosa maguirei		-	+			-			+
	Eugenia punicifolia	-								
	Chamaecrista papillata	-		+						
	Vernonanthura polyanthes		-		-					
	Diospyros hispida			+						
	Roupala montana		-			+		-	-	
	Byrsonima variabilis			+						
	Kielmeyera petiolaris		+	+			-	-		
	Psidium firmun					+				
Grassland	*Cambessedesia hilariana*						+		+	
	Richterago polymorpha		-			-	+		-	
	Actinocephalus bongardii	+				-				
	Paepalanthus argenteus			-	+	-		+	-	

M. maguirei (94). In the grassland habitat, *Paepalanthus argenteus* (61.34), *Richterago polymorpha* (50.32), *Cambessedesia hilariana* (29.13), *Actinocephalus bongardii* (23.51), and M. *guianensis* (21.15) had the highest IVIs. The most abundant species in this habitat were *R. polymorpha* (53), *P. argenteus* (44), and *Microlicia crenulata* (24).

Table 3. Vegetation structural variations (Mean ± SD) between two rupestrian habitats (rupestrian cerrado and Grassland) in Serra do Cipó, Brazil. * indicates significant values (p<0.05).

Attribute	"Cerrado"		Grassland	
	μ		μ	
Abundance*	106.88	± 9.10	26.18	± 6.29
Richness*	22.66	± 2.18	7.36	± 2.12
Relative density	9.36	± 0.79	10.52	± 1.65
Plant height (cm)*	118.29	± 6.03	59.97	± 9.83
Stem diameter (cm)*	0.130	± 0.01	0.05	± 0.01
Soil coverage	83.22	± 4.84	83.0	± 3.81

Discussion

Our results demonstrate that the structure of the arboreal-shrub vegetation and the species composition of two contiguous habitats in the mosaic of two rupestrian environments in Serra do Cipó are shaped by micro-environmental variation in soil chemistry. We found different species composition, greater richness and abundance, and plants with greater diameters and height sin the cerrado, where the soil is chemically more complex. This result reinforces that micro-environmental variation of the soil acts as important drivers of vegetation in rupestrian ecosystems (Giulietti *et al*. 1997; Rapini *et al*. 2008; Fernandes 2016; Coelho *et al*. 2016; Schaefer *et al*. 2016). Furthermore, the results also indicate that even in contiguous areas, a rupestrian ecosystem can possess high environmental heterogeneity, which favors the formation of microhabitat mosaics and thus high flora richness and several plant life-form strategies (e.g., Negreiros *et al*. 2014; Stradic *et al*. 2015; Neves *et al*. 2016; Mota *et al*. 2018).

We demonstrated that micro-environmental variation in soil chemistry represents strong filters that favor certain plant life forms. Our results show that the predominant life forms of rupestrian cerrado habitat were woody shrubs, sub-shrubs, and small palm trees. This was also where the soil had higher concentrations of chemical compounds and nutrient levels, when compared to the soil of the grassland habitat. However, small species, predominantly herbs, were dominant in the grassland habitat, where the soil had less nutrition. Plant life forms reflect a set of characteristics that determine the establishment and survival of plants in a given environment. As a result, the dominant life forms in a given community determine its vegetation structure (Araújo *et al*. 2011; Messias *et al*. 2011).

In rupestrian grassland communities, slight environmental differences can result in large differences in functional traits of plants, ranking the soil, characterized by its low fertility, high Al concentration and low water retention, as the most important environmental filter for the presence of highly stress-tolerant species (Negreiros *et al*. 2014). Some predominant life form adaptations, such as woody species with the capacity for annual regrowth and/or with subterranean structures for avoiding desiccation due to fire, are commonly found in rupestrian grasslands on rocky outcrops (Conceição *et al*. 2007). Therefore, plant life forms can be indicative of the environmental adaptation of a species in a given community, and indirectly provide information about the environment (Araújo *et al*. 2011; Schaefer *et al*. 2012). This pattern can be found in other environments where soil nutrients are scarce and where there is strong climatic pressures on plants, such as semi-arid and savanna areas of Brazil (Araújo *et al*. 2011; Neves *et al*. 2016; Mota *et al*. 2018). In such areas, there is pronounced environmental heterogeneity, which may influence species diversity, but mainly increases plant functional diversity (Araújo *et al*. 2011).

Nutrient availability and acidity, and species richness, were greater in the cerrado than in the grassland habitat. Acidity enhances soil solubility and carbonate, sulfate and phosphate concentrations (Mengel & Kirkby 1982; Bakker *et al*. 2005; Robins *et al*. 2013), which may explain the greater plant species richness of the cerrado habitat when compared to the grassland. Plants in the cerrado habitat were taller and had larger diameters, which can be favored by characteristics of the soil. Epigeal biomass formation by species in ferruginous rupestrian grasslands is closely related to aspects of the soil, such as water retention capacity, soil friability and granulometry (Teixeira & Lemos-Filho 2002). Additionally, basal area and vegetation structure of cerrado species are intimately related to soil characteristics, including the presence of clay and particle size, which enable greater physical support for roots (Assis *et al*. 2011).

Differences in the occurrence of species between the two studied habitats was largely associated with the higher acidity, Fe, Cu, Al, t and Mn of the cerrado, while in the grassland higher concentrations of Fe, OM, P and m had greater impact on species occurrence. In cerrado habitats, low basal saturation levels and restricted nutrient availability represent major challenges to plant nutrition (Arruda *et al*. 2017). Furthermore, cerrado soils differ in texture, acidity, Al, Ca and Mg concentrations (Mota *et al*. 2018). According to Oliveira *et al*. (2015), the low level of phosphorus in rupestrian grassland soils is an important environmental filter that favors root specialization strategies and greater leaf N:P proportions. Other factors, such as low resilience and low water retention capacity (Klink & Machado 2005; Negreiros *et al*. 2011), can also explain the heterogeneity of neighboring areas in rupestrian environments, which favor completely different vegetation types (Fernandes 2016).

In the grassland habitat, the establishment and abundance of some species, such as *C. hilariana,* were favored by the presence of P and Zn. Despite records of antagonist effects of P and Zn (Olsen 1972; Reis-Junior & Martinez 2002), their interaction can also result in increased Zn absorption facilitated by the presence of P (Wallace *et al*. 1978). In fact, higher soil iron (Fe) concentration, as our results indicate, is associated with low pH levels, which could facilitate the release of P in this habitat (Hinsinger 2001).

The species abundance of the cerrado habitat was five times greater than that of the grassland habitat, which can be explained by the nutrient concentration and shallow soils of the latter, which are impoverished due to the quartzite and sandstone content of the parental rock (Benites *et al*. 2003). Furthermore, such conditions, combined with regimes of frequent fire, association with the mycorrhizal community and topography, can modify the shrub-tree vegetation structure, and thus reduce biomass, increase mortality rates and reduce species recruitment rates (Hoffmann & Moreira 2002; Miranda *et al*. 2004; Carvalho *et al*. 2014). Additionally, differences in nutrient availability in the soil, such as Ca^2, may result indifferent floristic compositions of cerrado vegetation (Haridasan 2008).

Several studies in the cerrado have reported Fabaceae to be the most representative family (Giulietti *et al*. 2005; Pinto *et al*. 2009; Cheung *et al*. 2016; Torres *et al*. 2017). Likewise, Myrtaceae has been recorded as the richest family in cerrado habitats in Goiás, in central Brazil (Moura *et al*. 2010). For the grassland habitat, Asteraceae was the richest family, which is in concordance with other studies in the region (e.g. Mota *et al*. 2016; see also Conceição *et al*. 2016; Silveira *et al*. 2016; Mota *et al*. 2018).

In general, the results shown here corroborate the hypothesis that micro-environmental variation in soil chemistry is directly related to vegetation structure and influence species composition of plants in rupestrian environments. Furthermore, such soil heterogeneity yields different plant life form strategies for maximizing the acquisition of nutrients. Plants in rupestrian ecosystems are known for being highly adapted in order to survive, reproduce and maintain populations in such heterogeneous mosaic landscapes, and to deal with the constraints that this harsh environment presents.

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