The influence of soil on vegetation structure and plant diversity in different tropical savannic and forest habitats

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Abstract

Aims

Soil plays an important role in the formation and heterogeneity of habitats and thus can cause changes in vegetation structure and plant diversity. The differentiation between Cerrado/savanna and forest is well known, but the relationship between soil and habitats from savannic or forest formations still needs to be better understood, particularly in tropical ecotonal areas. We studied the association between attributes of plant communities, namely structure and diversity, and physicochemical characteristics of soils in the Caatinga domain at the transition to Cerrado in Brazil.

Methods

Chemical and physical analyses of soils were performed in samples of 38 plots from savannic formations and 30 plots from forest formations. Vegetation was characterized floristically and structurally in all plots, five habitats being assessed in each plant formation. Soil features and vegetation parameters were highly distinct among the different habitats.

Important Findings

In general, forest habitats were more nutrient rich than savannic formation. Furthermore, soil variables showed effects both on vegetation structure and on its species diversity, more pronouncedly in the savannic formations. Habitats were structurally distinct, and diversity differed between savannic and forest communities; however, a higher differentiation occurred when the savannic formation habitats were compared among them. Although plant diversity did not differ among forest formation habitats, soil attributes showed a close relationship with edaphic factors and can contribute for similar vegetation. The soil–vegetation relationship in highly diverse ecotonal landscapes is important from the conservation biology point of view and aid in the execution of proactive plans for the maintenance of biodiversity. Thus, we noticed that diversity and soil behaves distinctly between savannic and forest communities.

Keywords: Cerrado, dry forest, edaphic variation, vegetation–soil relationship, ecotone

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INTRODUCTION

The structure and diversity of tropical vegetation are determined by the discontinuous distribution of several biotic and/or abiotic factors, which act in different spatial and temporal scales (Dale 1999; Peña-Claros *et al.* 2012; Arruda *et al.* 2015a). At a local or regional scale, plant diversity may be influenced by abiotic conditions, but it may also depend on other ecosystem processes, such as biotic interactions and limitations to seed dispersal (Dalling *et al.* 2002; Peña-Claros *et al.* 2012). Among the abiotic factors, topography and soil type play a major role in the heterogeneity of habitats, thus contributing to physiognomic differentiation of the vegetation (Oliveira-Filho and Ratter 2002; Baldeck *et al.* 2013; Guerra *et al.* 2013). This ultimately results in changes on the structure of plant community and on their species diversity.

The wide variation in tropical landscapes in terms of soil age, erosion rates, topography and hydrology, among other factors, has effects on the structure and function of the ecosystems (Townsend *et al.* 2008; Becknell and Powers 2014). Among the edaphic factors, the nutrient content in the soil may affect parameters such as tree height and basal area and thus consequently influence the structure of tropical plant communities (Peña-Claros *et al.* 2012; Becknell and Powers 2014). According to the studies on tropical vegetation, plant species richness is positively related to soil fertility (Poulsen *et al.* 2006; Dybzinski *et al.* 2008; Neri *et al.* 2012), although several studies reported controversial results (Enright *et al.* 1994; Nadeau and Sullivan 2015), which therefore renders the performance of in-depth studies necessary, especially on tropical landscapes.

The knowledge on the abiotic heterogeneity within the structure of arboreal communities is fundamental to the conservation of tropical vegetation (Guerra *et al.* 2013), particularly in the transition areas. The northern region of Minas Gerais state poses a singular case in this context, as it is influenced by three major Brazilian phytogeographical domains: Cerrado, Caatinga and Atlantic Rainforest (Ab'Sáber 2003). This ecotonal zone shows a variety of phytophysiognomies that differ according to topography and soil characteristics (Brandão 2000; Arruda *et al.* 2013), revealing complex combinations of phytogeographical components from the adjacent biomes (Ab'Sáber 2003). Two types of plant formations can be distinguished: savannic and forest. In that sense, it should be highlighted that tropical forests, either deciduous or semideciduous, tend to occur over soils with higher nutrient availability, while the Cerrado phytophysiognomies (which are savannic formations) tend to occur over nutrient-poor soils (Oliveira-Filho and Ratter 2002; Ribeiro and Walter 2008; Arruda *et al.* 2013).

The Cerrado covers ~2 million km^2, supporting a mosaic of several physiognomies including savannas, grassy, woodlands and rupestrian fields (Ribeiro and Walter 2008), which almost 50% of total area was already lost (Klink and Machado 2005). On the other hand, deciduous forests cover up to 81 000 km^2

of the Brazil and is estimated that 52% have already been converted to some kind of human activity (Portillo-Quintero and Sánchez-Azofeifa 2010). The northern region of Minas Gerais state, is dominated by Cerrado and deciduous forests both actually covering 14 804.24 km^2 (24%) of its area. Recent studies have verified annual net loss of −1.2% per year for both vegetations in northern Minas Gerais (Espírito-Santo *et al.* 2016).

The terms habitat, formation and phytophysiognomy should be properly defined and understood. Habitat is the suite of resources and environmental conditions that determine the presence, survival and reproduction of individuals of a given species (Morrison *et al.* 2006; Sinclair *et al.* 2006). However, plant communities that are dominated by one particular life form, and which recur on similar habitats, are called 'formations' (Mueller-Dombois and Ellenberg 1974; Clapham and Radford 1980). Already phytophysiognomy is a morphological characteristic of the plant community in which can support different formations (Grabherr and Kojima 1993). The concepts of the terms listed above are fundamental to the context of this study, with implications for the conservation and management policies (see Veldman 2016).

Previous researches on biogeography and ecosystem dynamics have focused on the differentiation between forest and the Cerrado/savanna (Ratnam *et al.* 2011; Silva *et al.* 2013; Veldman 2016). However, with respect to establishing the relationships between all vegetation types and soil, little information is available (e.g. Assis *et al.* 2011). In this context, there is a large knowledge gap regarding the relationship between attributes of plant communities and soil characteristics in habitats inserted in the same landscape. Thereby, this study aimed to verify whether soil features (physical and chemical) determine the structure of vegetation and the diversity of species therein, in two types of tropical plant formations: savannic and forest. The following specific questions were addressed: (i) do vegetation structure, plant diversity and soil traits differ among the habitats in each plant formation? (ii) Does the soil traits influence the vegetation structure and plant diversity? (iii) If so, does the effects of soil traits differ across different formations? In particular, we expected greater plant diversity and structural complexity in habitats with more fertile soils, with similar effects on habitats within each formation.

MATERIALS AND METHODS

Study area

The study was conducted at the Caminhos dos Gerais State Park (CGSP; 14°48′S, 43°06′W and 15°18′S, 42°50′W), located in northern Minas Gerais, Brazil (Fig. 1). This conservation unit was created in 2007 and holds the largest area (56 237.37 ha) among the state parks in the region (Espírito-Santo *et al.* 2009). The CGSP is located at Serra Geral, an elevated topographic formation with scarped edges, at an averaged altitude of 1090-m above sea level, modeled in Proterozoic rocks
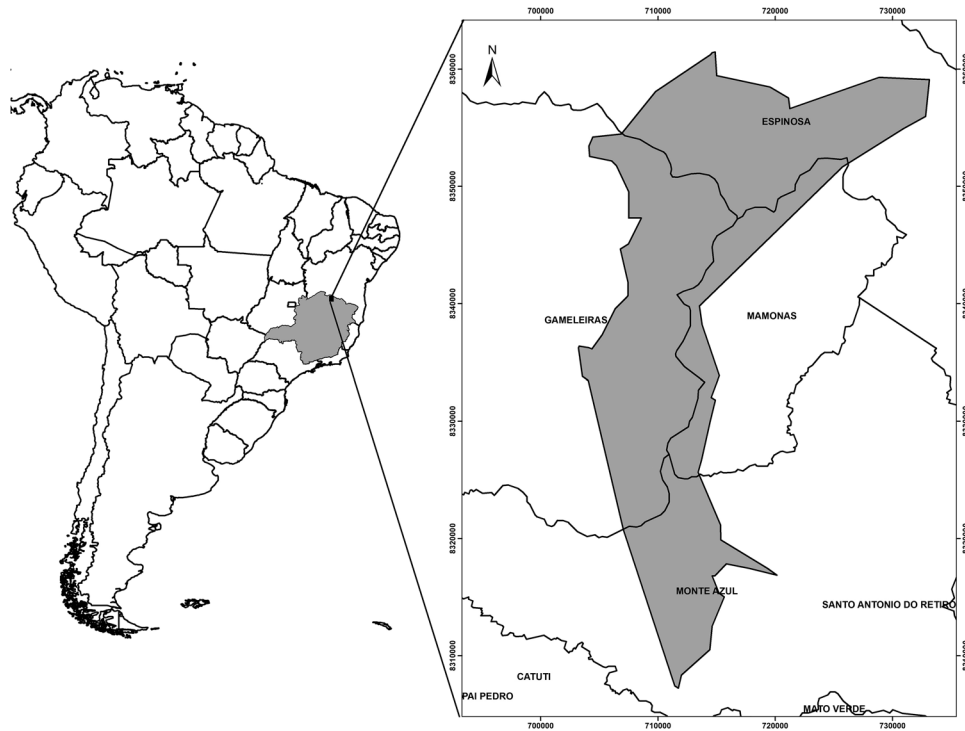
Figure 1: Location of Caminho dos Gerais State Park, Northern Minas Gerais state, Brazil.

(mid and late Precambrian) (Drummond *et al.* 2005), showing a wide geoenvironmental variation (see Rodrigues *et al.* 2015). According to the Köppen's climate classification, the climate of the studied region is BSh, which is a dry climate, semi-arid, with low latitude and altitude Semiarid (Alvares *et al.* 2013; Arruda *et al.* 2013). Mean annual precipitation is normally <750 mm, with a pronounced dry season from April to September (Antunes 1994; Fig. 2). Mean monthly temperatures range from 23 to 27.5°C (INMET 2014).

The phytophysiognomic mosaic in the CGSP ranges from fields to savanna vegetation, all of which were denominated in this study as savannic formation and forest formation. Each one of them was separated in five habitat types, defined by their vegetation and soil class (Table 1; see online supplementary Fig. S1). As savannic formations, we selected a Campo Cerrado, a Campo Rupestre, a Cerrado Rupestre and two habitats of Cerrado *sensu stricto*: early and late (Table 1). As for the forest formations, we sampled three habitats of Deciduous Seasonal Forest, namely Dry Forest over Acrisol, Dry Forest over Dystrophic Cambisol and Dry Forest over Eutrophic Cambisol; one habitat in a Semideciduous Seasonal Forest, called Riparian Forest; and a Caatinga *sensu stricto* (Table 1).

Considering the singularity of the sampled vegetations, we described each habitat: (i) Campo Cerrado is found in high altitudinal position, with shallow to moderately developed soils, characterized by high abundance of *Vochysia rufa* Mart.; (ii) Campo Rupestre is found in the highest mountain tops of CGSP, characterized by shrubby-herbaceous vegetation, and few shorter trees, with predominance of
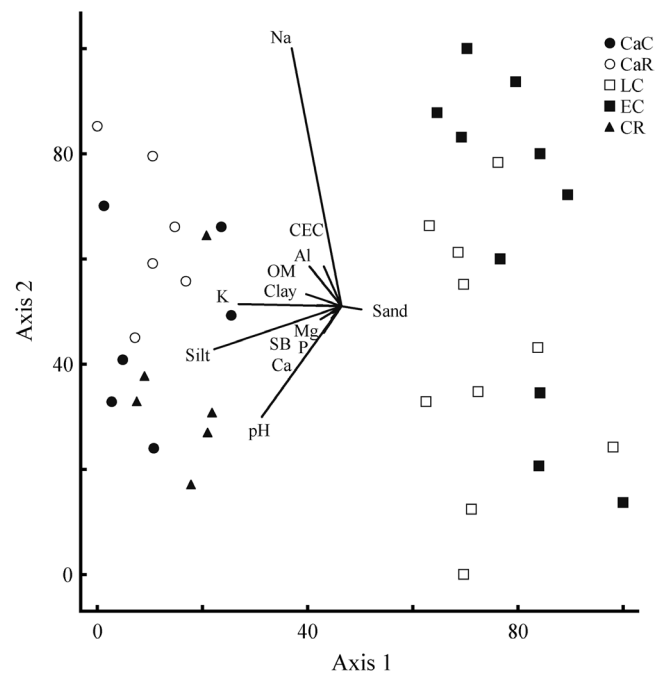

Figure 2: Ordering diagram of the principal component analysis (PCA) showing the distribution pattern of savannic habitats in function of soil characteristics. Campo Cerrado (CaC); Campo Rupestre (CaR); Late Cerrado (LC); Early Cerrado (EC); Cerrado Rupestre (CR).

Vellozia species; (iii) Cerrado Rupestre is found in mosaics dispersed at the CGSP on deeper soils, ranging from field to shrubby rupestrian grassland, in which share many species

Table 1: Habitats, plant formations, vegetation types, soil classes and UTM coordinates (Zone 23) at the Caminho dos Gerais State Park, Minas Gerais state, Brazil

Habitat	Vegetation formation	Phytophysiognomie	Soil class[a]	Altitude (m)	UTM N (m)	UTM E (m)
Late Cerrado (LC)	Savannic	Cerrado *sensu stricto*	Ferralic Arenosol (Dystric)	1074	8.343.179	713.310
Early Cerrado (EC)	Savannic	Cerrado *sensu stricto*	Ferralic Arenosol (Dystric)	1072	8.343.126	712.969
Campo cerrado (CaC)	Savannic	Campo Cerrado	Haplic Cambisol (Dystric)	1083	8.331.388	711.347
Cerrado Rupestre (CR)	Savannic	Cerrado Rupestre	Leptic Regosol (Dystric, Arenic)	1029	8.340.484	713.148
Campo Rupestre (CaR)	Savannic	Campo Rupestre	Lithic Leptosol (Dystric, Skeletic)	1104	8.339.117	709.362
Dry Forest over Acrisol (DFU)	Forest	Deciduous Seasonal Forest	Haplic Acrisol (Hyperdystric, Profondic)	526	8.354.194	705.208
Dry Forest over Dystrophic Cambisol (DFDC)	Forest	Deciduous Seasonal Forest	Leptic Cambisol (Dystric)	592	8.354.422	706.926
Riparian Forest (RF)	Forest	Semideciduous Seasonal Forest	Protic Arenosol (Dystric)	593	8.354.146	707.606
Caatinga *sensu stricto* (CA)	Forest	Deciduous Seasonal Forest	Leptic Cambisol (Dystric)	673	8.357.935	711.009
Dry Forest over Eutrophic Cambisol (DFEC)	Forest	Deciduous Seasonal Forest	Haplic Cambisol (Eutric)	597	8.314.685	715.675

[a]FAO–WRB.

with savanna (Cerrado *sensu stricto*); (iv) Late Cerrado is associated with deep and extremely drained soils, formed by unconsolidated Plio-Pleistocene material covering the Precambrian metasedimentary rock. The vegetation is savanna woodland, supporting a woody layer with height between 1.7 and 3 m, and an herbaceous layer dominated by grasses. (v) Early Cerrado has the same characteristic of the Late Cerrado; however, it is characterized by the earlier presence of *Eucalyptus* sp. plantations along its entire extension up until 2007, when the area was transformed into conservation area; (vi) Dry Forest over Acrisol supports deciduous vegetation on pediplain, with soils characterized by the mix between colluvial matters and metapelitic rocks from the Bambuí Formation; (vii) Dry Forest on Dystrophic Cambisol forests develops on soils of colluvial sediments; (viii) Dry Forest over Eutrophic Cambisol, deciduous forests on deep soils, most located in the mountain slope on the lithology of glacial origin with mafic elements; (ix) Riparian Forest has association with watercourse, and vegetation characterized like semideciduous forest, with trees forming a continuous canopy and few shrubby elements in understory; (x) Caatinga *sensu stricto* is the predominant habitat at the CGSP, with vegetation consisting of small to medium-sized woody plant. It is distinguished from a dry forest trees by its multiple stems, thorn and shorter height, usually <6 m (for more details, see Arruda *et al.* 2015a; Rodrigues *et al.* 2015; Schaefer *et al.* 2016).

Vegetation sampling

To study the effects of soil on the structure and diversity of the different habitats, permanent plots were randomly established. In each habitat, six 20 × 20 m plots were defined, except for the Late and Early Cerrado, in which 10 plots were performed. Despite the different sampling effort between formations (savannic vs forest), statistical procedures were addressed in order to minimize this unbalanced design. The plots were arbitrarily established, each plot in the same habitat was at least 150 m apart from each other. This distance was large enough to insure within-habitat formations variability in plant and soil parameters, which decreases the chance of a type I error and makes it less likely to find false differences among habitats formations. Our plots spatial distribution avoided the pseudoreplication design (i.e. 'clumped segregation'; *sensu* Hurlbert 1984) and maintained the principle of interspersion (Hurlbert 1984). In each plot from the savannic formations, all woody individuals were sampled (including monocots from the Velloziaceae and Arecaceae) with diameter at soil height (DSH) ≥ 3 cm. As for the plots in the forest formations, the sampling criterion for woody individuals was diameter at breast height ≥ 5 cm, at 1.3-m tall. Samples were collected from all individuals, which were identified at species level (or attributed to morphospecies) using the herbarium collection of the Federal University of Viçosa (UFV) and with the aid of specialists.

Soils

Three replicates of soil samples (0–20 cm) were collected in each of the 38 plots from the savannic formations and in the 30 plots from the forest formations. Samples were air-dried and sifted through a 2-mm mesh. Physical and chemical characteristics were determined at the Laboratory of Soil Analysis from UFV. The analyses included granulometry (sand, clay and silt contents); active acidity (pH) in water; exchangeable

acidity (Al); contents of Ca, Mg, K, Na and available P; sum of bases (SB); total cation exchange capacity (CEC) including micronutrients (Zn, Fe, Mn and Cu); and organic matter (OM). The mean value was then calculated to each plot. The soils were classified according to World Reference Base for Soil Resources (WRB) (ISSS Working Group RB 2015).

Data analysis

The differences in edaphic features from the different habitats were tested using generalized linear models (GLMs). In these models, each soil variable was regarded as a response variable, while the habitat variable was considered an explanatory variable. Due to the unbalanced sampling design (different number of plots for each habitat), the model variance were calculated through type II analysis of variance and using Gaussian distribution. This analysis is based on a hierarchical sum of squares (Langsrud 2003) and was performed using car package (Fox and Weisberg 2011) in software R$_{2.15.2}$ (R Development Core Team 2012). After, a contrast analysis was used in significant models in order to unite the levels within the categorical explanatory variable that did not differ significantly (e.g. amalgamation) (Crawley 2013). Finally, we performed residual analyses and evaluation of the adequacy of error distribution (Crawley 2013).

The 13 edaphic parameters were summarized in two variables (Axes 1 and 2) through the principal component analysis (PCA). A PCA was performed individually to each type of formation (savannic and forest). The variables were standardized through logarithmic transformation [$\log(x + 1)$] in order to equalize their contributions in the axis, except for pH, which is already given in a logarithmic scale. These analyses were carried out using software R2.15.2 (R Development Core Team 2012).

Habitat structure was described using the variables: abundance [individuals per plot (ind./plot)], density [individuals per hectare (ind./ha)], basal area (m^2) and mean height (m). The following variables relating to species diversity were also obtained from each plot sampled: species richness; dominance single species (number of individuals of the most common species divided by the total number of individuals, multiplied by 100), as proposed by Peña-Claros *et al.* (2012) (see online supplementary Table S1); Shannon diversity index; Simpson dominance index; and evenness index. All structure and diversity parameters were obtained using software Mata Nativa 3.0 (Cientec 2010), except for the dominance of a single species.

In order to verify the effects of soil on the vegetation structure and species diversity, GLMs were carried out using the above-mentioned structure and diversity variables as response variables. Edaphic variables, represented by the scores in Axis 1 of the PCAs, the habitats and the interaction between Axis 1 and the habitats were used as explanatory variables in each model. This procedure was made only with Axis 1 since it is the most explanatory axis in both PCAs. These models were

also adjusted for hierarchical sum of squares (Langsrud 2003) with type II analysis of variance and using Gaussian distribution. For all models, residual analyses were carried out in order to evaluate the adequacy in the assumed error distribution (Crawley 2013). All analyses were carried out in software R$_{2.15.2}$ (R Development Core Team 2012).

RESULTS

Soil characteristics

The studied habitats differed significantly in all soil characteristics (see online supplementary Table S2). In general, forest habitats were more nutrient rich than habitats from savannic formations (see online supplementary Table S2). For the savannic formation, eigenvalues of the first two PCA axes explained 74.28% of the variance (Axis 1 = 58.78%; Axis 2 = 15.5%) and only the Axis 1 demonstrated statistical significance (Monte Carlo, $P < 0.001$). Edaphic/environmental variables that showed a strong positive correlation with Axis 1 were sand and negative correlation were verified for silt, K, Mg, SB and Al; the variables positively correlated with Axis 2 were Na and CEC and negatively correlated was pH (Table 2; Fig. 2). The PCA of the forest formation showed that the eigenvalues of the first two axes explained 92.456% of the variance (Axis 1 = 86.898%; Axis 2 = 5.558%) and the Axis 1 was highly significant (Monte Carlo, $P < 0.001$). The Axis 1 showed strong positive correlation with Al and sand contents and negative correlation with pH, SB, Ca, Mg and silt; the Axis 2 was positively correlated with phosphorus content and a negatively correlated with clay (Table 2; Fig. 3).

Based on ordination diagram of plots generated by the PCA to data from savannic formation (Fig. 2), we verified that the first two axes discriminated a strong gradient among Na, pH and silt. The ordination diagram (Fig. 2) showed two distinct groups. The Axis 1 separated the Campo Cerrado, Campo Rupestre and Cerrado Rupestre from the Late and Early Cerrado. The Campo cerrado, Campo Rupestre and Cerrado Rupestre presented lower scores in the Axis 1, being related to high amounts of silt and pH, whereas the Late and Early Cerrado presented greater scores in the first axis, being related to high values of sand (Fig. 2). On the Axis 2, all habitats showed wide range in scores, making it difficult to complete separation of groups by this axis.

As for the forest formation, the ordination diagram of plots generated by PCA (Fig. 3), we verified that the first two axes discriminated a strong gradient between clay, phosphorus, CEC and pH. These axes segregated four groups of plots. The Axis 1 separated the Dry Forest over Eutrophic Cambisol from the Dry Forest over Acrisol and Riparian Forest, whereas the Axis 2 separated the Riparian Forest and Dry Forest over Dystrophic Cambisol from the Caatinga *sensu stricto*, Dry Forest over Acrisol and Dry Forest over Eutrophic Cambisol. The Dry Forest over Eutrophic Cambisol presented lower scores in the Axis 1, being related to high amounts of pH and CEC; Dry Forest over Acrisol and Riparian Forest presented

Table 2: Soil parameters in the first two axes of the respective soil PCAs for savannic and forest formation habitats

Soil characteristics	Savannic formation		Forest formation	
	Axis 1	Axis 2	Axis 1	Axis 2
pH (H_2O)	−0.787***	−0.387*	−0.99[ns]	−0.022[ns]
P (mg/dm^3)	−0.359*	−0.194[ns]	−0.362[ns]	0.646***
K (mg/dm^3)	−0.876***	0.005[ns]	−0.895***	0.151[ns]
Na (mg/dm^3)	−0.466**	0.854***	−0.513**	−0.007[ns]
Ca (cmol$_c$/dm^3)	−0.705***	−0.308[ns]	−0.947***	0.151[ns]
Mg (cmol$_c$/dm^3)	−0.838***	−0.299[ns]	−0.933***	0.182[ns]
Al (cmol$_c$/dm^3)	−0.687***	0.299[ns]	0.834***	−0.508**
SB (cmol$_c$/dm^3)	−0.837***	−0.196[ns]	−0.956***	0.189[ns]
CEC (cmol$_c$/dm^3)	−0.478**	0.393*	−0.837***	−0.279[ns]
OM (dag/kg)	−0.719***	0.081[ns]	−0.827***	−0.265[ns]
Sand (%)	0.796***	−0.045[ns]	0.81***	0.468**
Silt (%)	−0.922***	−0.111[ns]	−0.912***	−0.01[ns]
Clay (%)	−0.392*	0.003[ns]	−0.48**	−0.821***
Variation explained by PCA (%)	58.78	15.5	86.898	5.558

Significance levels were based on a Pearson's correlation between soil properties and PCA axes: *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, ns, non-significant.
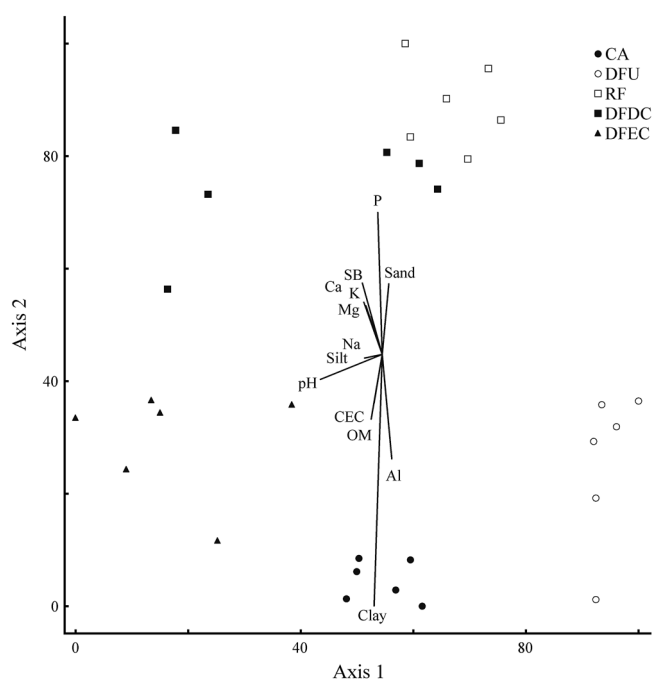

Figure 3: Ordering diagram of the principal component analysis (PCA) showing the distribution pattern of forest habitats in function of soil characteristics. Caatinga *sensu stricto* (CA); Dry Forest over Acrisol (DFU); Riparian Forest (RF); Dry Forest over Dystrophic Cambisol (DFDC); ; Dry Forest over Eutrophic Cambisol (DFEC).

higher scores in the first axis, being related to high values of sand (Fig. 3). In Axis 2, the Riparian Forest and Dry Forest over Dystrophic Cambisol presented higher scores, related with high values of phosphorus, and the Caatinga *sensu stricto*, Dry Forest over Acrisol and Dry Forest over Eutrophic Cambisol presented lower scores, related with high values of clay (Fig. 3).

Structure and diversity

The savannic formation habitats differed significantly in all structure and diversity characteristics, with the exception of species richness (see Table 3). On average, the Campo Rupestre had the highest abundance (155.7 ind./plot), largest basal area (1.4 m^2) and lowest height values (1.2 m). Mean individuals height was significantly higher in the Late and Early Cerrado (2.8 and 2.4 m) in comparison with the Cerrado Rupestre (2.8 m), Campo Cerrado (2.4 m) and Campo Rupestre (1.2 m). The mean densities varied significantly, with lowest densities in the Early Cerrado(1965 ind./ha) and Cerrado Rupestre (2083.3 ind./ha), followed by the Late Cerrado (2265 ind./ha), and with much higher values between Campo Cerrado (2654.2 ind./ha) and Campo Rupestre (3891.7 ind./ha), which did not differ. The lower density recorded by the Cerrado Rupestre (0.5 m^2) also accounts for reduced basal area recorded in this habitat, not differing from the basal area of the Late Cerrado (0.3 m^2). The most expressive habitats in terms of dominance of a single species were the Campo Rupestre (*Vellozia* sp.) and the Campo Cerrado (*Vochysia rufa*), represented by 63.3 and 53.7% of the sampled individuals, respectively. These two habitats also had the lowest values of Shannon, Simpson and evenness indexes.

In the forest formations, diversity parameters did not differ significantly among habitats, differences only were detected for structural parameters (Table 3). The abundance was highest in Dry Forest over Acrisol (59.8 ind./plot), but similar between Caatinga *sensu stricto* (59.3 ind./plot), Dry Forest

Table 3: Structure and diversity of the vegetation in different habitat formations (savannic and forest) at the Caminho dos Gerais State Park, Minas Gerais, Brazil

	Savannic formation habitats				
Response variables	LC	EC	CaC	CR	CaR
Structure					
Abundance (ind./plot)	90.6 ± 13.4[b]	78.6 ± 5[b]	106.2 ± 22.9[b]	83.3 ± 9.5[b]	155.7 ± 42.2[a]
Density (ind./ha)	2265 ± 334[b]	1965 ± 124.4[c]	2654.2 ± 572[a]	2083.3 ± 237[c]	3891.7 ± 1055[a]
Basal area (m^2)	0.3 ± 0[c]	0.6 ± 0.1[b]	0.6 ± 0.1[b]	0.5 ± 0.1[c]	1.4 ± 0.4[a]
Height (m)	2.4 ± 0.2[a]	2.8 ± 0.1[a]	1.9 ± 0.2[b]	2.1 ± 0.3[b]	1.2 ± 0.1[c]
Diversity					
Richness	16.9 ± 1.4[a]	17.5 ± 0.7[a]	14.7 ± 1.9[a]	16.7 ± 1.5[a]	12.7 ± 2[a]
DoA (%)	15.8 ± 3.1[b]	17 ± 3.7[b]	38.5 ± 15.8[a]	19.5 ± 3.6[b]	63.3 ± 10.3[a]
Shannon	2.3 ± 0.1[a]	2.4 ± 0.1[a]	1.7 ± 0.3[b]	2.2 ± 0.1[a]	1.4 ± 0.3[b]
Simpson	0.9 ± 0[a]	0.9 ± 0[a]	0.6 ± 0.1[b]	0.8 ± 0[a]	0.5 ± 0.1[b]
Evenness	0.8 ± 0[a]	0.8 ± 0[a]	0.6 ± 0.1[b]	0.8 ± 0[a]	0.5 ± 0.1[b]

	Forest formation habitats				
	DFU	DFDC	RF	CA	DFEC
Estruture					
Abundance (ind./plot)	59.8 ± 3.2[a]	50.3 ± 4.2[b]	39 ± 6.1[b]	59.3 ± 7.4[b]	45.8 ± 6[b]
Density (ind./ha)	1495.8 ± 80[a]	1258.33 ± 104.4[b]	975 ± 152.7[b]	1483.33 ± 183.8[a]	966.67 ± 75.7[b]
Basal area (m^2)	0.43 ± 0.02[c]	0.77 ± 0.04[b]	1.26 ± 0.17[a]	0.56 ± 0.04[b]	0.23 ± 0.04[c]
Height (m)	6.52 ± 0.23[c]	9.03 ± 0.16[a]	10.47 ± 0.27[a]	5.35 ± 0.23[c]	6.71 ± 0.19[b]
Diversity					
Richness	11.33 ± 0.9[a]	15.33 ± 1.48[a]	14.67 ± 0.99[a]	13.17 ± 1.56[a]	12 ± 1[a]
DoA (%)	36.65 ± 2.9[a]	22.3 ± 6.98[a]	23.06 ± 9.2[a]	15.75 ± 5.31[a]	16.53 ± 8.51[a]
Shannon	1.81 ± 0.1[a]	2.28 ± 0.12[a]	2.24 ± 0.13[a]	2.13 ± 0.17[a]	1.99 ± 0.1[a]
Simpson	0.78 ± 0.02[a]	0.86 ± 0.03[a]	0.86 ± 0.04[a]	0.85 ± 0.03[a]	0.082 ± 0.03[a]
Evenness	0.75 ± 0.02[a]	0.84 ± 0.03[a]	0.84 ± 0.05[a]	0.84 ± 0.03[a]	0.81 ± 0.03[a]

Data were averaged (± SE) at plot level for all habitats. Different letters in the same line indicate statistical differences among habitats determined by *post hoc* contrast tests ($P < 0.05$). DoA, dominance single species.

over Dystrophic Cambisol (50.3 ind./plot), Dry Forest over Eutrophic Cambisol (45.8 ind./plot) and Riparian Forest (39 ind./plot). Despite the statistical difference presented by Dry Forest over Acrisol in the parameter abundance, this habitat did not differ statistically from the Caatinga *sensu stricto* habitat regarding density of individuals (1495.83 and 1483.33 ind./ha, respectively). The densities of the other habitats were lower. In the case of Forest Dystrophic value was 1258.33 ind./ha, followed by Riparian Forest (975 ind./ha) and Dry Forest over Eutrophic Cambisol (966.67 ind./ha). The highest mean value for basal area was shown in the Riparian Forest (1.26 m^2). Regarding height of individuals, the highest values were observed in the Dry Forest over Dystrophic Cambisol and in the Riparian Forest (9.03 and 10.47, respectively).

Effect of soil on vegetation structure and diversity

Soil variables were more significantly related to vegetation variables (structure and diversity) in the savannic formations (11 variables) than in the forest formations (1 variable)

(see online supplementary Table S3). These results suggest that soil plays a more important role in the determination of structure and diversity in the savannic habitats. In general, among the analyzed soil–vegetation relationships, five vegetation variables were significantly affected by Axis 1 and seven by the interaction between Axis 1 and the habitat (see online supplementary Table S3).

Soil characteristics tend to have different effects on the structure and diversity of savannic and forest formation habitats (see online supplementary Table S3). The tree abundance in the savannic formation habitats was significantly influenced by the interaction between the habitat and Axis 1 (see online supplementary Table S3), with a significantly higher abundance in the Campo Rupestre (Table 3). However, in the forest formation habitats, there was no significant difference between structural parameters and soil characteristics. In the savannic formation, richness and Shannon, Simpson and evenness indexes were significant in relation to Axis 1, and the interaction between habitat and Axis 1 was significant for the dominance of a single

species and Simpson and evenness indexes. However, in the forest formations, habitats only species richness was significantly related to Axis 1 (see online supplementary Table S3). It should be noted that the edaphic influence differentiates some vegetation parameters among habitats from a same plant formation (see online supplementary Tables S4 and S5). The number of individuals increased with the soil axis (i.e. with increasing contents of OM and aluminum and decreasing contents of clay) in the Campo Cerrado, Campo Rupestre and Cerrado Rupestre and decreased in the both Early and Late Cerrado (see online supplementary Table S4). Further detail on the soil–vegetation relationship can be seen in online supplementary Table S4.

DISCUSSION

In this study, we asked how the vegetation structure, plant diversity and soil traits differ among the habitats in each plant formation, whether soil characteristics affect vegetation structure and plant diversity and whether the effect of soil varied across different formations. There were overall significant differences in vegetation parameters (structure and diversity) among the habitats (Table 3). Furthermore, soil variables showed effects on the vegetation structure and diversity (see online supplementary Table S3). And analyzing the different plant formations, soil characteristics showed effects on the vegetation structure and diversity more pronouncedly in the savannic habitats (see online supplementary Table S3).

Soil, structure and diversity across different habitats

The differences in the soils from the 10 studied habitats, in terms of texture and chemical composition, demonstrated the influence of environmental heterogeneity on the landscape at Serra Geral. These edaphic variations are commonly found in ecotonal areas (Arruda *et al.* 2013; Nunes *et al.* 2013; Rodrigues *et al.* 2013; Veloso *et al.* 2014) and may be the result of biotic processes that create edaphic gradients, instead of being single-handedly determined by the pre-existing edaphic conditions (Silva *et al.* 2013).

In the woody component, structural differences among habitats were evident in both savannic and forest formations. In savannic formation habitats, it is well established that the structure of vegetation can vary across the landscape, within topographic gradients that can be hundreds of meters long (Rossatto *et al.* 2012). Among the pronounced differences observed in the savannic formation, the Campo Rupestre surprisingly showed the highest basal area and the highest number of individuals. This result is inconsistent with other Campo Rupestre areas, considering that a great deal of studies excludes the monocot species from their floristic surveys (Lenza *et al.* 2011). Thus, the high number of individuals in the Campo Rupestre habitat is mainly due to the great number of *Vellozia* sp. representatives. Besides, the largest basal area detected in this habitat poses a sampling artifact, since

the DSH measurements of *Vellozia* sp. individuals were taken from the pseudostem. The largest part of the mass of this structure consists in persistent leaf sheaths around a slender woody stem (Ayensu 1973; Jacobi and del Sarto 2007). Such fact points to an overestimation of the basal area parameter, wherein the soil nutritional status is positively associated this structural parameter. The Campo Rupestre also presented the lowest mean height of woody individuals, likely as a result of a set of factors such as low soil nutritional status and the incidence of fire (Costa and Araújo 2007). As for forest formation, the Riparian Forest showed the highest frequency of taller individuals and largest basal area. A probable explanation may lie in the fact that the Riparian Forest can be considered a mesic habitat compared to the other sampled habitats of the forest formation, which can be regarded as xeric. Mesic habitats have better nutritional and productivity conditions compared to xeric (Murphy and Lugo 1986; Segura *et al.* 2003), which directly affects the structure of their plant communities. In contrast, the Dry Forest over Acrisol, which is located on the foothills at Serra Geral, showed high values for parameters density and number of individuals. The low chemical potential of the soil from this habitat in relation to the other sampled ones tends to influence the higher density and lower basal area of woody individuals. Thus, the structural complexity of the studied landscapes is strongly correlated with nutrient and water availability, and consequently with soil texture, similarly to the reports of Murphy and Lugo (1986), Segura *et al.* (2003), Rodrigues *et al.* (2013) and Veloso *et al.* (2014).

As for the diversity parameters, only phytophysiognomies belonging to the savannic formations showed significant differences among habitats (see online supplementary Table S3). The distinct soil types occurring in these formations (Table 1 and see online supplementary Table S2) may be responsible for such differences. According to several authors, soil characteristics are among the factors the most influence plant diversity in the Cerrado (Oliveira-Filho *et al.* 1989; Assis *et al.* 2011; Neri *et al.* 2012). The woody species showed higher abundance under environmental conditions (e.g. pedological) that are favorable to them. This explains the variation in other diversity parameters, such as the Shannon, Simpson and Pielou's evenness indexes. No significant difference in the diversity parameters was found in the forest formation habitats. Changes in water availability and soil nutritional status are important factors for the determination of species richness in forests (Balvanera *et al.* 2002; Guerra *et al.* 2013; Rodrigues *et al.* 2013). However, in our study, the differences in soil characteristics may not be so high as to the point of inducing expressive alterations in the species richness. Alternatively, changes in the species composition might also be considered, as such factor was not approached in the present study. Thereby, species composition may vary, forming groups of indicator species for each habitat (see Assis *et al.* 2011; Guerra *et al.* 2013), with not expressive difference in the species richness.

Soil–vegetation relationship

The effects of soil on the vegetation differed between the two formation types. Such singularity in the soil–vegetation relationships has also been reported to distinct forest types, namely rainforests and dry forests (Peña-Claros *et al.* 2012; Becknell and Powers 2014). Soil characteristics were mostly important in the savannic formation habitats, showing a significant relationship with all vegetation parameters (Tables 3 and online supplementary Table S4). However, the PCA Axis 1 was not significant for the structure and diversity parameters of the forest habitats, with the exception of the species richness (Table 3). A possible explanation is that, as soil characteristics differ between the types of plant formation, such difference propitiates the singular behavior of the soil–vegetation relationship in each formation. However, in the forest formation habitats, soil characteristics did not influence vegetation features across the habitats. Thus, nutrient and water availability (the latter of which could be assessed through soil texture) might be less limiting in the forest formations than in the savannic, exerting a similar influence on the soil–vegetation relationships in the different forest habitats.

As previously mentioned, there was no direct relationship between diversity parameters and soil characteristics in the forest habitats. This is in accordance with the results of Clinebell *et al.* (1995), which report that plant species richness has no direct relationship with edaphic properties, i.e. high nutrient concentration in the soil favoring some species in detriment of others. However, in savannic habitats, aluminum, sand and silt contents were the major soil attributes in relation to vegetation descriptors. The dominance of a single species, which had its highest value in the Campo Rupestre and Campo Cerrado, was positively correlated with sodium, aluminum, OM and silt contents and negatively correlated with sand. Nutrient contents were probably more limiting in these two habitats. The highest aluminum content is due to leaching and the consequent soil impoverishment, which result in competition for essential minerals and toxicity (Ruggiero *et al.* 2002), leading to the selection of aluminum-tolerant species. Canopy opening, although not assessed, may have an indirect relationship with the differentiation of diversity parameters (Poulsen *et al.* 2006; Assis *et al.* 2011).

In this study, the aluminum was also an important soil trait on the formation forest, where there was high variation at their level among different habitats. High aluminum concentrations were found in Dry Forest over Acrisol and Caatinga *sensu stricto* habitats. This edaphic condition restricts the establishment of some tree species not adapted to the scarcity of resources (Arruda *et al.* 2015b), which have higher nutritional requirements, as specialists species of Riparian Forest, Dry Forest over Dystrophic Cambisol and Dry Forest over Eutrophic Cambisol habitats.

CONCLUSION

The soil–vegetation relationship in such diverse landscapes is important from the conservation biology point of view because define habitat preference, and plant structure and diversity supported on each soil type and habitat formations; i.e. richest habitats in both plant and soil nutrient could sustain greater animal diversity and be preferable to conservation, whereas poorest habitats in both plant and soil nutrient could be preferable for cases of restoration. We believe that information provided here support the execution of proactive plans for the maintenance of biodiversity (Assis *et al.* 2011; Guerra *et al.* 2013). In our study, besides verify differences in plant structure among formations, we noticed that diversity is range distinctly between savannic and forest communities. Therefore, future studies in tropical landscapes need to include the distribution of species and their respective abundances in relation to edaphic variables in order to better understand the processes involved in the soil–vegetation relationship, especially in ecotonal areas.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plant Ecology* online.

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