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Forces driving the regeneration component of a rupestrian grassland complex along an altitudinal gradient

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Abstract This study aimed to document variation in the composition and structure of regenerating woody vegetation along an altitudinal gradient of a rupestrian grassland and to describe the relationship between species and characteristics of the soil. All woody plants with a diameter at ground height of ≤ 1 cm were collected in seven sampling sites at altitudes between 800 and 1400 m in Serra do Cipó (Minas Gerais State, Brazil). Phytosociological parameters and the Shannon diversity index were calculated and compared using Hutcheson's *t* test. Floristic composition was evaluated by nonmetric multidimensional scaling (NMDS) ordination with analysis of variance as a confirmatory analysis, in which the response variables were the axis of the NMDS. Correlation between soil characteristics and vegetation patterns was evaluated with multiple regression models and canonical redundancy analysis. For all analyses, we performed analysis of variation partitioning to decompose the explanation of spatial, soil, and altitudinal variation. A total of 809 individuals of 127 species belonging to 26 families were sampled. Species richness and structure varied among altitudes. Species diversity followed an altitudinal pattern and was higher at lower altitudes. Some soil variables, such as remaining phosphorus, base saturation, and structural components, were more strongly correlated with species distribution than the others. Although variation in altitude leads to changes in the composition of the regenerating woody species, variation in plant communities was determined by a combination of environmental factors, of which soil properties played an important role.

Keywords Altitude · Campo rupestre · Edaphic attributes · Espinhaço Mountain Range · Flora · Phytosociology

Introduction

Altitude is a geographic factor that is able to generate patterns of biological diversity due to the climate, soil, and vegetation changes that occur along its gradients (Whittaker 1960; Rahbek 1995; Lomolino 2001; Fritzsons et al. 2008; Rana et al. 2011). Environmental conditions that vary with altitude influence plant species distributions (Moreno et al. 2003), such that one of the most well-documented biogeographic patterns on Earth is the increase in plant diversity with decreasing altitude (e.g., Whittaker 1956; Hamilton 1975; Fernandes and Price 1988; Gentry 1988; Kitayama 1992; Huston 1994; Aiba and Kitayama 1999; Hussain and Malik 2012). However, several other studies have shown non-unimodal patterns for plant richness along altitudinal gradients (e.g., Fernandes 1992; Liberman et al. 1996; Wang et al. 2002; Joly et al. 2012), while yet others report peaks of diversity at intermediate elevations (e.g., Lomolino 2001; Sang 2009). Hence, a clear and accurate description of the distributional pattern of plant richness in relation to altitude is yet to be achieved

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(Wang et al. 2002). Mountains provide excellent opportunities to develop and test theories regarding the relationship between biodiversity and altitude, and empirical works are the most convincing tests when there are covariables that are not directly related to altitude (Korner 2007). Therefore, the study of the distribution of plant species along environmental gradients is important, particularly in several mountainous tropical regions where such knowledge is still needed.

Multiple environmental factors vary along altitudinal gradients, but few studies have attempted to interpret vegetation patterns associated with these factors (Wang et al. 2002). An altitudinal gradient basically corresponds to a temperature gradient (Kitayama 1992) and variation in other atmospheric variables, with implications for the distribution and survival of most organisms (Korner 2007). However, differences between distinct areas can also be attributed to soil characteristics (Moreno et al. 2008), and an altitudinal difference of a few hundred meters can cause significant changes in soil, climate, and vegetation (Fritzsons et al. 2008). For example, the decrease of nutrients, especially nitrogen, with increasing altitude was suggested as a cause for the decline of plant diversity and forest stature on tropical mountains (Grubb 1977; Aiba and Kitayama 1999). On the other hand, the effects of area and isolation likely contribute to the observed decreases in species richness with altitude (Korner 2007). However, the environmental processes responsible for structuring communities may also be spatially organized, so that spatial structure can corroborate false correlations between species and environment (Legendre et al. 2002; Peres Neto and Legendre 2010). Therefore, it is necessary to consider spatial structure in studies of correlations between components of vegetation and environmental variables.

The tropical flora of the southeastern Brazilian mountains represents an excellent opportunity for ecological studies. The main formation in these mountains is low-stature sclerophyllous vegetation called rupestrian grasslands, locally known as “campo rupestre”. This vegetation comprises a complex mosaic of plant communities with high species richness and many endemic species (Giulietti et al. 1987; Filgueiras 2002; Medina and Fernandes 2007). It occurs on a mosaic of soils of quartzite and igneous origin (Semir 1991; Benites et al. 2007) and is found mainly along the Espinhaço Mountain Range, generally above 900 m a.s.l., on shallow, Al-rich and water- and nutrient-deficient soils (Giulietti et al. 1987; Benites et al. 2007; Negreiros et al. 2009). These environments are highly diverse (Giulietti et al. 1987; Conceição and Pirani 2007; Carvalho et al. 2012; Gastauer et al. 2012) and represent a large proportion of the flora of the “Cerrado” (savanna) biome, as well as all tropical flora (Rapini et al. 2008; see Fernandes 2016).

Environmental heterogeneity and soil-climatic factors influence plant species composition in this environment and are partly responsible for the species diversity present in the rupestrian grassland complex (Ribeiro and Walter 2008; Carvalho et al. 2012). Floristic composition in this ecosystem may change within meters, and plant species density was argued to be directly associated with the soil substrate (Ribeiro and Fernandes 1999, 2000; Benites et al. 2001; Medina and Fernandes 2007; Carvalho et al. 2012). Therefore, more detailed studies on floristic diversity in this vegetation type are needed for understanding the relationship between species density and environmental conditions and for estimating the overall species richness of the region (Torres et al. 1997).

Although many studies have been conducted on the flora of rupestrian grassland vegetation in the Espinhaço Mountain Range (e.g., Giulietti et al. 1987; Conceição and Pirani 2007; Rapini et al. 2008; Nunes et al. 2008) making it the most studied plant typology in the state of Minas Gerais (Costa et al. 1998), only a few studies have assessed changes in its flora along altitudinal gradients (e.g., Nunes et al. 2008; Borges et al. 2011). Likewise, although essential for conservation and understanding the processes that determine the resilience of this ecosystem, studies on the natural regeneration of rupestrian grasslands are virtually nonexistent (see Medina and Fernandes 2007). Thus, focusing on natural regeneration is crucial to understand the behavior of different native species that compose this singular plant community. The presence of species in the early stages of regeneration indicates the flux of new species to the community, while a small number of these species indicate an interruption in the regeneration process (e.g., Menino et al. 2012). Due to a lack of research, the processes and patterns involved in the natural regeneration of rupestrian grasslands, and the factors that determine which species will colonize a given environment, are largely unknown. Furthermore, this knowledge has acquired legal significance, as a Brazilian law erroneously placed this vegetation under the domain of the Atlantic Forest (Law n. 11,428; Brasil 2006), and so knowledge regarding the colonization and regeneration of its species is necessary for the required environmental assessment strategies and plans (GWF, pers. inf.).

The present study aims to provide the very first information on the regeneration of woody species of the rupestrian grassland by attempting to answer the following questions: (1) Do floristic composition and structure of regenerating woody communities of the rupestrian grassland complex vary along an altitudinal gradient? (2) Is the floristic similarity among areas influenced by soil characteristics? (3) Is there an interaction between soil and altitude that promotes a pattern of plant diversity and distribution in the rupestrian grassland? Although we expect the diversity of the regenerating plant species to decrease with increasing altitude (e.g., Whittaker 1956; 1960; Hamilton 1975; Gentry 1988; Kitayama 1992), this diversity may also be influenced by soil characteristics independent of altitude (see Grubb 1977; Aiba and Kitayama 1999).

Materials and methods

Study area

This study was conducted in the rupestrian grasslands of Serra do Cipó from December 2010 to March 2011. Serra do Cipó is located in the southern portion of the Espinhaço Mountain Range between the latitudes of 19°12′–19°34′S and longitudes of 43°27′–43°38′W in the central region of the state of Minas Gerais of southeastern Brazil, (Melo Júnior et al. 2001). It encompasses the municipalities of Santana do Riacho and Jaboticatubas, and, according to the Köppen classification, the regional climate is tropical highland (Cw) with hot summers and pronounced dry seasons (Madeira and Fernandes 1999). The region experiences relatively cold winters and a narrow annual temperature range; the average annual temperature and precipitation are 21.2 °C and 1622 mm, respectively (Madeira and Fernandes 1999).

Serra do Cipó includes small and large patches of Atlantic Forest above 1300 m a.s.l., "cerrado" *stricto* sensu ("cerrado" *s. s.*; shrub-savanna) from 700 throughout 1400 m a.s.l., patches of seasonally dry forests at 800–900 m a.s.l. and riparian forest in drainages, while the rupestrian grasslands are distributed primarily between 900 and 1400 m a.s.l. (Giulietti et al. 1987). Although the soils in the region contain moderate levels of organic matter, they are highly acidic and macronutrient deficient, and have high aluminum saturation and a predominantly sandy texture (Negreiros et al. 2008).

Sampling of regenerating woody vegetation

The sampling area was established along an altitudinal gradient with sites stratified at approximately 100-m intervals from 800 to 1400 m for a total of seven altitudinal sites (Fig. 1–8; Table 1). At each altitudinal site, a 250-m north-to-south transect with 13 plots of 1 m^2 (1 m × 1 m) placed 20 m apart was established. In each plot, all regenerating woody plants (including seedlings, shrubs, and subshrubs, but excluding grasses and lianas) with a diameter at ground height (DGH) of ≤ 1 cm were inventoried, measured with a digital caliper, and labeled with a numbered aluminum plate that was affixed with nylon thread. Plants sampled in this category ($DGH \leq 1$) were considered juveniles or regenerating woody individuals (regeneration stratum). Even though they are non-woody, species that form rosettes were also included in the sampling because their young individuals are characteristic of the regeneration stratum and are an important component of this plant community (pers. obs.).

Species were identified through consultations with experts and/or the botanical literature. Biological material from all species was sampled, treated according to conventional herborization techniques, and stored at Montes Claros Herbarium (MCMG), located at the Universidade Estadual de Montes Claros (UNIMONTES), as part of a reference collection.

Soil samples were collected at the same 13 plots of each 250-m transect for evaluation of the effect of soil variables on species composition. We collected composite soil samples within the 100-m^2 plots in which adult woody plants were sampled (see Mota 2012 for details), where the 1 m × 1 m plots of regenerating woody plants were located. Following the protocol of EMBRAPA (1999), physical and chemical analyses of each composite sample were performed at the Laboratory for Soil Analysis at the Institute of Agricultural Sciences (Universidade Federal de Minas Gerais). The following soil variables were measured: water pH (pH), potassium (K), phosphorus (P-Mehlic), remaining phosphorus (P-rem), calcium (Ca), magnesium (Mg), aluminum (Al), hydrogen and aluminum (H + Al), sum of bases (SB), base saturation (V), effective cation exchange capacity (t), aluminum saturation (m), cation exchange capacity at pH 7.0 (T), organic matter (OM), and proportions of coarse sand (CS), fine sand (FS), silt, and clay.

Data analyses

The efficiency of sampling was evaluated from rarefaction curves constructed for each site using EstimateS software (Colwell 2013). Traditional quantitative parameters (Mueller-Dombois and Ellenberg 1974), including density, frequency, absolute and relative dominance, and importance value (IV), were calculated for each species at each altitude using the software FITOPAC 2.1 (Shepherd 2010). The alpha Shannon diversity index (H') was used to estimate the diversity within each altitude (Krebs 1989). A pairwise Hutcheson's t test with a significance level of 5 % was used to compare the variation in diversity between altitudes (Zar 1996). The seven sampled altitudes were coupled for comparisons (21 combinations) and Bonferroni correction was used to correct for multiple comparisons.

Variation in richness, abundance, basal area, and Shannon diversity index with respect to altitude was assessed using simple linear regression (Zar 1996). In this model, we used seven samples, one for each altitude.

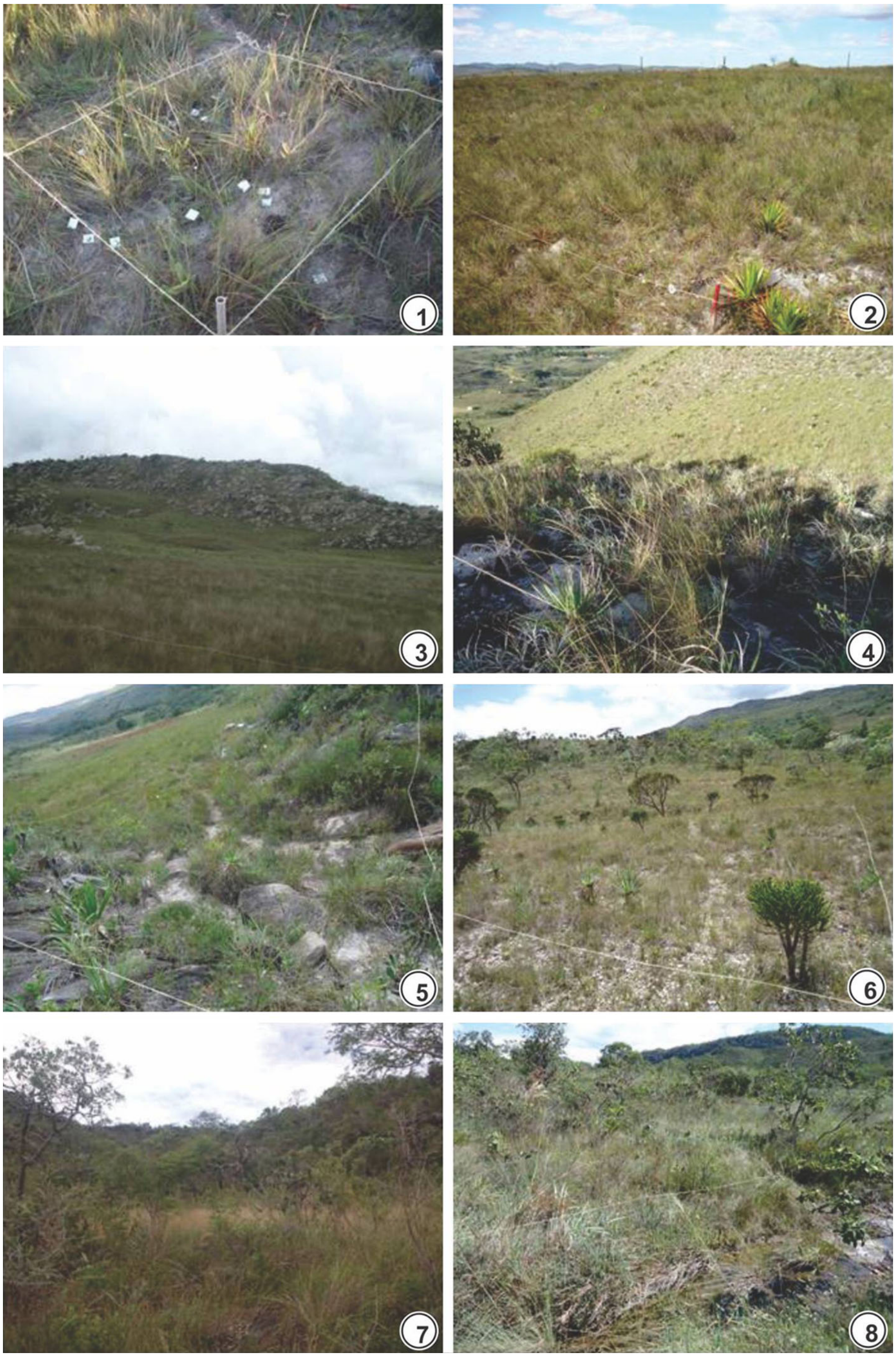

Fig. 1–8 Regenerating woody component of a rupestrian grassland complex sampled in 1-m^2 (1 m × 1 m) plots (**1**) in Serra do Cipó (Minas Gerais, southeastern Brazil) at different altitudes (2. 1400 m; 3. 1300 m; 4. 1200 m; 5. 1100 m; 6. 1000 m; 7. 900 m; 8. 800 m), between 800 and 1400 m. Photographers: Graciene da Silva Mota and Nayara Mesquita Mota

Variation in average richness, Shannon index, abundance, basal area, relative density, and absolute dominance was evaluated using multivariate analysis of variance with 1000 permutations (PERMANOVA) and a post hoc test with 5 % significance level and sequential Bonferroni correction using the software PAST 3.01 (Hammer 2013). For this purpose, a block design with the same number of plots and altitudes as the sampled treatments was established, in which we used the thirteen samples of each altitude.

To investigate variation in species composition and structure across the altitudinal gradient without direct interference from environmental and spatial variables, we applied NMDS (nonmetric multidimensional scaling; McCune and Grace 2002) coupled with the Sørensen coefficient as the similarity measure using the program PC-ORD 6.0 (McCune and Mefford 2011). The similarity of the floristic composition of the woody regeneration stratum among altitudes was determined using ANOVA (analysis

Table 1 Study area location in Serra do Cipó (Minas Gerais, Brazil) and characteristics of the vegetation at the sampling altitudes

Areas	Location (latitude and longitude)	Altitude (m)	Altitude description
Alto Palácio (AP)	19°16′59.3″S and 43°32′08.9″W	1420	Sandy bogs (seven plots) and peat bogs (six plots)
Quadrante 16 (Q16)	19°17′49.6″S and 43°35′28.2″W	1303	Peat bogs (seven plots), quartz gravel field (three plots), and prominent rocky outcrop (two plots)
Pedra do Elefante (PE)	19°17′43.0″S and 43°33′17.4″W	1255	Prominent steep rocky outcrop (seven plots), peat bogs (five plots), and quartz gravel field (one plot)
Cedro (CE)	19°13′56.5″S and 43°34′34.8″W	1101	Prominent rocky outcrop (nine plots), peat bogs (two plots), and sandy bogs (two plots)
Serra Morena (SM)	19°15′50.6″S and 43°35′10.3″W	1001	Ecotone site of "cerrado" and rocky outcrop [rupestrian "cerrado" according to Ribeiro and Walter (2008)], quartz gravel fields (five plots), and peat bogs (two plots)
Usina (US)	19°16′17.8″S and 43°36′18.1″W	977	Ecotone site of "cerrado" and rocky outcrop [rupestrian "cerrado" according to Ribeiro and Walter (2008)] (two plots), prominent rocky outcrop (seven plots), quartz gravel fields (two plots), and peat bog (one plot)
Rio Cipó (RC)	19°21′36.2″S and 43°36′25.2″W	824	Ecotone site of "cerrado" and rocky outcrop [rupestrian "cerrado" according to Ribeiro and Walter (2008)] (ten plots) and quartz gravel fields (three plots)

of variance) in which the response variable was the first axis of the NMDS. With respect to the SAC (spatial autocorrelation), we added spatial eigenvectors (filters) as additional predictors (Diniz Filho and Bini 2005) using the 'spacemakeR' package of R (Dray 2013). We progressively selected the MEMs (Moran's eigenvector maps) according to the method of Blanchet et al. (2008) using the 'packfor' package in R (Dray et al. 2013), and partitioning variance based on vegetation type using the 'varpart' function of the 'vegan' package (Oksanen et al. 2015) following Eisenlohr's (2014) script. We performed a Tukey's HSD test (Smith 1971) to determine the differences between pairs that were separated on this axis using the above MEMs as covariables. We confirmed the assumptions of the models following Eisenlohr (2013) and Eisenlohr (2014). To test normality of residuals we used Shapiro–Wilk test.

We constructed multiple linear models in order to determine the relationship between altitude, soil variables, and species composition. Three matrices were constructed that included the seven study areas. The first matrix contained the response variables (species composition), the second matrix the environmental variables (altitude and soil components), and the third matrix contained coordinate data. Prior to constructing models, we removed collinearities by performing a principal components analysis (PCA) to detect any redundant variables. For each set of redundant variables, we kept the variables that were most strongly correlated with the axis. We then performed a forward selection of environmental and spatial (MEMs) variables. To construct a linear model, we obtained the standardized coefficients for each selected variable. Finally, we partitioned the variance by separating the environmental effect from that exerted by space and the shared fraction between them, and tested each fraction with permutation-based ANOVA (Peres Neto et al. 2006), following the script of Eisenlohr (2014). We used the 'vegan,' 'spacemakeR,' and 'packfor' packages of R (Oksanen et al. 2015; Dray 2013; Dray et al. 2013).

A canonical redundancy analysis (RDA) was performed to confirm correlations between vegetation and soil variables (ter Braak 1987) using the software PC-ORD 6.0 (McCune and Mefford 2011). The primary matrix was composed of species abundance data for each site, while the secondary matrix included the soil variables with the variables selected by the PCA. To perform RDA, the environmental matrix should not contain correlated variables and must have a strong relationship with the response patterns of the variable (Peck 2010). We considered variables that represent a cutoff value >0.3 as significant.

Results

Floristic composition and structure of regenerating woody vegetation

Altogether, 809 individuals of 127 species belonging to 26 families and 13 unidentified morphospecies were recorded (Table 2). The family Fabaceae was the most represented (149 individuals), followed by Eriocaulaceae (102), Asteraceae (98), Melastomataceae (89), Lythraceae (61),

Table 2 List of families and species sampled in 91 1-m^2 plots in the Serra do Cipó (Minas Gerais, Brazil) altitudinal gradient with the respective importance value (IV) in each occurrence site and in the entire sampling area

Species	1400	1300	1200	1100	1000	900	800	Total
Annonaceae	–	–	–	–	–	–	7.97	1.75
Annona cornifolia A.St.-Hil.	–	–	–	–	–	–	7.47	1.41
Apocynaceae	–	–	–	–	–	–	3.76	0.98
Aspidosperma tomentosum Mart.	–	–	–	–	–	–	3.26	0.65
Aquifoliaceae	–	–	–	16.52	–	–	6.85	3.32
Ilex theezans Mart. ex Reissek	–	–	–	16.18	–	–	–	1.15
Ilex sp.	–	–	–		–	–	5.84	1.17
Arecaceae	–	–	–	–	–	6.10	–	1.19
Syagrus glaucescens Becc.	–	–	–	–	–	5.93	–	0.86
Asteraceae	–	4.51	55.72	73.79	67.98	45.59	29.18	34.32
Aspilia jolyana G. M. Barroso.	–	–	–	–	–	–	–	7.18
Baccharis axillaris Mart. ex Baker.	–	–	–	–	–	–	2.25	0.47
Baccharis dentata (Vell.) G. Barroso.	–	–	17.98	5.26	19.26	–	–	5.89
Baccharis elaeagnoides Steud. ex Baker	–	–	2.98	–	6.92	–	–	1.65
Baccharis sp.	–	–	–	–	10.27	–	–	1.58
Dasyphyllum reticulatum (DC.). Cabrera	–	–	–	–	–	6.02	–	1.07
Eremanthus incanus Less.	–	–	–	–	10.52		4.51	2.41
Eremanthus sphaerocephalus Baker.	–	–	2.84	–	–	3.54	–	1.11
Eremanthus sp.	–	–	–	–	2.49	–	–	0.46
Grazielia intermedia (DC.) R .M. King and H. Rob.	–	–	–	–	–	14.42	–	2.01
Gochnatia polymorpha (Less.) Cabrera	–	4.25	–	–	–	–	–	0.49
Lepidaploa sp. 1	–	–	–	–	–	2.81	–	0.52
Lessingianthus linearifolius (Less.) H.Rob.	–	–	–	37.75	–			2.90
Lychnophora pinaster Mart.	–	–	–	13.26	–	–	–	0.99
Lychnophora sp. 1	–	–	–	12.75	12.06	8.00	–	4.10
Lychnophora sp. 2	–	–	–	–	–	2.22	14.94	3.23
Mikania sp.	–	–	–	5.92	–	–	–	0.52
Pseudobrickellia brasiliensis (Spreng.) R. M. King and H. Rob.	–	–	–	–	–	4.80	–	0.70
Symphyopappus reticulatus (DC.) Baker	–	–	–	–	8.11	–	–	1.15
Vernonanthura falcifolia Mart.	–	–	–		4.09	–	–	0.64
sp. 1	–	–	–	–	–	5.20	–	0.90
Bignoniaceae	–	–	–	–	–	–	3.19	0.88
Handroanthus ochraceus (Cham.) Mattos	–	–	–	–	–	–	2.69	0.55
Bromeliaceae	–	–	4.99	–	–	–	–	1.18
Dyckia sp.	–	–	4.34	–	–	–	–	0.85
Celastraceae	–	–	3.72	–	6.73	–	–	2.05
Salacia crassifolia (Mart. exSchult.) G. Don	–	–	–	–	6.10	–	–	0.86
Salacia elliptica (Mart. ex Roem. Schult.) G. Don.	–	–	3.07	–	–	–	–	0.53
Clusiaceae	–	–	–	11.70	–	21.17	–	6.35
Kielmeyera lathrophyton Saddi	–	–	–	5.09	–	11.29	–	2.71
Kielmeyera rubriflora Cambess.	–	–	–	5.92	–	10.51	–	2.34
Dilleniaceae	–	–	–	–	–	19.15	–	3.54
Davilla rugosa Poir.	–	–	–	–	–	18.65	–	2.54
Eriocaulaceae	233.60	78.79	85.99	33.93	6.76	–	–	51.52
Actinocephalus polyanthus (Bong.) Sano.	106.51	–	–	–	–	–	–	7.56
Leiothrix crassifolia (Bong.) Ruhland	–	77.26	2.82	–	–	–	–	13.98
Leiothrix curvifolia (Bong.) Ruhland	–	–	–	–	6.13	–	–	0.86

Table 2 continued

Species	1400	1300	1200	1100	1000	900	800	Total
Paepalanthus planifolius Koern.	12.27	–	–	–	–	–	–	0.86
Paepalanthus sp. 1	–	–	–	26.51	–	–	–	8.41
Paepalanthus sp. 2	95.83	–	–	6.73	–	–	–	1.68
Paepalanthus sp. 3	16.98	–	81.21	–	–	–	–	18.06
sp. 1	10.42	–	–	–	–	–	–	0.84
sp. 2	–	–	4.30	–	–	–	–	0.84
Erythroxylaceae	–	–	–	21.14	35.13	–	–	7.54
Erytroxylum suberosum St. Hil.	–	–	–	20.10	32.61	–	–	5.87
Euphorbiaceae	–	–	–	5.89	–	–	2.75	1.62
Maprounea guianensis Aubl.	–	–	–	–	–	–	2.25	0.47
Sapium glandulosum (L.) Morong	–	–	–	5.55	–	–		0.50
Fabaceae	–	85.71	23.12	10.88	17.35	51.02	72.66	39.17
Acosmium dasycarpum (Vog) Yakovlev.	–	–	–	–	–	–	43.41	8.27
Andira vermifuga Mart. ex Benth.	–	–	–	–	–	–	8.25	1.55
Calliandra dysantha Benth.	–	80.45	–	–	–	–	–	13.92
Calliandra sp. 1	–	–	–	–	–	–	2.26	0.47
Calliandra sp. 2	–	–	–	–		–	4.09	0.80
Calliandra sp. 3	–	–	–	–	–	–	2.62	0.53
Chamaecrista sp. 1	–	10.88	–	–	–	–	–	1.44
Chamaecrista sp. 2	–	–	–	10.53	–	–	–	0.84
Chamaecrista sp. 3	–	–	2.82	–	–	–	–	0.47
Chamaecrista sp. 4	–	–	–	–	8.44	–	–	1.45
Chamaecrista sp. 5	–	–	–	–	–	–	11.73	2.41
Cousete sp.	–	–	5.42	–	–	–	–	0.99
Cratylia sp.	–	–	13.00	–	–	–	2.42	2.87
Dalbergia miscolobium Benth.	–	–	5.66	–	2.95	16.77	–	4.27
Mimosa sp. 1	–	–	–	–	–	30.70	–	4.19
Mimosa sp. 2	–	–	–	–	–	3.34	–	0.57
Stryphnodendron adstringens (Mart.) Coville	–	–	–	–	3.44	–	–	0.57
Stylosanthus guianensis (Aubl.) Sw.	–	–	–	–		–	3.14	0.62
Lamiaceae	–	–	–	–	–	5.55	–	1.71
Hyptis complicata A. St.-Hil. ex Benth.	–	–	–	–	–	2.98	–	0.59
Hyptis sp.	–	–	–	–	–	2.22	–	0.46
Lythraceae	–	29.06	5.49	12.01	4.09	45.03	–	15.43
Cuphea sp.	–	–	–	–	–	10.04	–	2.01
Diplusodon orbicularis Koehne	–	28.30	4.84	11.67	3.46	36.59	–	11.10
Malpighiaceae	–	–	–	11.60	–	4.78	54.42	13.39
Byrsonima crassifolia (L.) Rich.	–	–	–	–	–	–	18.04	3.38
Byrsonima intermedia A. Juss.,	–	–	–	–	–	4.44	2.29	1.06
Byrsonima pachyphylla A. Juss.	–	–	–	11.26	–	–	2.80	1.42
Heteropterys byrsonimifolia A. Juss.	–	–	–	–	–	–	29.31	5.53
Malvaceae	–	–	–	–	–	–	5.02	1.21
Blepharocalyx salicifolius (H.B.K.) Berg.	–	–	–	–	–	–	4.52	0.87
Melastomataceae	26.22	9.07	55.58	12.47	33.96	18.58	24.50	23.43
Lavoisiera subulata Triana	–	–	25.75	–	2.50	–	–	5.31
Lavoisiera macrocarpa Naudin.	7.38	–	15.42	–	–	–	–	3.23
Lavoisiera sp.	–	–	2.90	–	–	–	–	0.49
Leandra sp.	–	–	–	–	–	3.28	–	0.62

Table 2 continued

Species	1400	1300	1200	1100	1000	900	800	Total
Marcetia taxifolia (A. St.-Hil.) DC.	–	–	4.50	–	11.29	–	–	2.27
Miconia albicans (Sw.) Triana	–	–	–	–	–	–	2.39	0.49
Miconia coralina Spring	–	–	–	11.78	6.07	–	–	2.10
Miconia ferruginata DC.	–	–	–	–	7.89	3.87	–	2.00
Miconia sp. 1	–	–	–	–	–	–	5.07	1.49
Miconia sp. 2	–	–	–	–	2.81	–	3.36	1.16
Microlicia sp.	–	–	–	–	–	2.56	–	0.49
Trembleya laniflora Cogn.	–	–	–	–	–	2.45	–	0.48
Tibouchina sp.	–	–	–	–	3.89	–	3.21	0.91
sp. 1	–	4.17	2.99	–	–	–	–	1.50
sp. 2	4.39	–	–	–	–	–	–	0.52
sp. 3	16.03	–	3.07	–	–	–	–	0.53
sp. 4	–	–	–	–	2.50	7.21	–	1.38
sp. 5	–	–	–	–	–	–	2.95	0.59
sp. 6	–	–	–	–	–	–	5.75	1.10
sp. 7	–	–	–	–	–	–	5.92	1.19
Myrtaceae	8.81	–	4.74	19.99	24.76	41.56	33.64	18.56
Myrcia guianensis (Aubl.) Kuntze	–	–	–	17.15	10.56	40.21	6.95	8.94
Myrsine guianensis(Aubl.) Kuntze.	–	–	4.09	–	5.88	–	22.02	6.91
Psidium pohlianum O. Berg	–	–	–	–	8.55	–	–	1.42
sp. 1	7.40	–	–	–	–	–	–	0.47
sp. 2	–	–	–	5.03	–	–	–	0.47
Nyctaginaceae	–	–	–	–	16.69	19.92	44.30	16.53
Eugenia aurata O.Berg	–	–	–	–	–	–	3.19	0.64
Guapira venosa (Choisy) Lundell	–	–	–	–	10.53	9.30	16.28	6.38
Guapira noxia (Netto) Lundell	–	–	–	–	3.64	–	–	0.59
Neea theifera Oerst.	–	–	–	–	–	9.77	27.08	6.94
Ochnaceae	–	21.79	4.21	–	3.23	6.93	–	6.41
Ouratea semisserrata (Mart. and Nees) Engl.	–	21.28	3.56	–	2.60	6.59	–	5.07
Rubiaceae	–	–	3.60	17.60	47.86	2.81	4.08	11.96
Cordiera sessilis (Vell.)Kuntze	–	–	–	–	30.32	–	–	4.32
Cordiera sp.	–	–	–	–	12.76	–	–	2.26
Palicourea rigida Kunth.	–	–	–	17.25	–	2.64	3.58	2.45
Sabicea brasiliensis Wernham	–	–	–	–	–	–	7.51	1.42
sp. 1	–	–	–	–	–	–	–	0.50
sp. 2	–	–	2.95	–	2.57	–	–	0.47
sp. 3	–	–	–	–	4.14	–	–	0.64
Velloziaceae	–	53.23	41.63	52.48	25.94	11.82	4.01	25.46
Barbacenia sp. 1	–	–	–	–	–	–	–	0.73
Barbacenia sp. 2	–	5.34	–	14.88	–	11.65	–	2.61
Vellozia albiflora Pohl.	–	–	–	–	20.46	–	–	2.77
Vellozia epidendroides Mart. ex Schult. and Schult.	–	32.16	29.61	–	–	–	–	11.67
Vellozia nivea L. B. Smith. and Ayensu.	–	–	5.38	–	–	–	–	1.11
Vellozia sp. 1	–	14.45	–	–	–	–	–	2.61
Vellozia sp. 2	–	–	–	–	–	–	3.50	0.69
Vellozia sp. 3	–	–	2.84	–	–	–	–	0.47
sp. 1	–	–	–	27.57	–	–	–	2.12
sp. 2	–	–	–	11.87	3.58	–	–	1.54

Table 2 continued

Species	1400	1300	1200	1100	1000	900	800	Total
Verbenaceae	–	–	5.57	–	–	–	–	1.29
Lippia sp.	–	–	4.92	–	–	–	–	0.95
Vochysiaceae	–	–	5.63	–	–	–	–	1.30
Vochysia rufa Mart.	–	–	4.98	–	–	–	–	0.97
Unidentified	–	–	–	–	–	–	–	7.91
sp. 1	27.17	–	–	–	–	–	–	1.71
sp. 2	–	9.60	–	–	–	–	–	1.19
sp. 3	–	7.47	–	–	–	–	–	1.20
sp. 4	–	–	3.33	–	–	–	–	0.60
sp. 5	–	–	–	–	2.96	–	3.17	1.14
sp. 6	–	–	–	–	7.62	–	–	1.02

The absence of IV values indicates the absence of the species on the respective site

and Velloziaceae (57), altogether accounting for nearly 70 % of all sampled individuals. Eriocaulaceae had the highest IV, followed by Velloziaceae and Melastomataceae. The most diverse genera were *Vellozia* (six species) and *Chamaecrista* and *Miconia* (five species each). The species with the highest IV were *Paepalanthus* sp. 3, *Leiothrix crassifolia* (Bong.) Ruhland, *Calliandra dysantha* Benth., *Vellozia epidendroides* Mart. ex Schult. & Schult., and *Diplusodom orbicularis* Koehne. The species with the highest IV at each site were *Acosmium dasycarpum* (Vog) Yakovlev. (800 m), *Myrcia guianensis* (Aubl.) Kuntze (900 m), *Erytroxylum suberosum* St. Hil (1000 m), *Lessingianthus linearifolius* (Less.) H.Rob. (1100 m), *Paepalanthus* sp. 3 (1200 m), *Calliandra dysantha* Benth. (1300 m), and *Actinocephalus polyanthus* (Bong.) Sano. (1400 m).

The rarefaction curve for the total area exhibited a tendency toward stabilization (Fig. 9). At higher altitudes (800 and 900 m), the rarefaction curves did not stabilize, while at lower altitudes there were fewer species. A clear pattern of variation in species richness with altitude is apparent from the rarefaction curves.

Of the sampled species, 35 were found at two or more altitudes, while no species occurred at all altitudes (Table 2). The most common species was the restricted native and threatened species *Diplusodom orbicularis* Koehne (Medina and Fernandes 2007), which was found at all except at the highest (1400 m) and lowest (800 m) altitudes. More than 92 (70 %) of the species were found only at one altitude: 24 at 800 m, 15 at 900 m, 16 at 1000 m, 8 at 1100 m, 16 at 1200 m, 8 at 1300 m, and 5 at 1400 m. The altitudes sharing the greatest number of species were 800 and 1000 m with four species, whereas the altitude pairs of 1000 and 1200, 1000 and 1100, 900 and 1100, and 800 and 900 each shared three species, and 900 and 1000 m shared two. The highest species richness (37 species) and abundance (154 individuals) of regenerating woody species were observed at the altitudes of 800 m and 1200 m, respectively (Table 3). The highest species density occurred at 1300 m, while the highest dominance was observed at 1200 m. According to linear regression analysis, abundance and basal area did not vary across altitudes ($P = 0.357$ and $P = 0.845$, respectively), but species richness decreased with altitude ($n = 7$, $r^2 = 0.816$, $P < 0.01$, $y = -0.0821x + 135.79$, Fig. 10). More than 80 % of the variation in species richness was explained by altitude.

Species richness also varied significantly among altitudes (PERMANOVA: $df = 90$; $F = 2.99$; $P < 0.001$, Table 3). Plant species richness was significantly higher at 800 and 900 m, and lowest at 1400, 1300, and 1100 m (Table 3). Abundance ($df = 90$; $F = 2.28$; $P < 0.001$, Table 3) and absolute dominance ($df = 90$; $F = 3.21$; $P < 0.001$, Table 3) varied among altitudes. The 800- and 1200-m sites had the highest dominance values, while the sites at 1100, 1300, and 1400 m had the lowest.

The diversity (H') for the entire sampled area (0.091 ha) was 4.14 (Table 3) and decreased with increasing altitude ($n = 7$, $r^2 = 0.821$, $P < 0.05$; $y = -0.236x + 3.61$; Fig. 11). According to PERMANOVA, Shannon index varied significantly among sites ($df = 90$; $F = 4.25$; $P < 0.001$). Sites can be grouped into three classes according to the significance of the Hutcheson's t test followed by Bonferroni correction: high altitude (1300- and 1400-m sites), intermediate altitude (1100-m and 1200-m sites), and low altitude (800- to 1100-m sites) (Table 3). The 1100-m site was placed into two groups because its diversity value did not differ from that of the sites at 800, 900, 1000, and 1200 m, while H' at the 1200-m site was significantly different from the H' at all other sites except 1100-m site (Table 3).

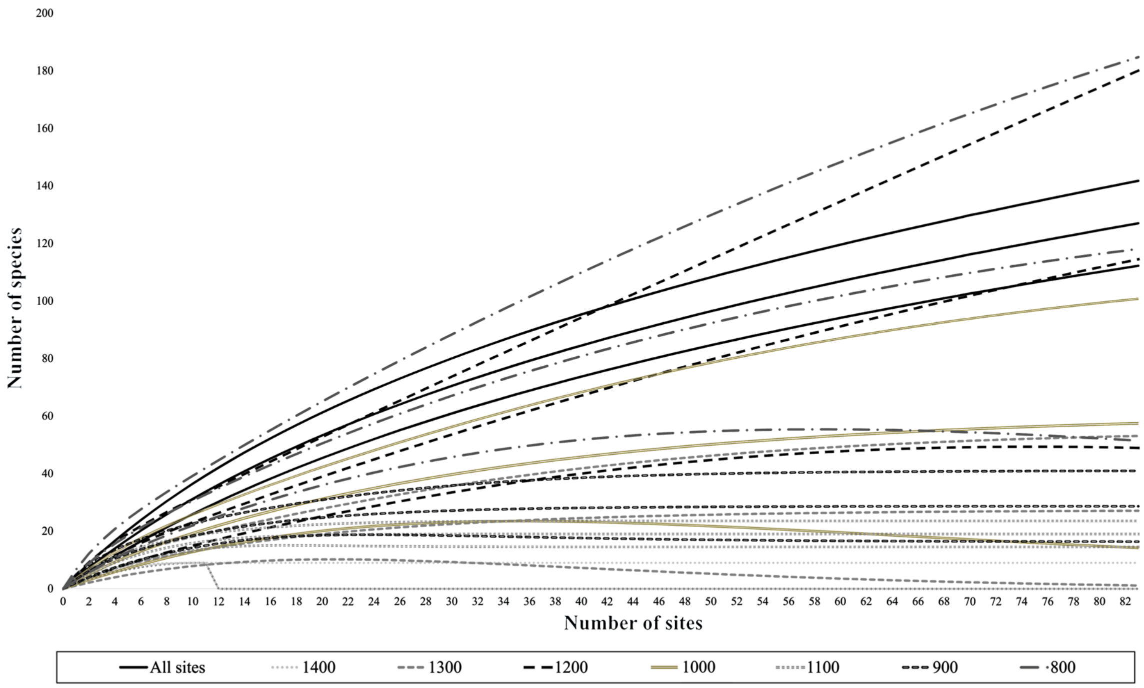

Fig. 9 Rarefaction curves of the regenerating woody component of a rupestrian grassland complex (Serra do Cipó, southeastern Brazil) of each altitude (1400, 1300, 1200, 1100, 1000, 900 and 800 m) and all sites

Floristic similarity

The NMDS ordination (Fig. 12) indicated a significant correlation between altitude and species composition. The ordination axis explained 87.7 % of the variation, with 52.8 % explained by the first axis and 35.0 % by the second (35 %). The first axis separated the sites at the lower altitudes (800 and 900 m) from those at the higher altitudes (1300 and 1400). Plots of the sites at 1200, 1100, and 1000 m were dispersed. It was not possible to identify variation in altitude with the second axis; however, it was able to separate the plots at 1100 m. The first axis revealed a significant correlation with altitude composition ($df = 81$, $F = 103.4$, $P < 0.0001$), after considering the effects of spatial autocorrelation. Tukey's HSD test showed that the highest three sites were significantly different from the lowest four sites.

Soil attributes

The collected soils were acidic, and especially so at higher altitudes (1100 through 1400 m) which exhibited lower average pH values (pH < 5). The altitude of 1400 m had the highest average levels of Al, Mg, H + Al, Ca, effective cation exchange capacity, and cation exchange capacity. The highest average levels of organic matter were found at

Table 3 Shannon diversity index (*H′*), number of individuals (*n*), number of species (*S*), number of families (*F*), absolute density (AD ind ha^{-1}), absolute frequency (AF), basal area (BA cm^2 ha^{-1}), and absolute dominance (ADo cm^2 ha^{-1}) values of the regeneration woody community of rupestrian field complex, sampled in different altitudes at Serra do Cipó (Minas Gerais, Brazil)

Altitude (m)	*H′*	*N*	*S*	*F*	AD	AF	BA	ADo
1400	1.56a	49a	09a	04	49000a	190a	0.000950a	0.95ab
1300	1.80a	146ab	13a	08	136363a	263a	0.000237a	0.21b
1200	2.58b	154ab	29ab	13	119230a	369a	0.002647a	2.03a
1100	2.80bcd	58a	22a	13	48333a	258a	0.000651a	0.54ab
1000	3.12d	127ab	36ab	13	114545a	536a	0.001159a	1.05a
900	2.97cd	136b	31b	14	104615a	523a	0.000969a	0.75ab
800	3.06cd	145ab	37b	15	111538a	500a	0.001927a	1.48a
Total	4.14	809	127	26	623.076	2.276	0.011000	8.11

Numbers following the same letters represent significance values >0.05

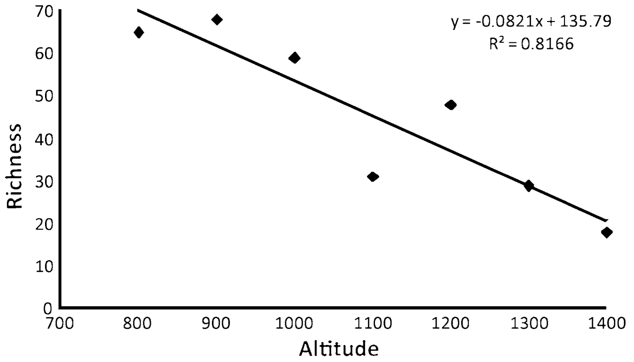

Fig. 10 Species richness of the regenerating woody component of a rupestrian grassland complex (Serra do Cipó, southeastern Brazil) sampled at seven altitudes (800–1400 m)

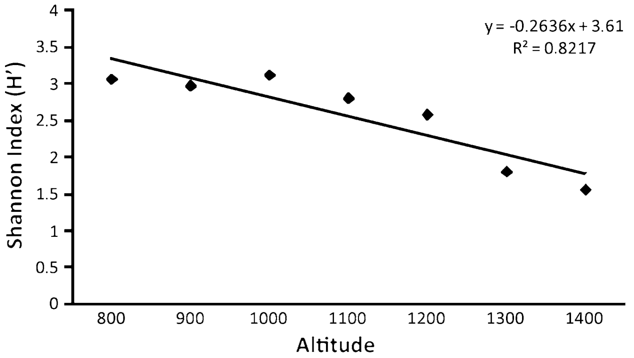

Fig. 11 Shannon diversity index for the regenerating woody component of a rupestrian grassland complex (Serra do Cipó, southeastern Brazil) sampled at seven altitudes within the rocky field complex at Serra do Cipó, MG

the altitudes of 1200 and 1400 m. On the other hand, the altitudes of 800 and 1200 m had higher average levels of K, whereas the altitudes of 1100 and 1300 m had the lowest. The greatest average proportion of fine sand was found in the soils at 1100 and 1400 m, and the highest proportion of coarse sand was at 800, 1100, and 1300 m, silt at 800 and 900 m, and clay at 800 and 1100 m.

Relationship between environmental data and vegetation

For the correlation between community data and environmental variables (soils and altitude), altitude, V, Al, P-rem, and silt were significant and could be used to predict the variation in community data ($F = 1.266$, $P < 0.002$), as well as the spatial predictors ($F = 1.617$, $P < 0.001$). The variation explained by the spatial factors (12 %) was highest among fractions [*a*], [*b*], and [*c*] in the variance partitioning. The environment explained 2 %, and the spatially structured environment explained 4 % of the variation in species distribution. The residual fraction of variation was 82.4 %. In the RDA graph (Fig. 13), the first axis was positively correlated with the proportion of silt levels (0.67), base saturation (V; 0.52), and K (0.47) and negatively correlated with fine sand (FS; −0.61) (Fig. 13).

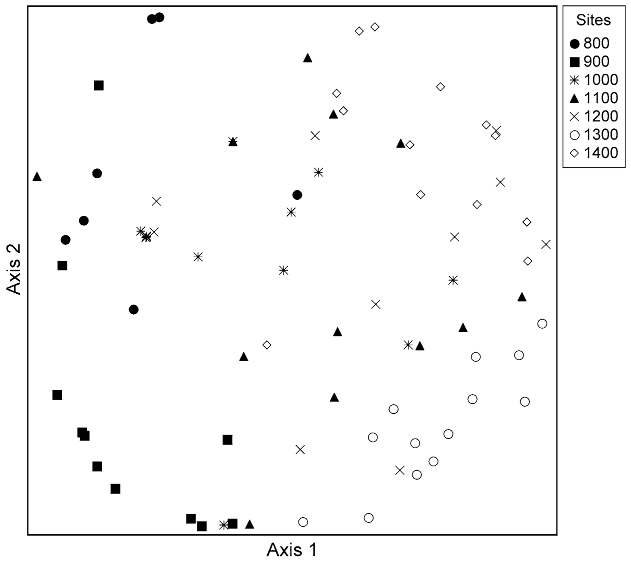

Fig. 12 NMDS ordination of regenerating woody vegetation based on the Sørensen coefficient as the measure of similarity among altitudes in a rupestrian grassland complex (Serra do Cipó, southeastern Brazil)

Discussion

Even in tropical mountains and within a relatively short altitudinal gradient, altitude causes changes in plant species composition and diversity. Such variation is also related to soil components at different altitudes. This study highlights the high species diversity and rarity of the vegetation of the rupestrian grassland complex at Serra do Cipó and the influence of environmental variation on plant diversity.

The families (Asteraceae, Eriocaulaceae, Lythraceae, Fabaceae, and Melastomataceae) and genera (*Lychnophora*, *Eremanthus*, *Paepalanthus*, *Miconia*, and *Vellozia*) of the regenerating strata found in this study have been considered characteristic of the rupestrian grassland (Romero 2002). Not surprisingly, elements of other vegetation types, especially "cerrado" *s. s.*, are common in the rupestrian grassland ecosystem (Rapini et al. 2008), including some of the most abundant species detected in this study: *Guapira venosa* Lundell (typical of semideciduous, deciduous, and gallery forests), *Erytroxylum suberosum* (*cerrado s.s.*), and *Acosmium dasycarpum* (Vog) Yakovlev. (semideciduous, deciduous, gallery forests and "cerrado" *s.s.*) (Oliveira Filho 2005). Pinto et al. (2009) found that the woody vegetation in a rupestrian

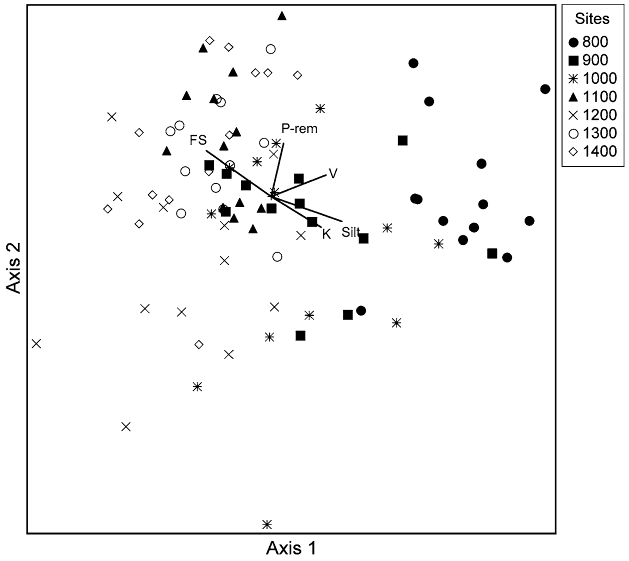

Fig. 13 Ordination diagram of the canonical redundancy analysis (RDA) of significant soil variables and sampling altitudes according to the distribution of the 127 species sampled in 90 1-m^2 plots at different altitudes of a rupestrian grassland complex of Serra do Cipó, and the correlation between the following variables: *FS* fine sand proportion, *P-rem* remaining phosphorus, *V* base saturation, *Silt* silt proportion, *K* potassium level

"cerrado" was composed mostly of species typical of *cerrado s.s.* vegetation, with smaller contributions from species characteristic of "cerrado" forest formations and endemic rupestrian grassland species. However, species of Eriocaulaceae had the highest IV, as these species have a large basal area and are common in the study area, especially at higher altitudes. Species of Eriocaulaceae are characterized by spiral leaves in rosettes or along the stems (Miranda and Giulietti 2001). They are extremely common in rupestrian grasslands (Costa et al. 2008) and contributed a significant basal area in the present study. In this study, floristic composition differed markedly among altitudes, as has been shown in altitudinal zones in the Atlantic Forest (Moreno et al. 2003). Vegetation patches vary in structure at different altitudes; as altitude increases both plant size and species richness are reduced (e.g., Whittaker 1956; 1960; Hamilton 1975; Gentry 1988; Kitayama 1992; Rocha and Amorim 2012). Structural aspects varied significantly between altitudes; however, again no altitudinal pattern was observed and, in other words, basal area, density, and dominance had no clear relationship with altitude. Species and habitat characteristics at each altitude may be confounding dominance values. The altitudes with higher dominance were 800 and 1200 m, and vegetation structure at 800 m had woody plant species with greater height and basal area. At this altitude, higher temperatures, lower wind velocity, and deeper soil (authors' pers. inf.) ensure better conditions for colonization by woody species and seedling development. In the same manner, this elevation presents a dominance of "cerrado" physiognomy (Table 1). At an altitude of 1200 m, the influence of *Paepalanthus* sp. 3 was determinant for basal area and, consequently, for the dominance values. In contrast, at 1100, 1300, and 1400 m dominance values were low. These differences may have been the result of fewer individuals being sampled at 1100 and 1400 m altitudes, or by the presence of individuals with lower basal area at the 1300-m site (high abundance of *Caliandra dysantha*). Medina and Fernandes (2007) argued that low abundance of emergent seedlings at this altitude could be related to high seed dormancy. Only detailed studies on seed dormancy in the rupestrian grassland can address this hypothesis.

The diversity found in the present study for the total sampling area ($H' = 4.14$) may be considered high, even for rupestrian grasslands (Conceição and Giulietti 2002; Conceição et al. 2005, 2007; Conceição and Pirani 2007; Gastauer et al. 2012; Mota 2012). However, it should be recognized that the different altitudes sampled encompass heterogeneous areas with different environmental factors that may contribute to the high diversity observed (Medina and Fernandes 2007; Carvalho et al. 2012). Sampling in the present study incorporated several habitat types commonly found in the rupestrian grasslands of Serra do Cipó (see Carvalho et al. 2012; Table 1). Therefore, these environmental variations likely contributed to the increased diversity of species in the area. The geomorphological features of each particular area, such as elevation, depression, and the general shapes of mountains, may also contribute to high local and regional diversity. In addition, the high species richness of the rupestrian grassland has a strong relationship with different substrates (Conceição and Giulietti 2002), while the relevance of the surrounding vegetation matrix cannot be neglected (e.g., Jacobi et al. 2007).

The highest species richness and diversity were found at lower altitudes, hence providing support for the altitudinal gradient hypothesis (Whittaker 1960; Lomolino 2001). Bhatt and Purohit (2011) also reported a decline of species richness with increasing altitude in a study conducted on a 1600–2200 m altitudinal gradient in the Himalayan region, while Sharma et al. (2009) showed the same trend for temperate forests (see also Huston 1994). On the other hand, highest plant diversity at mid-altitude has also been reported (Wang et al. 2002; Sang 2009; Joly et al. 2012). However, our study focused on a type of vegetation (rupestrian grasslands) that is naturally restricted to high altitudes (above 900 m). In this scenario, the regenerating woody species had a strong negative response to an increase in altitude. The regenerating community at the lower altitude had more species from the "cerrado" *s.s.*, which contribute to the local diversity. The 1000-m site is a good example of an altitudinal transition zone, as it was the most diverse and contained species typical of high altitudes as well as of neighboring vegetation. Therefore, regional peculiarities and the relationship between sampled altitudes and neighboring phytophysiognomies seem to affect regenerating species composition, presumably through dispersion and colonization events.

In another sense, the presence of rocky outcrops in different proportions among the altitudes is another environmental characteristic that may influence variation in species composition and floristic similarity among sites. Some species prevail in areas with shallow soils using the fractures of the rocks for establishment (Conceição and Giulietti 2002; Negreiros et al. 2008). For example, the 1400-m elevation presents a more homogeneous area, with no rocky outcrops, and comprises a rupestrian grassland landscape (Table 1), with the most stressful physical conditions, which limit colonization by woody species resulting in low species diversity. Besides, rupestrian grassland vegetation occurs mostly at altitudes above 1100 m, and in this altitude, regenerating species of Eriocaulaceae and Velloziaceae prevail (Romero 2002). Korner (2007) attributes the high diversity at low altitudes to the effects of regional peculiarities and general altitude phenomena. Thus, in the study region, this pattern is probably a result of climatic trends and altitude, with strong roles played by light, UV radiation, and other factors such as wind velocity. These factors, unmeasured in our models, appear to have a significant contribution since the residual fraction was high in the partitioning of the variance of our study.

Typically, rupestrian grassland soils have low pH, phosphorus, and base saturation values (Vincent and Meguro 2008) and little organic matter; they are generally porous and friable (Reatto et al. 1998) as well as nutrient poor, with yellowish hues, sandy textures, and high levels of exchangeable aluminum (Benites et al. 2003). According to the RDA results, the soil variables distinguished some plots, although there was only slight variation in soil characteristics between altitudes in relation to fertility. For all chemical variables measured, remaining phosphorus, potassium, and base saturation were related to plots, but this relationship was not sufficient to separate the plots according to altitude. Communities that include species that are more demanding with respect to soil nutritional status occur where the potassium availability is higher (Moreno et al. 2008). The plant species of rupestrian grasslands differ in their responses to variation in soil fertility (Negreiros et al. 2009), so that soil nutritional deficiency favors only species adapted to nutritional stress (Grime 2006). According to Grime (2006), certain common features of vegetation types are immediately apparent among sites with severely nutrient-deficient soil, such as rosette species and a high proportion of dicotyledons being of creeping habit. Therefore, availability of nutrients appears to be one of the factors that allow the establishment of tree species (with higher nutritional requirements) at lower altitudes and perhaps in specific locations at higher altitudes that act as islands of resources.

In rock outcrops, physical characteristics of the soil, such as the influence of particle size on soil penetration by roots, water retention capacity and permeability, and low root/shoot ratios (Negreiros et al. 2009; Messias 2011), can determine features of the vegetation and affect plant colonization. The physical characteristics of the soil, specifically fine sand and silt, differed among the study plots. Fine sand showed a strong relationship with the distribution and composition of regenerating species at 1100 and 1400 m, while proportions of silt were higher at lower altitudes (1000, 900, and 800 m), and likely affected species richness. Thus, structural characteristics of soil are generally responsible for the heterogeneity of this habitat because variation in these characteristics affects species composition. This conclusion corroborates the results of Messias (2011), who found a strong relationship between species composition and variables associated with soil particle size, as well as the results of Negreiros et al. (2008) who found that soils differ significantly in texture in the rupestrian grasslands at Serra do Cipó. Carvalho et al. (2012) attributed the high diversity of the rupestrian grasslands of Serra do Cipó to heterogeneity in the physical attributes of soil among habitats.

In turn, it is likely that the proportion of fine sand and silt in the soil influences the similarity between locations, as this factor distinguished some plots. Furthermore, there were significant differences in the soils of some endemic legumes in the rupestrian grasslands of Serra do Cipó with respect to sand, silt, and clay (Negreiros et al. 2008). On the other hand, features of microtopography, such as the presence of rock outcrops, can have a crucial influence on rupestrian grassland flora (Benites et al. 2007), and may explain the low response of the environmental variables in the variance partitioning. The dispersion of the 1200-m plots, for example, may be due to the presence of large, steep outcrops at the site, which may limit the number of taxa (see also Conceição and Giulietti 2002). Thus, the lithology and geomorphology of the sampling area (Messias et al. 2012) and substrate (Conceição and Giulietti 2002) could have an important role in plant distribution in rupestrian grasslands.

Our study highlighted the relevance of altitude, physical soil characteristics, base saturation, potassium, and remaining phosphorus levels on the composition, structure, and richness of regenerating woody species along an altitudinal gradient in Brazil. Studies elsewhere have also shown strong plant response to similar environmental factors (e.g., Odland 2009; Sang 2009; Eisenlohr et al. 2013; Gentili et al. 2013; Graham et al. 2014). Other important contributors to variation in species diversity and composition were immediacy altitudes and habitat microtopography, which may influence the abrupt changes in richness and composition in a given altitudinal gradient. Restricting factors interfere with colonization by establishing limits to plant recruitment and establishment. These factors act as strong environmental filters mainly at higher altitudes where they restrict colonization by woody species and favor stress-tolerant ones (Grime 2006; Graham et al. 2014). It is likely that this has resulted in communities with phylogenetically closely related species at higher altitudes (Machac et al. 2011), such as mostly monocots, many of which are endemic. Additional studies are needed to investigate these possibilities.

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