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Regenerative potential of the soil seed bank along an elevation gradient of rupestrian grassland in southeastern Brazil

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Abstract: The objective of this study was to determine the species richness and abundance of the seed bank and the influence of soil attributes along an elevation gradient (800–1400 m a.s.l.). We examined the floristic similarity among areas and determined the regional diversity along this gradient in Serra do Cipó (Minas Gerais, Brazil). A total of 1975 individuals from 149 species were germinated. Richness and abundance were not linearly related to elevation, and exhibited a threshold at 1200 m. The low degree of similarity among the areas reflects environmental heterogeneity, resulting from a rich mosaic of habitats, distinguished by the substrate configuration, continuity of vegetation, floristic composition, and proportion of exposed rock. The diversity between plots of different areas ($\beta 2$) contributed to regional diversity, and species turnover was the most important factor. The physical variables and base saturation, which had high spatial heterogeneity, may be the most important factors with which to determine species turnover and β diversity. The studied seed bank is strongly influenced by edaphic variables, with a gradient of increasing acidity and proportion of fine sand, and decreasing proportion of clay and organic matter, with elevation. In addition, species richness was influenced by cation exchange capacity, organic matter, and base saturation.

Key words: altitude, beta-diversity, floristic similarity, natural regeneration, edaphic variables.

Résumé : L'objectif de cette étude était de déterminer la richesse et l'abondance en espèces d'une banque de semences et l'influence des attributs du sol le long d'un gradient d'élévation (800-1400 m a.s.l.). Les auteurs ont examiné la similarité floristique entre les régions et déterminé la diversité régionale le long de ce gradient dans la Sierra do Cipó (Minas Gerais, Brésil). Un total de 1975 individus appartenant à 149 espèces a été conduit jusqu'à la germination. La richesse et l'abondance en espèces n'étaient pas reliées de façon linéaire à l'élévation et elles atteignaient un seuil à 1200 m. Le faible degré de similarité entre les régions reflète l'hétérogénéité environnementale résultant d'une riche mosaïque d'habitats qui se distinguent par la configuration du substrat, la continuité de la végétation, la composition floristique et la proportion de roche exposée. La diversité entre les lots de différentes régions (β 2) contribuait à la diversité régionale, et le renouvellement des espèces en constituait le facteur le plus important. Les variables physiques et la saturation basique, qui présentaient une hétérogénéité spatiale élevée, pourraient être les facteurs les plus importants qui déterminent le renouvellement des espèces et la diversité β . La banque de semis étudiée est fortement influencée par les variables édaphiques, le gradient d'acidité et la proportion de sable fin étant croissants et la proportion d'argile et la matière organique, décroissantes, en fonction de l'élévation. Par ailleurs, la richesse en espèces était influencée par la capacité d'échange cationique, la matière organique et l'argile, et l'abondance, par la capacité d'échange cationique, H + Al, la matière organique et la saturation basique. [Traduit par la Rédaction]

Mots-clés : altitude, diversité bêta, similarité floristique, régénération naturelle, variables édaphiques.

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Introduction

Mountains possess great biodiversity and high levels of endemism, and are considered unique environments for detecting the impacts of global climate change (Spehn et al. 2010). Elevation is correlated with a wide variety of factors that influence plant establishment and regulation, including precipitation, climatic variation, and soil characteristics (Kharkwal et al. 2005; Sharma et al. 2009). Decades of research has led to general hypotheses regarding species distribution along elevation gradients, with one of the most reported patterns being a decrease in plant species richness with increased elevation (e.g., Whittaker 1956; Hamilton 1975; Gentry 1988; Toledo-Garibaldi and Williams-Linera 2014). At higher elevations, temperature, wind, and soil instability may limit plant growth (Callaway et al. 2002). However, the seed bank does not seem to be a single standard for richness and abundance in relation to altitude. Cummins and Miller (2002), studying Calluna vulgaris in Scotland, did not find significant variation of seed density as a function of altitude. These authors concluded that soil fertility and seed rain (authochthonous and allochthonous seeds that are dispersed in the area) had a greater influence than altitude. Funes et al. (2003), studying a seed bank on a mountain in the central region of Argentina, found an increase in richness and density with increasing altitude. Ortega et al. (1997), studying seed bank in a gradient in Spain, found the opposite result, with increased richness in the lower areas and dominance of annual species, and a decrease in the higher areas and dominance of perennial species. The lack of altitudinal pattern of soil seed banks (see also Lippok et al. 2011; Oke and Okunola 2008) reinforces the importance of studies of regenerative potential in the soil of mountaintop regions.

The Serra do Cipó is a mountainous region in Brazil, where the predominant vegetation is the rupestrian grasslands (locally called campos rupestres), associated with quartzite formations. They form a mosaic of plant communities adapted to the environmental constraints provided by its highly infertile soils, and have high levels of aluminum, a pronounced seasonal drought, intense light exposure, and strong and constant winds (Benites et al. 2007; Negreiros et al. 2009; Carvalho et al. 2012). This phytophysiognomy is one of the most studied grasslands in Brazil, especially with regard to its flora (e.g., Giulietti et al. 1987; Conceição and Pirani 2005, 2007; Rapini et al. 2008; Borges et al. 2011). Studies of the established vegetation in this area, for both woody and rosette species (Mota et al. 2017), and natural regeneration (Mota et al. 2016) have shown a pattern of decreasing species richness and abundance with increasing elevation. In these studies, the process of species turnover was the determining factor for diversity, as well as the greater floristic similarity between areas of similar elevations. In addition, some edaphic variables (mainly phosphorus

and base saturation) were found to be determinants of vegetation distribution (Mota et al. 2016, 2017).

Several studies have revealed the vulnerability of rupestrian grasslands to global climate change (Bitencourt et al. 2016), biological invasions (Barbosa et al. 2010), and increased pressure on natural resources (Fernandes et al. 2014), because the vegetation is very diverse and exhibits great variability in species composition. Investigations of the processes and patterns involved in the natural regeneration of rupestrian grasslands, and the factors that determine species colonization, are needed (Mota et al. 2016). The potential regeneration of an area is influenced by seed rain, seed and seedling banks, and regrowth of individuals (Garwood 1989). Species composition and abundance of seed banks vary with the degree of disturbance and, as a consequence of geographic location, elevation, climate, and soil (Williams-Linera 1993; Cummins and Miller 2002). Because of high elevation, irregular relief, and the presence of rocky outcrops, the soils of rupestrian grasslands possess a high erosion index (Benites et al. 2003). Loss of soil structure results in difficulties in the absorption and retention of rainwater and soil reserves, leading to desiccation of seeds and loss of germination capacity (Carmo et al. 2012). Gulshan and Dasti (2012) showed that soil composition plays an important role in seed germination. The influence of soil on seed germination is based on the transmission of light through the soil, which includes particle size, moisture content, particle color, and the presence of organic matter (Tester and Morris 1987). These data reinforce our hypothesis that the physical and chemical characteristics of the soil influence the germination of the seeds that are buried in it, composing the seed bank. Thus, even at shallow depths, sometimes formed only of an organic layer upon rock, soils in these high-mountain areas represent an important factor for the occurrence of vegetation (Benites et al. 2001). However, there are still only a few studies on the regenerative potential of rupestrian grasslands through the soil seed bank (Medina and Fernandes 2007; Le Stradic 2012).

We investigated the composition, richness, abundance, and diversity (α and β) of the seed bank along a seven areas at different elevations. We also evaluated similarity in the composition of the seed bank among different areas and the influence of edaphic factors on the distribution of species. Therefore, we aimed to answer the following questions: (i) Do richness and abundance of seed in the soil seed bank decrease linearly with increasing elevation? (ii) Is local diversity (α) lower than the diversity among areas (β), and is the process of turnover the main source of variation in beta diversity throughout the elevation gradient? (iii) Is there greater floristic similarity among areas more proximate altitudinally than among areas more proximate geographically? (iv) Does soil influence the composition and distribution of seed-bank species along the analyzed gradient? We

Fig. 1. Geographic location of Serra do Cipó showing the Espinhaço Mountain Range in Minas Gerais, and indicating the sampling sites (800–1400 m a.s.l.).



expected the seed bank to exhibit the same general patterns observed for aboveground vegetation in relation to elevation, soil variables, and consequently, distribution of diversity.

Materials and methods

Study area

The study was conducted in areas of rupestrian grasslands in Serra do Cipó, located in the southern portion of the Serra do Espinhaço (19°12′-19°34′S, 43°27′-43°38′W), in the central area of the state of Minas Gerais, southeastern Brazil (Fig. 1). The region has a highland tropical Cwb Köppen climate with a rainy season between November and February and mean annual temperature and rainfall of 20 °C and 1500 mm, respectively (Madeira and Fernandes 1999). The rainy season is concentrated from November to February, and the dry season is most pronounced from June to August (Fernandes et al. 2016). The sampling area was delimited along an elevation gradient with seven sampling areas: 800, 900, 1000, 1100, 1200, 1300 and 1400 m a.s.l. (for more details see Mota et al. 2016, 2017). The areas of 800, 900, and 1000 m were considered low-elevation areas, 1100 and 1200 m as intermediate, and 1300 and 1400 m, as high-elevation areas.

Seed-bank sampling

Seed-bank sampling was performed during four periods: July 2014, February 2015, September 2015, and February 2016. Data gathered from the four sampling periods were then assembled in one database. Therefore, we analysed all of the results as one data record. In each area, we sampled 13 plots (100 m²), spaced 10 m from each other, previously installed to survey woody vegetation (Mota et al. 2017). In each plot, four equidistant points were marked at 3 m from the plot edge. Samples of superficial litter and soil were collected at the depth of 0-5 cm (4500 cm³), using a 30 cm × 30 cm template. A total of four soil samples and four litter samples were collected per plot and combined to form one composite plot sample for each category (litter and soil). The litter and soil samples from each plot were then divided into two and packed in plastic trays (22 cm \times 12 cm \times 8 cm). The litter samples were arranged on sterilized sand, according to the methodology adapted from Pereira et al. (2010).

To assess species germination for each sampling period, each pair of soil and litter samples were distributed in greenhouses on the campus of Universidade Estadual de Montes Claros (Unimontes), in Montes Claros (Minas Gerais, Brazil), under two light conditions (direct light and 50% shade). Fifty-six plastic trays containing sterile sand were also distributed in each greenhouse to control for contamination by the local seed rain. Four such control trays were added to each treatment, formed by 13 trays containing soil or litter collected in each plot of the seven areas. All of the samples were irrigated twice a day (once during the morning and once in the afternoon).

The germination method (Brown 1992) was used to evaluate the seed bank. Samples from each area were monitored weekly over a 12-week period by counting and morphotyping all of the individual plants that sprouted. After plant establishment, or with the appearance of reproductive structures, individuals were removed, herborized, identified, and deposited in the Montes Claros Herbarium (MCMG) of Unimontes. Identification of the botanical material was performed with the assistance of experts and specialized botanic literature. The classification of species into families followed the Angiosperm Phylogeny Group IV system (APG IV 2016).

Physicochemical soil analysis

The relationship between the seed bank and the physicochemical composition of the soil was done using data collected by Mota and colleagues in 2012 (Mota et al. 2016). Samples composed of superficial soil (0–20 cm in depth) from each plot were analyzed according to the protocol of Embrapa (1997), which included measuring pH (pH in water), K (levels of potassium), P-Mehlich (phosphorus), P-rem (remaining phosphorus), Ca (calcium), Mg (magnesium), Al (aluminum), H + Al (potential soil acidity), SB (sum of bases), V (base saturation), t (effective cation exchange capacity), m (aluminum saturation), *T* (cation retention capacity), OM (organic matter), and proportions of clay (<0.02 mm), silt (0.02–0.05 mm), fine sand (0.05–0.2 mm), and coarse sand (0.2–2 mm).

Data analysis

Species composition

The cumulative values for abundance and species richness were determined for each plot, at each elevation, addressing the four sampling periods. Plants that died during the experiment were only included in the calculation of abundance. To determine whether variation in elevation determined abrupt changes in species richness and abundance, we used the segmented function of the "segmented" package (Muggeo 2008), applying the glm.nb function of the MASS package (Ripley et al. 2017), with negative binomial error distribution for the overdispersion of the count data. This analysis tests for the existence of ecological thresholds that occur when a model with a breakpoint explains more variation than a linear model (Magnago et al. 2015). To determine whether elevation influenced species richness and abundance, we constructed generalized linear models (GLMs) in which levels of elevation were grouped through contrast analysis (Crawley 2013). If the level of aggregation was not significant, and did not change the deviation explained by the null model, the levels were pooled. The models were submitted to residual analysis to identify the most appropriate error distribution. These analyses were performed within the R environment (R Core Team 2015).

Beta diversity

To evaluate differences in species composition among areas (β diversity), we carried out an additive partitioning analysis (Veech et al. 2002). In additive partitioning, $\gamma = \alpha + \beta$, with α (alpha diversity) representing the diversity within each plot, β (beta diversity) the diversity among plots of different areas, and γ (gamma diversity) the diversity of the entire gradient analyzed. The β diversity was subdivided into β 1 (diversity among plots at the same area), and $\beta 2$ (species turnover among areas at different areas). Diversity values for α and β were calculated using the sampled species richness of the seven areas at different elevations using the "Vegan" package (Oksanen et al. 2017) within the R environment (R Core Team 2015). A method using 1000 randomizations was applied to measure the divergence between observed values and the null model for three diversity components used here $(\alpha, \beta 1, \text{ and } \beta 2).$

For partitioning $\beta 2$ diversity, we used the beta.multi function (using the Sørensen index) of the "Betapart" package (Baselga and Orme 2012). To determine which component was the main feature of β diversity nestedness (species accumulation) or turnover (species substitution) — β diversity was determined using the Sørensen (β_{SOR}) and Simpson (B_{SIM}) indices (Baselga 2010). B_{SOR} represents total β diversity and includes both turnover and nestedness. B_{SIM} does not consider differences in species richness and, therefore, represents only the spatial substitution of species, or turnover. Thus, the total loss of species due to nestedness (β_{NES}) is given by the difference between these indices ($\beta_{\text{NES}} = \beta_{\text{SOR}} - \beta_{\text{SIM}}$).

Similarity among areas

The similarity of seed-bank species composition among areas (800 to 1400 m a.s.l.) was determined through the nonmetric multidimensional scaling (NMDS) using the Sorensen similarity index (Hammer 2012), calculated from species presence/absence matrices in PCORD for Windows, version 6.0 (McCune and Mefford 2011). Analysis of variance (ANOVA) and the Tukey test were used to compare the axes obtained from NMDS among areas. Area was used as the explanatory variable and axes as the response variable. To verify whether the most similar areas are those that have the smaller geographical distance between them, the geographical distance between the areas was measured in kilometres with the aid of the software Google Earth Pro version 7.3.3832, using the geographical coordinate data for each area.

Soil analysis

To compare soil variables among areas, GLMs were constructed using pH, K, P-Mehlich, P, Ca, Mg, Al, H + Al, SB, V, t, m, T, OM, and proportions of coarse sand (CS), fine sand (FS), silt, and clay as response variables and areas as the predictor variable. When significant differences were observed among areas, the data were submitted to contrast analysis through the aggregation of levels (Crawley 2002). All of the models were submitted to residual analysis to identify the most appropriate error distribution (Crawley 2002). To test whether the physicochemical properties of the soil influence the distribution of seed-bank species at different elevations, a canonical correspondence analysis (CCA) was performed in PCORD for Windows version 5.0 (McCune and Mefford 2011). Only the species with more than 10 individuals were used, which was equivalent to 30 species, 15 identified at the species level, 11 at the genus level, and 4 at the family level. After the preliminary CCA, the nonsignificant soil variables and those with high redundancy (>0.5) were eliminated, keeping only the soil properties that had a close relationship with species abundance: cation exchange capacity (t), base saturation (V), organic matter (OM), potential soil acidity (H + Al), proportion of fine sand (FS), and proportion of clay. The Monte Carlo permutation test was used to evaluate the significance of the model (Ter Braak 1987).

To investigate the effect of edaphic variables on seedbank richness and abundance at each elevation, GLMs were constructed with the variables selected through the CCA (>0.5). Thus, the global model included potential soil acidity (H + Al), effective cation exchange capacity (t), base saturation (V), organic matter (OM), fine sand, and clay as predictor variables. Within the R environment (R Core Team 2015), GLMs (Generalized Linear Models) were created using the glm.nb function of the MASS package (Ripley et al. 2017), with negative binomial error distribution for the overdispersion of the count data. Using the dredge function of the "MuMIn" package (Barton 2016), all possible combinations of the variables included in the global model were tested, with the most decisive factors for richness and abundance being identified through the AICc (Akaike's Information Criteria of Second Order), with the best model being the one with the lowest AICc value (Burnham et al. 2011).

We analyzed stratified spatial heterogeneity to verify whether the soil attributes are spatially stratified. The value of *q* indicates the percent of the variance of an attribute explained by the stratification, in which 0 indicates no spatial stratified heterogeneity and 1 indicates perfect spatial stratified heterogeneity (Wang et al 2016). So, *q*-values were calculated to demonstrate how soil variables were spatially stratified.

Results

Richness and abundance of soil seed bank along an elevation gradient

A total of 1975 individuals were recruited in the soil seed bank, representing 22 families and including 149 taxa. Of these taxa, 41 were identified to the species level, 55 to genus, and 44 to family, while 9 remained unidentified (Appendix Table A1). The dominant families were Poaceae (40 species), Cyperaceae (35), Melastomataceae (14), and Asteraceae (12). The most abundant species were *Rhynchospora consanguinea* (354 individuals), *R. riedeliana* (154), *Rhynchospora* sp. 3 (129), *Rhynchospora* sp. 4 (139), and *Bulbostylis* sp. (90), which together comprised 42% of the germinated individuals.

Species richness and abundance did not show a linear relationship with elevation ($p \ge 0.05$). Instead, a threshold for richness (Fig. 2A) and abundance (Fig. 2B) was identified through finding a breakpoint at the elevation of 1200 m a.s.l. (Table 1), which showed an abrupt decrease for richness and abundance from this altitude onwards. Both richness ($F_{[6.84]} = 53.621$, $p \le 0.001$; Fig. 3A) and abundance ($F_{[6.84]} = 80.663$, $p \le 0.00$; Fig. 3B) varied among areas. The seed bank in areas at 800, 900, 1100, and 1200 m a.s.l. had greater richness than those at 1000, 1300, and 1400 m. The highest abundance was observed at 1200 m areas at 800, 900, 1000, 1100, and 1400 m.

Variation in β diversity along an elevation gradient

The additive partitioning of species diversity revealed that gamma diversity (γ) is formed mainly by species turnover between areas ($\beta 2 = 70\%$), followed by species turnover among the plots of the same area ($\beta 1 = 24.5\%$). Local diversity (α) represented only 5.8%. Thus, beta di-

versity (β) represented 94.5% of the regional diversity of the seed bank in the studied area. The three components of diversity were statistically different from that expected by the null model (Fig. 4). The observed value for β 1 was lower than that expected by chance, while the observed values of β 2 and α were higher. The decomposition of β 2 diversity revealed that species turnover between areas is the main component of β_{SOR} diversity ($\beta_{SOR} = 0.61$, $\beta_{SIM} = 0.49$), representing 81% of β diversity; nestedness explained only 19% ($\beta_{NES} = 0.11$).

Floristic similarity between areas and elevations

The NMDS ordering analysis (Fig. 5) showed that areas which are more proximate altitudinally had greater similarity than areas more proximate geographically (Supplementary data, Table S1¹). As can be seen in Fig. 5, although areas at 800 and 900 m have the largest geographical separation (almost 10 km distance), were similar floristically. Similarly, areas at 1300 and 1400 m (6.03 km apart) were also similar floristically, as were the intermediate areas of 1000, 1100, and 1200 m, despite the geographical distance between them. The first axis segregated the lower areas (800 and 900 m) from the highest areas (1300 and 1400 m), while the intermediate areas (1000, 1100, and 1200 m) remained scattered between both groups. The first axis (F = 2.89, $P \le 0.05$) and the second axis (F = 5.62, $P \le 0.05$) revealed a significant correlation with the elevation composition. However, Tukey's honestly significant difference (HSD) test showed no significant differences among areas, and therefore, indicated a low degree of similarity. Only six species were common to all of the areas: R. consanguinea, R. riedeliana, Rhynchospora sp. 3, Rhynchospora sp. 4, R. tenuis, and Echinolaena inflexa.

Soil attributes and distribution of seed bank along an elevation gradient

The soil analyses indicated that all of the analyzed parameters varied significantly among areas (Table 2). The *q*-values indicated that soil variables were spatially stratified, at least to some degree. pH was the soil attribute that was least heterogeneous (0.23), compared with base saturation, which was the variable with the highest spatially stratified heterogeneity (0.69). Despite to base saturation, the physical attributes were the variables with highest spatially stratified heterogeneity. In general, the soils were acid, especially those at intermediate and high elevation (pH < 4.99). The area at 1300 m a.s.l. had a lower concentration of potassium, while the areas at 800 and 1400 m had higher levels of magnesium. The areas at 1200 and 1400 m possessed higher levels of aluminum, whereas the area at 1400 m had higher levels of calcium. Base saturation was higher at 800 m, while the sum of bases did not differ between the areas at 800 and

¹Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2017-0162.

Fig. 2. Species richness (A) and abundance (B) of germinated seeds along an elevation gradient in Serra do Cipó, Brazil, with a breakpoint at 1200 m a.s.l.



Table 1. Results of the generalized linear models for abundance and richness of the seed bank along an elevation gradient in Serra do Cipó, Minas Gerais, Brazil.

Variables	Model	df	AICc
Richness	One-segmented	5	497.668
	Linear model	3	515.748
	Null	2	517.599
Abundance	One-segmented	5	682.893
	Linear model	3	728.152
	Null	2	726.056

Note: Values are degrees of freedom and AICc parameters. Onesegmented is the model with one breakpoint. 1400 m. The effective cation exchange capacity was lowest at 1300 m and highest at 1400 m, while aluminum saturation was highest at 1200 m and lowest at 800 m. The highest levels of organic matter were found at 1200 and 1400 m, and the lowest at 800 and 1000 m. Regarding physical variables, the areas at 800 and 900 m had lower amounts of fine sand and greater amounts of silt, while the area at 900 m also exhibited a greater amount of clay.

The first two axes of the CCA (Fig. 6) possessed eigenvalues of 0.32 (axis 1) and 0.23 (axis 2), and explained 5.8% and 4.2% of the total data variance, respectively. The eigenvalues for the two ordination axes were low, indicating that there is low species substitution along the gradient. On the other hand, species–environment correlations were high for both axes: 0.81 (axis 1) and 0.79

Fig. 3. Species richness (A) and abundance (B) of germinated seeds along an altitudinal gradient in Serra do Cipó, Brazil. Values are the mean \pm SD (n = 13). Different letters indicate significant differences ($p \le 0.05$) between means.



Fig. 4. Additive diversity partitioning for the seed bank of an elevation gradient in Serra do Cipó, Brazil. The component α represents the percent of the number of germinated species per plot; β 1 represents β diversity due to the percent of species among plots; β 2 represents the percent of species among different areas. Observed values were compared statistically with the expected values (*, p < 0.001).



(axis 2). Furthermore, the Monte Carlo permutation test indicated that abundance was significantly correlated with soil attributes (p < 0.05).

Plots located at different areas were segregated, and the organization of these plots formed three groups (Fig. 6A). The first group, in axis 1, comprised plots at 1300 and some at 1400 m; the second group, in axis 2, comprised plots at elevations of 800 and 1100, and some at 900 m; and the third group, in axis 1, comprised plots at 1000 and 1200, and some at 1400 m. Internal correlations between environmental variables and the first two ordination axes (Table 3) showed that the environmental variables most strongly correlated with axis 1 were clay (positive correlation); H + Al; t (effective cation exchange capacity); OM (organic matter); and fine sand (negative correlation), while the environmental variable most strongly correlated with axis 2 was V (base saturation), which exhibited a negative correlation. The seed bank at all plots located at 1300 m, and some at 1400 m, was positively correlated with the variables V and clay. Most of the plots at 1100 m negatively correlated with organic matter, while those at 1000 m were positively related. Those areas located at 1200 m positively correlated with H + Al, t, and fine sand, and negatively correlated with V and clay; and some plots of the areas at 800, 900, and 1000 m were dispersed.

The CCA ordination of species (Fig. 6B) suggests that Symphyopappus brasiliensis, Paspalum multicaule, Digitaria cf. bicornis, Schwenkia americana, Phylanthus sp., Rhichardia sp. 2, and Cyperus sp. 3 are more abundant in areas with higher availability of clay and base saturation, while Baccharis platypoda, Polygala glochidiata, R. consaguinea and Bulbostylis sp. are more related to areas with a greater amount of organic matter. On the other hand, R. tenuis subsp. austro brasiliensis, R. riedeliana, Axonopus sp. 3, and Borreria sp. are predominant in areas with low organic matter content. Homolepis longispicula, Schyzachyrium tenerium, and Eragrostis articulata were found to be related to areas with higher potential acidity, effective cation exchange capacity, and a greater amount of fine sand.

Species richness at 1000, 1100, and 1200 m a.s.l. was mainly affected by effective cation exchange capacity (t); in the areas at 1100 and 1300 m by organic matter (OM); and at 1100 m by clay. Seed abundance was mainly affected by the variable t at 1100 m; OM at 1100 and 1300 m; clay at 1100 m; H + Al at 1400 m; and base saturation (V) at 1200 m. None of the environmental variables analyzed explained the variation in species richness and abundance of germinated seeds at 800 and 900 m, abundance at 1000 m, and richness at 1400 m (Supplementary data, Table S2).

Discussion

Do richness and abundance of seed in the soil seed bank decrease with elevation?

Richness and abundance of the soil seed bank did not decrease with the increasing elevation, according to the adult woody and regenerating vegetation in the same areas/plots of this study (Mota et al. 2016, 2017). The results also do not corroborate general patterns of the distribution of plant diversity, which indicate decrease in richness with increasing elevation (e.g., Whittaker 1956; Hamilton 1975; Gentry 1988; Kitayama 1992; Aiba and Kitayama 1999; Hussain and Malik 2012; Shaheen et al. 2015). However, several studies have shown a nonunimodal pattern for plant richness along elevation gradients (Lieberman et al. 1996; Wang et al. 2002; Joly et al.





Table 2. Analysis of variance with generalized linear models and *q*-statistic values of edaphic variables at the seven elevations studied in Serra do Cipó, Minas Gerais, Brazil.

	Elevation (m	a.s.1.)							
Edaphic variable	800	900	1000	1100	1200	1300	1400	F	q
pН	5.15±0.07a	5.05±0.06a	5.18±0.06a	4.99±0.05b	4.80±0.11b	4.78±0.16b	4.70±0.08b	4.278	0.23
P-Merlich	2.91±0.37a	1.16±0.13b	1.16±0.12b	1.15±0.08b	2.70±0.46a	1.02±0.18b	2.38±0.33a	11.313	0.40
P-Rem	32.60±0.07b	30.30±0.06c	32.81±0.06b	29.12±0.05c	24.86±0.11c	39.26±0.15a	33.90±0.08b	44.628	0.33
K+	49.45±3.88a	31.66±2.80b	30.08±4.90b	33.06±2.60b	41.15±5.45a	15.32±0.64c	25.06±3.82b	67.030	0.38
Ca++	0.25±0.02b	0.20±0.00b	0.20±0.00b	0.21±0.01b	0.21±0.01b	0.20±0.00b	0.28±0.03a	5.318	0.25
Mg ⁺⁺	0.15±0.01a	0.10±0.00b	0.10±0.00b	0.11±0.01b	0.10±0.00b	0.10±0.00b	0.17±0.02a	13.23	0.44
Al	1.43±0.07b	1.69±0.20b	1.62±0.22b	1.87±0.12b	2.48±0.24a	1.29±0.111b	2.66±0.24a	7.895	0.36
H + Al	1.95±0.13b	5.08±0.70a	2.47±0.36b	5.87±0.62a	5.86±0.58a	1.99±0.16b	5.89±0.47a	15.985	0.53
SB	0.53±0.03a	0.38±0.01b	0.38±0.01b	0.40±0.02b	0.42±0.02b	0.34±0.00	0.52±0.04a	10.893	0.42
t	1.96±0.09a	2.07±0.21b	1.99±0.23a	2.27±0.13b	2.90±0.25b	1.60±0.11a	3.18±0.25c	8.3283	0.37
т	72.64±1.07c	78.67±2.49b	79.41±1.35b	82.01±0.76b	84.04±1.53a	77.57±1.41b	82.81±1.69b	6.233	0.31
Т	2.48±0.14b	5.46±0.71a	2.85±0.37b	6.27±0.64a	6.28±0.59a	2.40±0.15b	6.41±0.47a	15.449	0.52
V	21.92±1.10a	8.74±1.24c	15.10±1.24b	7.04±0.68c	7.39±0.73c	14.91±0.80b	8.55±0.87c	32.257	0.69
OM	3.51±0.17c	5.037±0.48b	3.57±0.41c	5.59±0.48b	6.90±0.65a	3.57±0.19c	6.90±0.58a	11.201	0.44
CS	17.84±1.08a	4.18±0.68c	17.65±1.48a	4.88±0.45c	12.80±1.09b	18.17±1.36a	9.35±1.41b	28.683	0.67
FS	62.77±1.01d	72.59±1.16b	67.11±1.66c	81.12±1.20a	75.66±0.97b	73.74±1.40b	78.49±1.26a	25.623	0.64
Silt	11.54±0.68a	12.46±1.20a	8.15±0.77b	5.54±0.40c	6.00±0.51c	4.92±0.43c	7.85±0.57b	19.23	0.55
Clay	7.85±0.53c	10.77±0.36a	7.08±0.66d	8.46±0.79b	5.54±0.33e	3.08±0.29g	4.31±0.21f	30.847	0.66

Note: Values followed by a different letter are significantly (p < 0.01) different. Abbreviations for edaphic variables are defined in the text.

2012), while others describe a peak of diversity at intermediate elevations (Fernandes 1992; Lomolino 2001; Sang 2009). In fact, there was an increase in abundance up to 1200 m a.s.l. and a stabilization of richness between 800 to 1200 m, whereas above this elevation both species abundance and richness decreased. This threshold at the intermediate elevation of 1200 m may be related to both the environmental conditions provided by the elevation and the composition of species present in the area. For example, the greater abundance at 1200 m may be related to the occurrence of species of the genus *Rhynchospora* and *Bulbostylis*, which comprised 44% of the observed total abundance. Both genera belong to the family Cyperaceae, which preferentially occurs on poorly drained soils such as swamps, marshes, river banks, and puddles (Ardissone 2014). In some of the plots **Fig. 6.** Canonical correspondence analyses (CCA): plot ordination diagrams (A) and seed-bank species (B) based on the distribution of the number of individuals of 30 species with 10 or more individuals in 91 plots among seven elevations in rupestrian grasslands in Serra do Cipó, Brazil, and their correlation with soil variables: OM, organic matter; *t*, cation exchange capacity; *V*, base saturation; H + Al, potential soil acidity; FS, fine sand; and clay.



Table 3. Analysis of the results from the canonical correspondence analysis (CCA) of the abundance of 149 seed-bank species sampled in 91 plots among seven elevations of rupestrian grasslands in Serra do Cipó, Minas Gerais, Brazil.

	Intraset correlati	ons	Edaphic	variables			
Edaphic variables	Eixo 1	Eixo 2	H + Al	Т	V	ОМ	FS
H + Al	-0.052	-0.772					
t	-0.129	-0.793	0.774				
V	0.261	0.700	-0.85	0.589			
OM	0.089	-0.970	0.799	-0.784	-0.678		
FS	-0.511	-0.536	0.555	0.283	-0.635	0.403	
Clay	0.694	0.183	0.107	-0.166	0.092	-0.16	-0.248

Note: The values represent the internal correlations (intraset) between the soil characteristics and the first two ordering axes, and the matrix of weighted correlations between potential soil acidity (H + AI), effective cation exchange capacity (t), base saturation (V), organic matter (OM), proportions of fine sand (FS), and clay.

in the area at 1200 m the soil was flooded, which may have influenced the abundance of these species. This finding indicates that there is variation in the pattern of distribution of plant species by stratum along the studied gradient.

Elevation modifies the climatic conditions, influencing the composition, richness, abundance, and density of seeds in the soil (Funes et al. 2003; Ma et al. 2010; Lippok et al. 2013). The lower richness and abundance in the higher areas (1300 and 1400 m) may be associated with low temperatures, and consequently, low embryonic metabolic rates and slow consumption of seed reserves, favoring greater seed longevity (Murdoch and Ellis 1992). However, other factors can act on the soil seed bank in response to variation in elevation, such as seed rain potential, soil type and conditions, presence of anthropic activities, and evaluated seasons, among others (Cummins and Miller 2002; Funes et al. 2003; Ma et al. 2010; Lippok et al. 2013). For example, there was low species richness and abundance in the area at 1000 m. Soil type and area steep declivity of the terrain may facilitate the transport of seeds to lower regions, thereby changing the deposition of seed rain on this site.

Is local diversity (α) lower than the diversity among areas (β), and is the process of turnover the main source of variation in beta diversity throughout the gradient analyzed?

Our results corroborate the hypothesis that diversity among areas (β) contributes more to regional diversity (γ) than does local diversity (α). This greater contribution of β diversity to γ diversity means that more species are added to the community, owing to differences in composition between plots within the same area and between areas of different elevations (see Veech et al. 2002). In addition to differing from that expected by chance, β diversity was higher, indicating that this diversity component contributed to the global richness of seed-bank species in the studied gradient. Although α diversity had a small contribution to regional diversity, local conditions are also important and cannot be disregarded when assessing the regional species pool (Cain et al. 2011). In this way, the partition of diversity should not be restricted to the scale of the landscape, and regional subsets should be considered, to better understand the environment as a whole (Margues and Schoereder 2013). However, the value of β 1 being below the value expected by chance indicates that there is a high degree of similarity in species between plots of the same area, and structure and habitat conditions as a whole (Beck et al. 2012; Neves et al. 2013). The component β 2 contributed more to γ diversity than β 1 and α , with 70% of the seedbank diversity being caused by differences between areas. In association with this, turnover was the main component of $\beta 2$ diversity decomposition, indicating that mountain-top communities are not nested subsets of communities of lower elevations, but instead are communities with different species compositions. This result could be related to the high level of environmental heterogeneity of the sampled areas, with different types of habitats being found within a single area (Carvalho et al. 2012; Mota et al. 2016, 2017). We can also assume that diversity along the gradient can be shaped by different environmental filters that act on the exclusion or inclusion of species in certain communities (Cain et al. 2011). Thus, the dispersal ability of species, and their local abiotic conditions and species interactions, for example, can act as filters, causing differences in species composition between areas and increasing turnover along the studied gradient. Other studies with plants and other taxa, like insects, also point to turnover as the main component of $\beta 2$ diversity (Marques and Schoereder 2013; Nunes et al. 2016a; Mota et al. 2017). These data showed that the seed bank of the Serra do Cipó presents high regional diversity, caused by differences among areas, with high species turnover.

Is there greater floristic similarity between areas more proximate altitudinally than among areas more proximate geographically?

The low degree of similarity found in the seed bank between areas, even among those closest to each other, is contrary to what was expected and observed in studies carried out for woody plant community in the areas (Mota et al. 2016, 2017). These results reflect environmental heterogeneity and the influence of edaphoclimatic factors on the composition of rupestrian grassland species (Carvalho et al. 2012).

Seed dispersal is an important step in the reproductive cycle of most plants, through which seed distribution occurs among diverse habitats, and can promote their deposition in particular sites suitable for germination and seedling establishment (Howe and Smallwood 1982). However, even when taken to adjacent areas, away from the mother plant, many seeds cannot germinate and establish. Several factors contribute to the reproductive success of the diaspore, such as soil conditions, temperature, water conditions, light, and presence of dormancy (Nunes et al. 2016b). Altitude modifies climate, interfering in several of these factors and thus in the composition and establishment of the plants (Kharkwal et al. 2005; Sharma et al. 2009). In this study, altitude was more important than geographic proximity for floristic similarity. In addition, the close similarity between the areas at 800 and 900 m and at 1300 and 1400 m may be related to physiognomic characteristics. Both of the lower areas have a predominance of shrub-tree species characteristic of the cerrado, sensu stricto, with a transition to the rupestrian grasslands (Mota et al. 2017). Likewise, areas at higher elevations have a predominantly grassy, herbaceous stratum with few shrub species in rocky outcrops in these areas (Mota et al. 2017). Areas at both 1000 and 1100 m possess species characteristic of cerrado sensu stricto and rupestrian grassland, with the presence of rocky outcrops (Mota et al. 2017).

In addition to E. inflexa, five species of Rhynchospora were common in the seven studied areas. Species of the families Cyperaceae and Poaceae are well represented in rupestrian grasslands (Medina and Fernandes 2007; Rapini et al. 2008; Le Stradic et al. 2015). When comparing the species of the seed bank sampled in our study with the species sampled by Le Stradic et al. (2015) in areas also in Serra do Cipó, it is noted that 24 identified species of the seed bank are present in established vegetation. Of these species, 79% are species of Cyperaceae and Poaceae. Le Stradic et al. (2015) found Lagenocarpus tenuifolius on stony substrates, Panicum cyanescens and Paspalum hyalinum on sandy substrates, and Tatianyx anarctes and Homolepis longispicula on both substrate types. The presence of vegetation species established in the seed bank reflects the regenerative potential of the rupestrian fields of Serra do Cipó.

Does soil influence the composition and distribution of seed-bank species along the elevation gradient?

Soil influences the composition and distribution of seed-bank species and, among the edaphic variables analyzed, the most important were effective cation exchange capacity (t), H + Al, organic matter (OM), base saturation (V), fine sand (FS), and clay. Considering these edaphic variables, which were related to the seed bank, only V was important in the distribution of regenerating woody vegetation (Mota et al. 2016), and H + Al, OM, and V in the distribution of adult woody vegetation (Mota et al. 2017) in the studied elevation gradient. Furthermore, differences were observed among areas in the edaphic variables of the soil as a result of the gradient analyzed. The areas at intermediate and high elevations possessed more acidic soils, with greater aluminum saturation. Although this high concentration of aluminum is harmful to plants, because at low pH, phosphorus, which is a critical element in vegetation development (Sarmiento 1984), can precipitate with aluminum and make it less available to plants (Le Stradic et al. 2015), rupestrian grasslands species are adapted to this conditions

Intermediate areas, such as those at 1000 and 1200 m, have high cation exchange capacity (t), which favors nutrient assimilation (Conceição and Pirani 2005), influencing seed richness at 1000 m, and seed richness and abundance at 1200 m. This edaphic variable represents the capacity to gradually liberate several nutrients in the soil, favoring the maintenance of its fertility for an extended period of time (Ronquim 2010). As with the soils of the area at 1100 m, some of the plots at 800 and 900 m have low cation exchange capacity, and these soils must have the capacity to retain cations in a reduced exchangeable form. On the other hand, OM was important in the areas at 1100 and 1300 m (in the selection of models). Organic matter plays a significant role in nutrient recycling, buffering the soil from abrupt changes in pH, construction and maintenance of its structure, and adsorption and storage of water, as well as increasing cation exchange capacity (Vargas and Hungria 1997). Areas with low OM content, such as observed at 800 m (in the CCA), usually possess sandy soils with a low capacity for effective cation exchange. Therefore, these soils possess a low buffering capacity and a high potential for base leaching, as well as possible sulfur and micronutrient deficiency (Tomé Junior 1997).

The base saturation (*V*) is also indicative of soil fertility. According to the saturation percentage described by Ronquim (2010), the soils of the studied areas are considered to have low fertility, which is in agreement with other studies in rupestrian grasslands (Benites et al. 2003; Negreiros et al. 2008; Schaefer et al. 2016). The seed bank was related to *V* in all plots in the area at 1300 m and some of the plots in the area at 1400 m. It was also an important edaphic variable in the variation in seed-bank abundance in the area at 1200 m. Areas located at the 292

highest elevations, such as at 1300 m, also had a strong relationship with clay, which occurred in smaller proportions in the soils of these areas compared with the higher levels in the soils of the lower areas. Clay also influenced seed-bank richness and abundance in the area at 1100 m. Clay provides greater nutrient retention capacity (Raven et al. 2001; Le Stradic et al. 2015) and has an important ecological role in increasing soil fertility (Conceição and Pirani 2005). Another important physical variable is the proportion of fine sand, which was particularly important in the area at 1200 m (in the CCA), indicating that the predominant texture of these soils is sandy. Sandy soils are, generally, highly susceptible to erosion and, due to the presence of large pores, cannot retain water, which causes excessive drainage and nutrient leaching (Prado 1995). Sandy soils also have a low cation exchange capacity, which comes almost exclusively from organic matter (Tomé Junior 1997). In the spatially stratified heterogeneity analysis, base saturation, coarse sand, clay, fine sand, and silt presented greater *q*-values of 0.69, 0.67, 0.66, 0.64, 0.55, respectively (0 indicates no spatially stratified heterogeneity and

1 indicates perfect spatially stratified heterogeneity) (Wang et al. 2016). We note that physical variables and base saturation may be the most important factors for determining species turnover and β diversity.

High levels of H + Al usually occur in soils that are rich in organic matter and have very low pH (Tomé Júnior 1997), such as the soils of the areas at 1200 and 1400 m, which have a low pH and high levels of H + Al and organic matter. Thus, the observed results show the complexity and heterogeneity of the sampled areas, where each area possesses different important edaphic variables that affect the richness, abundance, and composition of the seed bank. The richness and abundance of the seed bank was influenced mainly by t in the lower areas, negatively by the clay in the higher areas, and positively by the fine sand and H + Al in the higher and intermediate areas, and negatively by the OM in the lower areas. In addition, in the gradient evaluated (800-1400 m) in Serra do Cipó, some species found in this study were characteristic of a certain areas, such as Cyperus sp. 2, Schizachyrium sp. 2, and Borreria sp. 2 at 800 m; Lychnophora pinaster, Lagenocarpus tenuifolius, Diplusodon orbicularis, and Marcetia taxifolia, at 900 m; Rhynchospora recurvata, Stylosanthes sp., and Turnera sp. 2 at 1000 m; Ageratum fastigiatum, Lagenocarpus rigidus, and Panicum sp. at 1100 m; Bulbostylis cf. conifera, Tibouchina heteromala, Trembleya lanifolia, and Trachypogon spicatus at 1200 m; Schizachyrium sp. 3, Croton sp. 1, Mimosa sp., and Miconia sp. 2 at 1300 m; and Xyris sp., Schizachyrium cf. sanguineum, and Tatyanix anarcites at 1400 m. These species vary in their occurrence and abundance in the seed bank along the elevation gradient, and may be indicative of the environmental variation at each area localized to a different elevation. Thus, there is vast biological complexity in this environment, which was

attested to by the studies of the aboveground vegetation (Mota et al. 2016, 2017) and verified by the present study.

The analyses presented here show that seed bank of Serra do Cipó does not show a linear pattern of increase or decrease in richness and abundance with elevation, and that the soil, although extremely poor in nutrients, acid and thin in some places, is largely responsible for the high β diversity and changes in richness, abundance, and composition between areas. In addition, the soil attributes of the areas contribute to the low similarity between the areas. The high β diversity, the predominance of species turnover in the studied gradient, and the low similarity among areas reflect the high species richness in this ecosystem of great environmental heterogeneity. Understanding the factors that influence the seed banks in response to changes in soil, elevation, and consequently, climatic conditions, expands our knowledge about vegetation at high elevations, especially that of rupestrian grasslands.

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Appendix

Appendix Table A1 appears on the following pages.

Table A1	. Germinated species	, their respective fam	ilies, voucher,	and occurrence	ce in each area i	n the evaluated	elevation gradier
(800-1400) m a.s.l.) in Serra do	Cipó, Minas Gerais,	Brazil.				

Family	Species	800	900	1000	1100	1200	1300	1400	Voucher
Amaranthaceae	Alternanthera sp.							Х	5143
	Amaranthus sp.		Х		Х				5144
Apocynaceae	Oxypetalum cf. strictum	Х			Х				5145
Asteraceae	Ageratum fastigiatum (Gardner) R.M. King & H. Rob.				Х				5146
	Aspilia sp.		Х		Х	Х			
	Baccharis platypoda DC.	Х	Х	Х	Х	Х			5147
	Baccharis sp. 1					Х			
	Lychnophora cf. ericoides		Х	Х	Х	Х			5148
	Lychnophora pinaster		Х						
	Senecio sp.	Х		Х		Х			5149
	Symphyopappus brasiliensis (Gardner) R.M. King &	Х	Х	Х	Х	Х			5150
	H. Rob.								
	Species 1		Х		Х			Х	
	Species 2		Х	Х					
	Species 3	Х							
	Species 4	Х				Х			
Bromeliaceae	Species 1			Х		Х			
Chloranthaceae	Hedyosmum brasiliense Mart. ex Miq.		Х						
Cyperaceae	Bulbostylis cf. conifera					Х			5151
	Bulbostylis sp.	Х	Х	Х	Х	Х			5152
	Species 1				Х	Х			
	Species 2						Х		
	Species 3		Х	Х					
	Species 4						Х	Х	
	Species 5			Х	Х			Х	
	Species 6	Х				Х	Х		
	Species 7	Х							
	Species 8						Х		
	Species 9							Х	
	Species 10						Х		
	Species 11	Х							
	Species 12	Х			Х				
	Cyperus sp. 1	Х				Х		X X X X X X X X X X X X X X X X X X X	5153
	Cyperus sp. 2	Х							
	Cyperus sp. 3	Х							5154
	Cyperus sp. 4	Х		Х					5155
	Cyperus sp. 5	Х			Х				
	Fimbristylis sp.	Х	Х			Х	Х		5156
	Lagenocarpus rigidus Nees				Х				5157
	Lagenocarpus sp.				Х				
	Lagenocarpus tenuifolius (Boeckeler) C.B. Clarke		Х				Х	Х	5158
	Rhynchospora cf. emaciata	Х	Х		Х	Х	Х	Х	5159
	Rhynchospora consanguinea (Kunth) Boeckeler	Х	Х	Х	Х	Х	Х	Х	5160
	Rhynchospora recurvata (Schrad. ex Nees) Steud.			Х					5161
	Rhynchospora riedeliana C.B. Clarke	Х	Х	Х	Х	Х	Х	Х	5162
	Rhynchospora sp. 1				Х	Х		Х	5163
	Rhynchospora sp. 2		Х					Х	
	Rhynchospora sp. 3	Х	Х	Х	Х	Х	Х	Х	
	Rhynchospora sp. 4	Х	Х	Х	Х	Х	Х	Х	5164
	Rhynchospora sp. 5	Х							
	Rhynchospora sp. 6							Х	
	Rhynchospora tenuis Link	Х	Х	Х	Х	Х	Х	Х	5165
	Rhynchospora tenuis subsp. austro brasiliensis	Х		Х	Х	Х		Х	5166
	T. Koyama								

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Table A1 (continued).

Family	Species	800	900	1000	1100	1200	1300	1400	Voucher
Euphorbiaceae	Chamaesyce sp. 1		Х						5167
1	Chamaesyce sp. 2		Х						
	Croton sp. 1	Х					Х		5168
	Croton sp. 2	Х			Х				5169
	Species 1					Х			
Fabaceae	Chamaecrista desvauxii (Collad.) Killip				Х	Х			5170
	Mimosa sp.						Х		
	Stylosanthes sp.	Х		Х					
Krameriaceae	Krameria sp.		Х						
Lamiaceae	Hyptis complicata A. StHil. ex Benth.		Х		Х				5171
	Species 1					Х			
Lythraceae	Diplusodon orbicularis Koehne		Х						5172
Malvaceae	Species 1				Х				
	Species 2			Х					
	Species 3		Х						
Melastomataceae	Cambessedesia sp					Х			
	Marcetia taxifolia (A. StHil.) DC.		Х						5173
	Species 1					Х			
	Species 2		х			Х			
	Species 3	Х							
	Species 4					Х			
	Species 5		х						
	Species 6		X						
	Miconia sp. 1		X						
	Miconia sp. 2					х	Х		
	Microlicia sp. 1		Х	Х					
	Microlícia sp. 2					Х			
	Tibouchina heteromalla (D. Don) Cogn.					Х			5174
	Trembleva laniflora (D. Don) Cogn.					Х			5175
Myrtaceae	Species 1			Х					
Phyllantaceae	Phyllanthus sp. 1		Х						
5	Phyllanthus sp. 2	Х	Х	Х	Х				
Poaceae	Axonopus aureus P. Beauv.	Х	Х			Х			
	Axonopus siccus (Nees) Kuhlm.	Х							
	Axonopus sp. 3	Х	Х			Х			
	Axonopus sp. 4		Х	Х	Х				
	Axonopus sp. 5			Х					5178
	Digitaria cf. bicornis	Х	Х	Х	Х	Х	Х		5177
	Echinolaena inflexa (Poir.) Chase	Х	Х	Х	Х	Х	Х	Х	5179
	Eragrostis articulata (Schrank) Nees	Х	Х	Х	Х	Х		Х	5176
	Homolevis longisvicula (Döll) Chase	Х	Х	Х		Х	Х	Х	5180
	Mesosetum loliiforme (Hochst.) Chase		Х		Х				5181
	Panicum cvanescens Nees ex Trin.					Х	Х		5182
	Panicum sp.				Х				
	Paspalum erianthum Nees ex Trin.		Х					Х	5183
	Paspalum hvalinum Nees ex Trin.					Х			5184
	Paspalum multicaule Poir.	х	х		х				5186
	Paspalum sp. 1	X			X				5185
	Paspalum sp. 3				X	х			5187
	Paspalum sp. 4		х						5188
	Paspalum sp. 5			Х					
	Species 1	х		X	х				
	Species 3		Х						
	Species 4			Х					
	Species 5	х							
	Species 6	X							
	Species 7					х			
	Species 8	х			Х	X		х	
	L				-	-		-	

Family	Species	800	900	1000	1100	1200	1300	1400	Voucher
	Species 9	Х				Х			
	Species 10	Х			Х	Х			
	Species 11	Х							
	Species 12					Х			
	Species 14		Х						
	Schizachyrium cf. sanguineum							Х	5189
	Schizachyrium sp. 1				Х				
	Schizachyrium sp. 2	Х							
	Schizachyrium sp. 3				Х		Х		
	Schizachyrium sp. 4							Х	
	Schizachyrium tenerum Nees				Х	Х	Х	Х	5190
	Trachypogon spicatus (L.f.) Kuntze					Х			5191
	Tatianyx arnacites (Trin.) Zuloaga & Soderstr.							Х	5192
Polygalaceae	Polygala glochidata Kunth	Х			Х	Х			5193
Portulacaceae	Portulaca cf. oleracea				Х	Х			
Rubiaceae	Borreria sp. 1	Х	Х		Х			Х	5194
	Borreria sp. 2	Х							
	Declieuxia sp. 1		Х						5195
	Declieuxia sp. 2					Х			
	Diodella apiculata (Willd. ex Roem. & Schult.)					Х			5196
	Delprete								
	Richardia sp. 1	Х				Х	Х		5197
	Richardia sp. 2	Х	Х		Х				5198
	Species 1					Х			
	Species 2		Х						
	Species 3				Х				
Solanaceae	Schwenckia americana Rooyen ex L.		Х		Х	Х			5199
	Solanum sp.					Х			5200
Turneraceae	Turnera sp. 1			Х					
	Turnera sp. 2		Х						5201
Xyridaceae	Xyris sp.							Х	
Unidentified	Species 1		Х						
	Species 2	Х							
	Species 3					Х			
	Species 4		Х						
	Species 5		Х						
	Species 6				Х				
	Species 7				Х				
	Species 8					Х			
	Species 9		Х			Х			