

## Shared-role of vegetation types, elevation and soil affecting plant diversity in an old-tropical mountain hotspot

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**Abstract:** Despite the exceptional species richness and endemism, the environmental drivers of plant diversity along old tropical mountains remain under- explored. The respective importance of vegetation types, elevation, slope, and soil to drive diversity across life-forms is poorly addressed. Here, we tested whether environmental variables drove local and regional plant diversity along an old tropical mountain according to the three main life-forms: graminoids, herbaceous and woody species. We sampled all Angiosperm species on 180 plots across five elevations, at the tropical old-mountain region of Serra do Cipó, South-eastern Brazil. We assessed soil, slope, and vegetation types, and calculated richness and beta-diversity, applying generalized least square models, linear mixed-models and partial Mantel tests to test for relationships. Richness of graminoids and herbaceous species increased with greater elevation and more nutrient-impooverished soils, while woody richness showed the inverse pattern. Beta-diversity was primarily driven by species turnover, correlated with elevation and soil and higher in less dominant vegetation types, with unique species. Despite the limited elevational range in these old mountains, it still played an important role in filtering woody species, while fostering graminoid and herbaceous species. Conservation and restoration actions need to foster the high regional diversity supported by the old mountain heterogeneous landscape and the diversity of life-forms, especially the dominant and highly diverse grassy component.

**Keywords:** Beta-diversity; *Campos rupestres*; Cerrado; Grassland; Herbaceous; Species turnover

## 1 Introduction

The distribution of plant diversity is shaped by a range of factors, including biotic interactions, dispersal limitation, and abiotic filtering (Kraft et al. 2014; Le Bagousse-Pinguet et al. 2017). Elevation, a classical gradient in the ecological literature, primarily driven by climatic variations, is important leading to high regional species turnover (Lomolino 2001; Fontana et al. 2020; Birks 2021). Locally, elevation might show a humped-shaped pattern or decrease local plant diversity upwards, acting as an environmental filter (Kamimura et al. 2022; Moradiet al. 2020). Different from young and snowy mountains, with sharp elevation ranges above 4,000 m, old tropical mountains often reach as high as 2000 m, and elevation might show a positive effect on diversity (e.g., Mattos et al. 2019, 2021; Silveira et al. 2019), whereas biotic interactions, dispersion limitation and other environmental variables, such as soil and vegetation types, might be also add explanation in the diversity distribution (Le- Bagousse-Pinguet et al. 2017; Abrahão et al. 2019; Silveira et al. 2019).

In old tropical mountains, soil texture and chemical composition inherited from long erosion processes, play determinant roles to govern plant occurrences and distribution (Carvalho et al. 2014; Le Stradic et al. 2015; Mattos et al. 2019, 2021). Soils are generally shallow, acidic and nutrient-poor at the mountain top, constraining species assemblages and selecting for trait adaptations to cope with soil conditions (Carvalho et al. 2014; Schaefer et al. 2016; Cunha-Blum et al. 2020). Heterogeneity of microhabitats supports a mosaic of vegetation types and high species turnover, leading to high beta- diversity (e.g., Andriano et al. 2020; Araújo et al. 2022). Vegetation types are not linearly distributed along the elevational gradient in tropical mountains but are rather shaped by local topography and soil granulometry (Carvalho et al. 2014; Le Stradic et al. 2015, 2018b; Schaefer et al. 2016), which also represent strong drivers of plant diversity.

Environmental factors driving community assemblage are different among life-forms: on one hand, woody species might be limited by elevation, low fertility, shallow soils, coarse texture, acidity, and steeper slopes (Mota et al. 2018; Mattos et al. 2019). On the other hand, graminoid and herbaceous species might cope to such edaphic conditions and occupy available niches at higher elevations and poor soils (Mattos et al. 2021; Rocha and Pinto 2021). Herbaceous species can show a variety of adaptations, such as dauciform or sand-binding roots, that increase nutrient acquisition and allow their occurrence in harsh environments, as the rocky outcrops (Oliveira et al. 2016; Abrahão et al. 2019). Moreover, different vegetation types reflect variations in soil depth and water infiltration, changing in the dominance and richness among life-forms (Carvalho et al. 2014; Le Stradic et al. 2018b; Silveira et al. 2019).

The environmental filtering hypothesis predicts higher tolerance with increased environmental stress, in which less species establishes and persist under a given level of abiotic stress (Grime 2006; Enquist et al. 2015). However, these predictions contrast with the remarkable high diversity that can be observed within certain plant communities in the tropics (Wright et al. 2004), even in stressful environments (Chesson et al. 2004; Freschet et al. 2011; Gross et al. 2013). The Espinhaço Range, located in Brazil, is the oldest South American mountain range

and support a **mosaic** of vegetation types, primarily the *campos rupestres* i.e., megadiverse tropical grasslands with scattered shrubs, above 900 m, and also two Cerrado physiognomies from the Savanna biome in the lowlands. The megadiverse flora shows than 1800 species recorded within 200 km (Alves et al. 2014; Caminha-Paiva et al. 2022). Identifying the environmental factors leading to changes in diversity is of primary importance to better understand and predict how global environmental changes will impact these plant communities (Le Bagousse-Pinguet et al. 2017).

In this study, we assessed whether vegetation types, elevation, slope, and soil impacted plant diversity along an old tropical mountain. We tested the effects of environmental variables on the local and regional diversity, for the whole pooled community and for three life-forms: graminoid, herbaceous and woody species. We expected that local richness of the woody life-form would be limited in higher elevations, steep, and poorer soils (Mota et al. 2018; Bueno et al. 2021; Gastauer et al. 2021). The opposite pattern was expected for graminoids and herbaceous species (Shaeffer et al. 2016; Mattos et al. 2019). Among the environmental drivers considered, soil and vegetation types should be more important locally, while elevation, slope, and vegetation types should be major determinants of regional diversity by supporting high species turnover.

## 2 Materials and Methods

### 2.1 Study area

We carried out the study in the Serra do Cipó mountains, at the southern portion of the Espinhaço Range (19°10' - 19°20' S and 40°30' - 40°40' W), Minas Gerais State, Brazil. The Espinhaço Range is the oldest and the second longest mountain chain in South America, extending for 1200 km SW-NE in the countryside, reaching 2100 m of altitude (Morellato and Silveira 2018; Silveira et al. 2019). Areas up to 900 m a.s.l. are mainly covered by different physiognomies of cerrado. Between 900 and 1100 m a.s.l., there is a transitional zone hosting both cerrado and the *campos rupestres*, whereas above 1100 m a.s.l. the landscape is dominated by *campo rupestre* (Silveira et al. 2019). *Campos rupestres* represent a mosaic of open vegetation types including wetlands, grasslands, and outcrops, and comprises one of the most speciose and endemic flora of the tropics (for details see Morellato and Silveira 2018; Silveira et al. 2016, 2019). The regional climate is a subtropical highland climate (Cwb), with dry and cold winters from April/May to October and wet and warm summers from October/November to April (Köppen 1948). Minimum monthly temperatures vary from 10°C to 19°C, and maximum temperatures vary from 25°C to 30°C; mean annual rainfall is 1,313 mm (Le Stradic et al. 2018a; Abrahão et al. 2019).

### 2.2 Sampling design

Five study sites were selected ranging from 824 m to 1420 m a.s.l. (see Mattos et al. 2019, 2021 for details). The sites integrate the Long-Term Ecological Research – *Campos rupestres* Serra do Cipó program (LTER-CRSC; Silveira et al. 2019). Six vegetation types were identified: four vegetation types belonging to the *campos rupestres*: rocky outcrops (RO), sandy grasslands (SG), stony grasslands (StG), and wet grasslands (WG), and two Cerrado vegetation types: cerrado shrubland (CS) and cerrado sensu stricto or cerrado woodland (CW) (Table 1, see Silveira et al. 2019).

At each site, we established four transects of 270 m, along which we systematically established nine 1 m<sup>2</sup> plots every 30 m, summing up 36 plots per site and 180 plots in total (see Mattos et al. 2019 for details). In each plot, all Angiosperm species were surveyed monthly from April to October 2016 to ensure exhaustive plant collection and guarantee species identification. Species were classified according to three life-forms: graminoid (including Poaceae, Cyperaceae, Xyridaceae, Rapateaceae), herbaceous (non-graminoid species without lignin tissue) and woody (non-graminoid species with lignin tissue) (Data uploaded to Zenodo). Species were identified with the help of specialists, using identification keys and herbarium collections (Mattos et al. 2019). Species names and synonyms have been checked with Plantminer (Carvalho et al. 2010) and follow Flora 2020 (Brazil Flora Group 2021). Herbarium specimens are lodged at the Herbarium Rioclaurensis (HRCB) of São Paulo State University.

We surveyed 454 species from 59 families in 180 plots, including all Angiosperms. The richest families were Poaceae (101 species and 1046 records), Asteraceae (40 spp.; 180 records), Cyperaceae (36 spp.; 500 records) and Xyridaceae (37 spp., 206 records). The woody species represented 157 species, herbaceous species

had 145 species, and graminoid species accounted for 138 species. The highest richness was sampled in rocky outcrops (224 species), and the lowest was sampled in wet grasslands (78 species).

**Table 1** Main characteristics of the six vegetation types considered along the environmental gradient at Serra do Cipó, Espinhaço Range, Brazil.

Vegetation types	Main characteristics
Rocky outcrops (RO)	Dominated by scattered evergreen sclerophyllous shrubs growing on soil patches formed on depressions among the bare rock surfaces (Benites et al. 2007).
Sandy grasslands (SG)	Formed by a continuous herbaceous layer, dominated by graminoids along shallow coarse soils with low water-holding capacity, imposing water deficit conditions for plants during part of the year (Le Stradic et al. 2015; Oliveira et al. 2016).
Stony grasslands (StG)	Dominated by grasses and subshrubs, found along smoother topography, with stony lag deposits and soil surfaces covered by gravel and quartz concretions (Le Stradic et al. 2015).
Cerrado Woodland (CW)	Formed by a dense woodland of fire-adapted trees and a restricted herbaceous layer. This vegetation type occurs in the lowlands over deep sandy and nutrient poor soils with high levels of aluminium saturation.
Cerrado shrubland (CS)	Dominated by an herbaceous-grassy layer with scattered small shrubs and trees. Can be found up to 1000 m of elevation.
Wet grasslands (WG)	Dominated by a tall herbaceous layer with scattered small shrubs, occurring in low lying areas where soils are waterlogged during the summer months, retaining some of the moisture during the dry season (Carvalho et al. 2012).

## 2.3 Environmental variables

For each plot, we recorded the vegetation type (Table 1), and measured the slope with an inclinometer and the geographical coordinates with a GPS (Appendix 1). We sampled soil during the rainy season, using four pooled subsamples taken at each corner of each plot from the upper layer (0 – 20 cm). Soil samples were sent to the Federal University of Lavras, in which chemical composition was determined through the variables: pH, N, P, K, Mg<sup>2+</sup>, Ca<sup>2+</sup>, Al<sup>3+</sup>, sum of bases (SB), base saturation (V%), Al saturation (m%), and cation exchange capacity (CEC), and the physical composition through the proportions of sand, silt and clay (Appendix 1, Mattos et al. 2019). Environmental variables were used as predictors, while diversity indices were used as response variables.

## 2.4 Data analysis

Locally, we calculated the species richness of all Angiosperms species for the whole community and for each life-form using the number of species with the ‘vegan’ package (Oksanen et al. 2022). Beta diversity was calculated using the ‘betapart’ package (Baselga 2012) through the Sørensen index of multiple-site dissimilarity between plots and vegetation types. We decomposed the dissimilarity for each single pair of plots, considering the number of shared and unique species in the poorest and richest plots (Baselga and Orne 2012). We analysed the relative local contribution to beta diversity (LCBD) of each vegetational type using the ‘beta.div’ function in the ‘adespatial’ package (Dray et al. 2021). LCBD quantifies the contribution of individual sites to total beta diversity within a given region, in which high values for a given site are indicative of high dissimilarity between the community and other sites in the region (Legendre and De Cáceres 2013). In our case, LCBD represents the degree of contribution of each vegetation type to the beta diversity, in terms of their species composition, indicating the ecological uniqueness of each vegetation type (Heino and Grönroos 2017). LCBD indices were tested for significance by using 999 independent permutations within the species distribution among vegetation types (Table 2).

We applied different statistical tests due differences in the variable’s natures. To answer how local richness varies among vegetation types (categorical variable), we applied linear mixed models (LMM) by using the ‘lmer’ function of the ‘lme4’ package (Bates et al. 2015), with vegetation types as fixed factors and transects as random factors, to account for different vegetation types across transects. Then, we applied Tukey post-hoc tests to evaluate differences between the vegetation types using the ‘emmeans’ package (Lenth et al. 2019).

To test whether local richness was related to elevation, slope, and soil variables (fixed factors - continuous variables), we applied generalized least squares fitted linear models (GLSs), accounting for spatial autocorrelation (Beguéria and Pueyo 2009), for the whole community and for each life-form. To remove the differences between means (variation between intercepts) and differences in variance in our models, we first standardized all variables, by using z- scores (mean of 0 and a unit standard deviation) and established the best-fitting model for each group based on the multi-model approach (Burnham and Anderson 2002) using the ‘dredge’ function of the ‘MuMIn’ package (Barton 2019). We used the lowest value of Akaike’s information criteria, corrected for small sample sizes (AICc). Finally, we assessed the percentage of variance explained by each environmental factor, using the ratio of estimate value of each factor by the total estimate in the models (Le Bagousse-Pinguet et al. 2017). We performed GLS models using the ‘gls’ function in the ‘nlme’ package (Pinheiro et al. 2021; Appendix 2).

We partitioned beta-diversity into nestedness and species turnover (Baselga 2010) considering all Angiosperms and the three life-forms. We calculated beta diversity as the breadth of groups (vegetation types) in the ordination space, using the mean distance of plot scores to group centroids in a principal coordinates analysis, so each plot had a single observation (Anderson et al. 2006). This procedure allows us to assess the multivariate homogeneity of group dispersions (variances) between plots of each vegetation type. Then, beta- diversity variation among plots and vegetation types was tested using LMMs, in which the plot distances were used as response variables, vegetation types were used as fixed effects, and transects as a random factor to account for different vegetation types across the transects. LMMs were fitted using the ‘lmer’ function of the ‘lme4’ R package (Bates et al. 2015).

To answer whether beta diversity was correlated with elevation, slope, and soil (continuous) variables, we used the distance-based approach, of comparison of matrices through partial Mantel tests (Manly 1991; Legendre 2000). Here, we assessed the relationship between the pairwise dissimilarities in the community and differences in the environment (Anderson et al. 2010), considering that the rates of species turnover can be dependent on random events modelled by space and geographical distance (Tuomisto et al. 2012). To disentangle the relative contribution

of environmental and spatial factors on beta diversity, we used variation partitioning analyses (Legendre 2000). First, we built four distance matrices based on the Euclidean distances of environmental variables and the geographical coordinates of each plot, removing highly correlated soil variables from the analyses (Pearson's  $r > |0.7|$ ) (see Mattos et al. 2019, for details). Collinearity between environmental variables was also checked according to the variance inflation factor (VIF), in which VIF of 4 or higher were omitted (Zuur et al. 2010). We then ran partial Mantel tests through 999 randomizations to test whether total beta diversity, nestedness and species turnover were correlated with the environmental distance-matrices, using geographical coordinates to account for the spatial structuring of variables (Manly 1991; Legendre 2000). All analyses were performed in R (R Development Core Team 2021).

### 3 Results

#### 3.1 Species richness in the environment

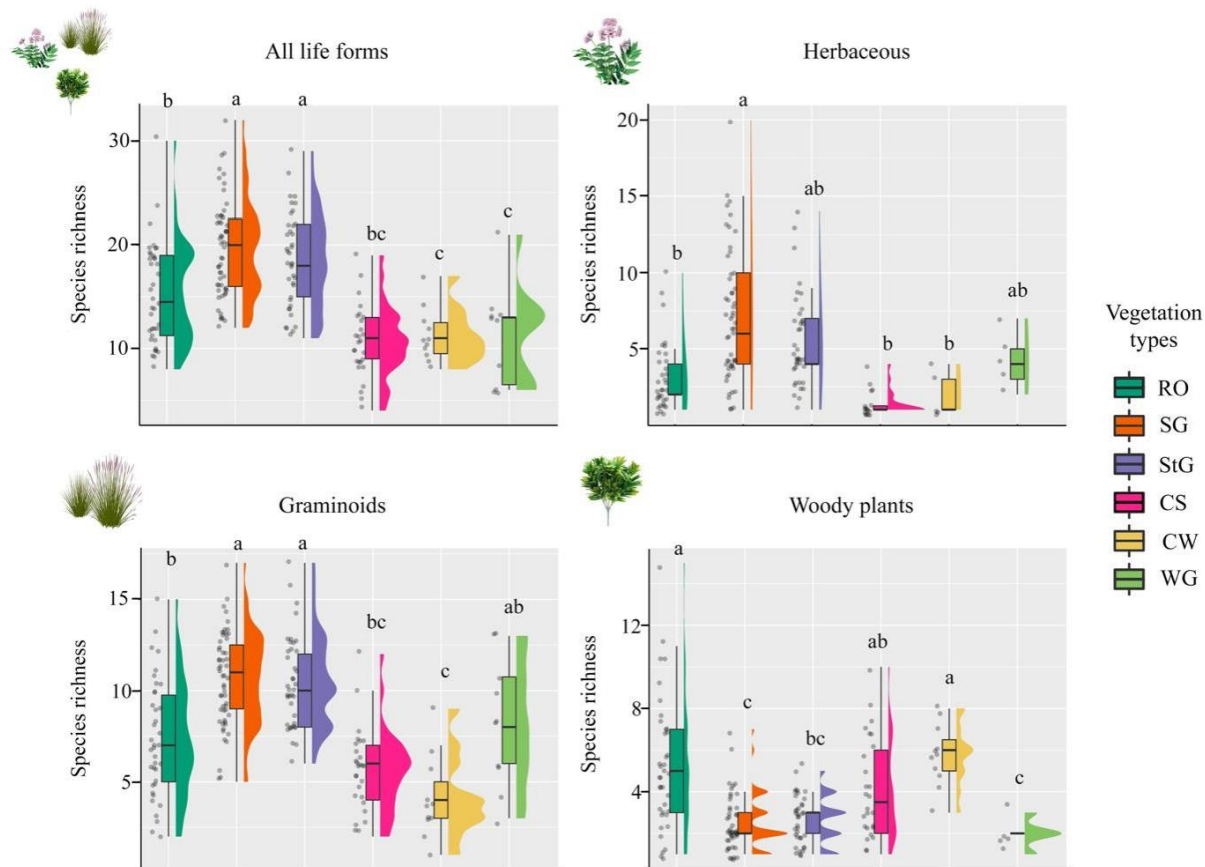
The total number of species was higher in sandy, stony and rocky outcrops, as the number of graminoid species (Fig. 1). Herbaceous species' richness was highest in stony grasslands, followed by sandy and wet grasslands, compared to the rocky outcrops and two cerrado vegetation types (Fig. 1). Whereas graminoid species occurred in all vegetation types, herbaceous species barely occurred in the cerrado (Fig. 1). Woody species were richer in the rocky outcrops and in the two cerrado vegetation types (Fig. 1).

After accounting for the spatial structure of environmental variables, richness was high overall and varied according to the life-forms. Local richness of the whole community was positively related to elevation and pH (i.e., less acidic soils) and negatively related to soil P (Fig. 2). Richness of graminoid and herbaceous species were also positively related to elevation and pH and negatively related to soil nutrients, P and K for graminoids and N for herbaceous species (Fig. 2). Woody richness followed an inversed pattern, negatively related to elevation and higher slopes, not related to soil variables (Fig. 2). The variance of richness explained by each environmental variable in the models selected is shown in the pie charts, along with the unexplained variance (Fig. 2).

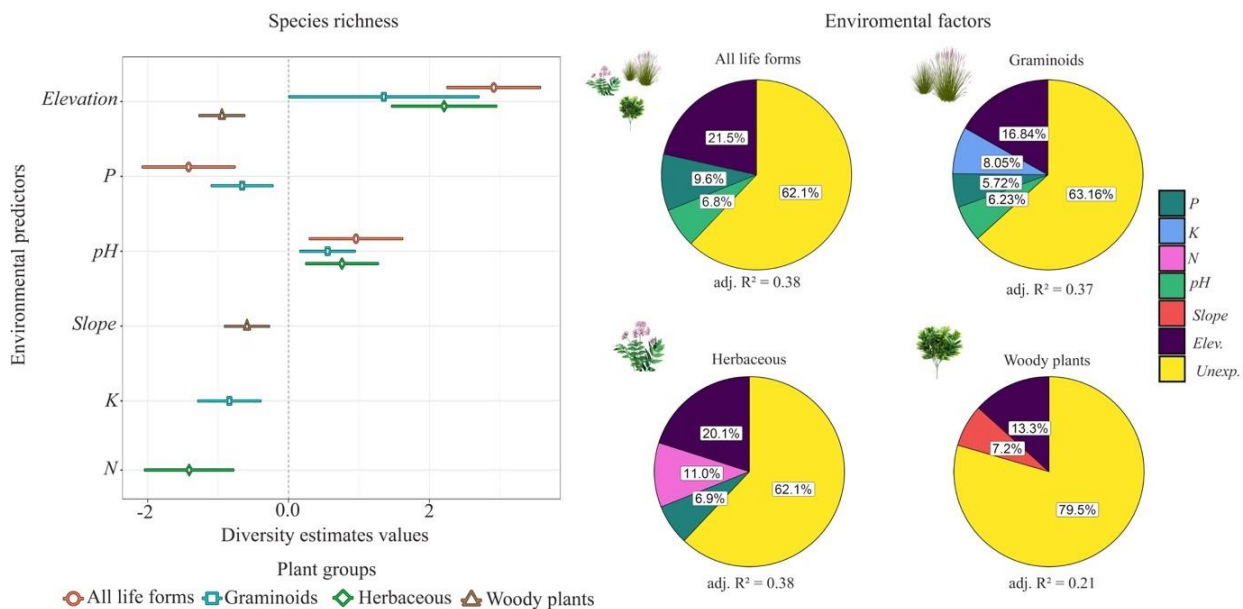
#### 3.2 Local contribution to regional diversity and shared species

We analysed the number of shared species between vegetation types through LCBD, to understand the species exchange among vegetation types, and the contribution of unique species to regional diversity. The three *campos rupestres* dominant vegetation types i.e., stony and sandy grasslands, and rocky outcrops, shared more species (Fig. 3). Stony and sandy grasslands were an important pool of species for graminoid and herbaceous species (Fig. 3). Both vegetations showed relatively low proportion of unique species (15 and 25%, respectively, Fig. 3). Rocky outcrops were rich in species, shared many species with other vegetation types (154 species), but also presented many unique species (31%), acting as an important source of diversity of all life-forms (Fig. 3). Wet grasslands and the two cerrado (CW and CS) presented a relatively low number of species (approximately 80 species) and yet hosted the largest proportions of unique species (above 30%, Fig. 3, Table 2), highly contributing to regional diversity. Cerrado shrubland and woodland shared most of the species between themselves – woody species – and less species with *campos rupestres*' vegetation types (Fig. 3).

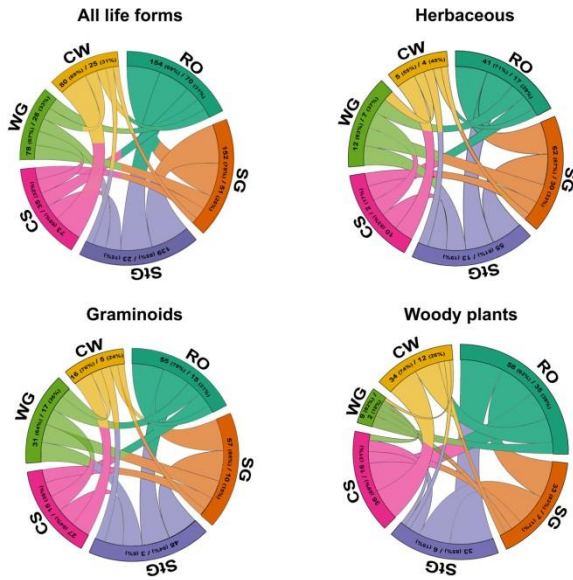
Beta diversity was primarily driven by species turnover (96.3%), positively correlated with differences in elevation (36%, Fig. 4) and in soil (23%; Fig. 4). There was very low nestedness (3.7%). Mantel tests showed that the species turnover for graminoid species drive the overall community, but there were weak correlations for herbaceous and woody species with elevation and soil dissimilarities (Table 2). Although species dissimilarity increased with variation in elevation and in soil composition, only 36% of the total turnover variation was explained by these two factors. Partial Mantel tests and combining environmental variables did not increase the strength of the relationships. At the regional scale, species turnover was significantly lower for stony and sandy grasslands compared to the other vegetation types, both considering all life-forms or only graminoid species (Fig. 5). Species turnover of herbaceous and woody species did not vary according to vegetation types (Fig. 5).



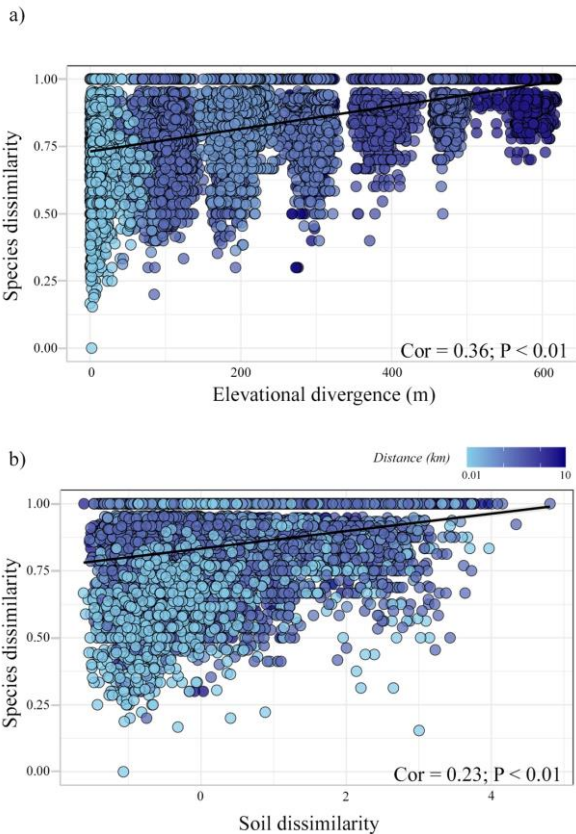
**Fig. 1** Boxplots of species richness and their respective distributions (line-charts) from the *campos rupestres* of Serra do Cipó, Brazil. Values shown to the entire plant community and split into the three main life-forms: graminoids, herbaceous, and woody species. Different letters indicate significant differences between vegetation types ( $P < 0.05$ ) after LMM analysis. Vegetation types were: RO: rocky outcrops; SG: sandy grassland; StG: stony grassland; CS: cerrado shrubland; CW = cerrado woodland; WG = wet grassland. Each boxplot displays the minimum, first quartile, median, third quartile, and maximum values of species richness per vegetation type.



**Fig. 2** Results of four generalized least squares fitted linear models (GLSs), considering the spatial autocorrelation ( $P < 0.05$ ), and relating the effects of elevation, soil, and slope on richness in the *campos rupestres* of Serra do Cipó, Espinhaço Range, Brazil. Models were built for all plant species and depicted into the three main life-forms (graminoids, herbaceous and woody species). On the left, significant effects are shown, following the GLS models ( $P < 0.05$ ). Positive effects are on the right, and negative effects are on the left side of the dashed line. On the right side, the relative importances of environmental variables of each model are shown in percentages: Elev. = Elevation, soil P – phosphorus, pH, slope, soil K – potassium, and soil N – nitrogen, Unexp. = Unexplained variance.

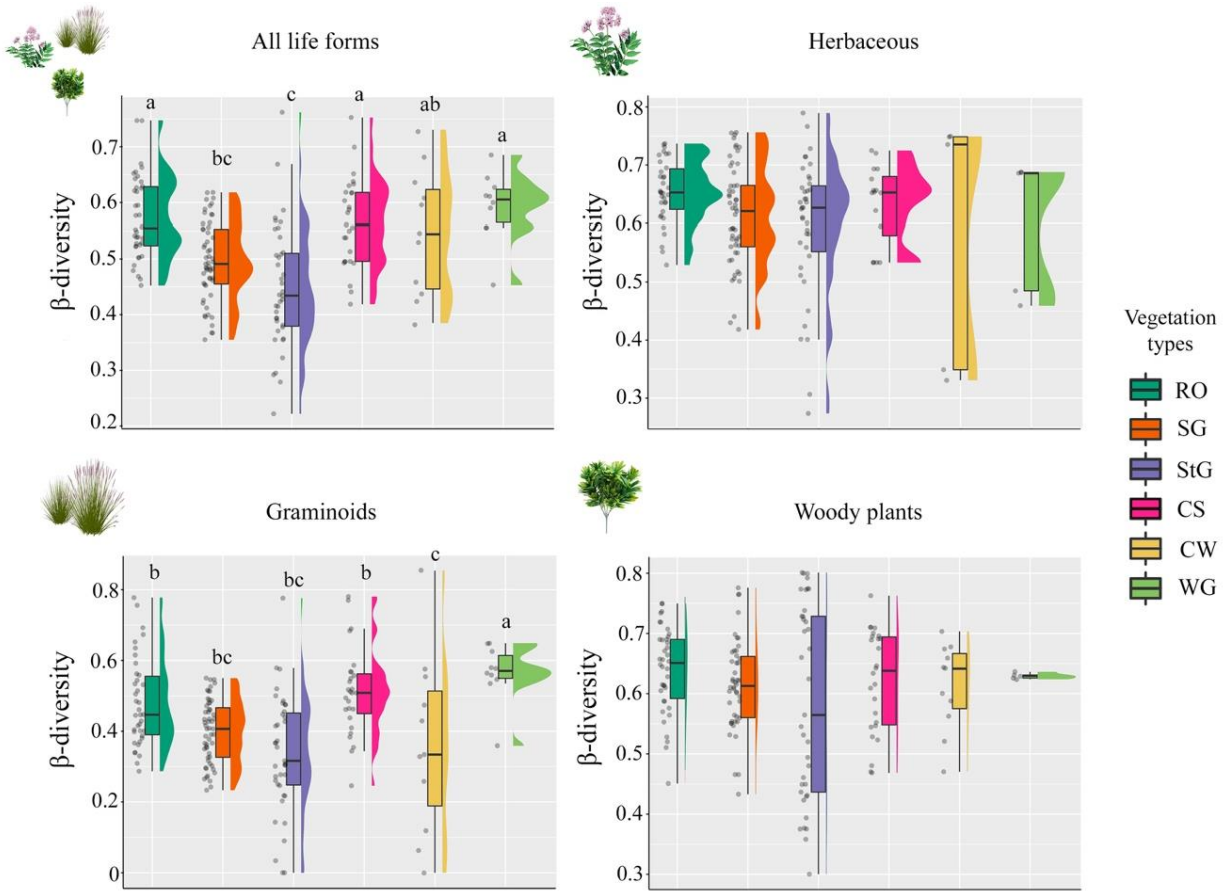


**Fig. 3** Chord diagram showing the shared species (non-unique species) among vegetation types of Serra do Cipó, Espinhaço Range, Brazil. The number species and the unique species (and associated percentages) are presented to the overall community and to three life-forms: graminoids, herbaceous and woody species. The proportion of species between each pair of vegetation types is represented by the width of the edges connecting that pair. Vegetation types: RO: rocky outcrops; SG: sandy grassland; StG: stony grassland; CS: cerrado shrubland; WG = wet grassland; CW = cerrado woodland.



**Fig. 4** Linear relationships between the distance matrices of (a) elevation divergence (m) and (b) soil dissimilarity (considering chemical and physical variables, uncorrelated and standardized, see Methods for further information) and the species dissimilarity (species turnover, the main component of the beta- diversity) of the *campos rupestres* of Serra do Cipó, Espinhaço Range, Brazil. Partial Mantel tests after 999 permutations were used to test for these relationships (correlation and  $P$  values shown), using a distance- matrix with the coordinates of each plot to account for the spatial structuring of environmental variables. The spatial distance between plots is shown in blue intensity, varying from 0.01 to 10 km. Results depicted into the three life-forms are shown in [Table 2](#).





**Fig. 5** Boxplots indicating the variation in composition dissimilarity associated with species turnover, i.e., the major component of beta-diversity, of the six vegetation types of the *campos rupestres* of Serra do Cipó, Espinhaço Range, Brazil. Significant differences after LLM analysis are indicated by different letters ( $P < 0.05$ ). Analyses were done to the pooled community, and depicted into three life-forms: graminoids, herbaceous and woody species, and for vegetation types: RO: rocky outcrops; SG: sandy grassland; StG: stony grassland; CS: cerrado shrubland; CW = cerrado woodland; WG = wet grassland.

**Table 2** (a) Local contribution to the overall beta-diversity (LCBD, values range from 0 to 1) of each of the six vegetation types. RO: rocky outcrops; SG: sandy grassland; StG: stony grassland; CS: cerrado shrubland; CW = cerrado woodland; WG = wet grassland; Elevation: Elev.. Significant differences ( $P < 0.05$ ) are highlighted with \*, and indicate increased values tested against the null distribution. (b) Coefficient of correlation from partial Mantel tests ( $r$ ) between beta diversity and elevation, slope, and soil variables corrected for the spatial structuring of the environment, and their respective  $P$  values. Analyses were applied to the whole community and to each of the three life-forms: graminoids, herbaceous and woody species. Grouping environmental variables did not increase the Mantel –  $r$  coefficients in the analysis, so only single correlations are shown.

(a)					(b)				
LCBD	Comm.	Graminoids	Herbaceous	Woody	Beta-Div	Comm.	Graminoids	Herbaceous	Woody
RO	0.14	0.15	0.16	0.14	Elev. $r$	0.36	0.34	0.10	0.14
SG	0.14	0.13	0.13	0.15	Elev. $P$	< 0.001*	< 0.001*	< 0.001*	< 0.001*
StG	0.15	0.12	0.14	0.15	Soil $r$	0.24	0.21	0.09	0.10
CS	0.17	0.18	0.17	0.17	Soil $P$	< 0.001*	< 0.001*	< 0.001*	< 0.001*
CW	0.21*	0.22*	0.20*	0.20*	Slope $r$	0.069	0.033	0.029	0.068
WG	0.19*	0.20*	0.20*	0.19*	Slope $P$	0.03*	0.172	0.113	0.01*

## 4 Discussion

Along old tropical mountains at the Serra do Cipó, not only elevation, but also soil, slope, and vegetation types drove plant species diversity. The heterogeneity of vegetation types is an important source of diversity, emphasizing the role of the environmental mosaic to promote biodiversity at regional scale (Marx et al. 2017; Vasconcellos et al. 2020; Qian et al. 2021). Drivers of diversity and the direction of the patterns were different for graminoid, herbaceous or woody species. Richness of graminoid and herbaceous species increased with elevation and nutrient impoverished soils, contrary to woody species. Both graminoid and herbaceous species represented a large share (64.3%) of the plant species diversity regionally, highlighting their extreme relevance for the

conservation of open ecosystems (Mattos et al. 2019, 2021), especially considering current anthropogenic threats (Fernandes et al. 2016, 2020). A combined effect of elevation, edaphic conditions and vegetation types supports the high biodiversity in the *campos rupestres* and might have shaped its long evolution (Mattos et al. 2019, 2021; Vasconcellos et al. 2020). Constrained edaphic conditions at higher elevations, including shallow, highly leached, and nutrient-poor soils, are related to plant species' specializations, such as *Vellozia* roots capability of dissolving quartzite rocks (Abrahão et al. 2020; Cunha-Blum et al. 2020). Increased fertility is expected to decrease species richness due to the dominance of a few species (Venterink 2011), but in low productivity sites, extremely constrained soil conditions may represent a major species filter, reducing herbaceous' species dominance and promoting richness. In *campos rupestres*, plant species are highly adapted to extremely low soil P content and even show P-toxicity symptoms (Lambert et al. 2010; Oliveira et al. 2015). Nutrient-poor sites at high elevations might have acted as refuge in the past, and play the role of islands nowadays, favoring in-situ speciation and species diversity (Vasconcelos et al. 2020). Whereas graminoid and herbaceous species were able to overcome these restrictions, as we observed increasing richness under low P, N and K (see also Oliveira et al. 2015; Abrahão et al. 2020), constraining edaphic conditions were unfavorable for woody species.

Vegetation types contributed differently to local and regional plant diversity and among life-forms. While the most common vegetation types, stony and sandy grasslands, were locally richest, they contributed the least to the regional species turnover, hosting fewer unique species. Sandy and stony grasslands are the matrix of *campos rupestres* and represent the largest pools of species, while cerrados, rocky outcrops and wet grasslands retained a larger proportion of unique species, contributing to the high regional diversity. Both wet grasslands and rocky outcrops correspond to habitats within the matrix of grasslands, with lower fire frequency, acting as islands for speciation (Marx et al. 2017; Vasconcellos et al. 2020). Wet grasslands show specific edaphic conditions, including coarser texture and regular flooding, that might select for singular environmental pressure to species establishment. In the cerrado, relatively higher fertility, especially of N and P, favor shrubs and trees, not typical of the *campos rupestres sensu stricto* (Silveira et al. 2016). The rocky outcrops presented highest woody richness, and a relatively high regional diversity for the pooled community, as for graminoid and herbaceous species. This vegetation type, typical of *campos rupestres* and of the landscape of Espinhaço range (Morellato and Silveira 2018), may act as a refugium for species sensitive to environmental disturbances of surrounding grasslands, such as fire, explaining the high species richness and uniqueness of this habitat (Mattos et al. 2019, 2021; Vasconcellos et al. 2020).

## 5 Conclusion

By depicting the diversity of the vascular plant communities into life-forms, we show that the three life-forms, i.e. graminoid, herbaceous and woody species, respond differently to the environmental gradients and within the vegetation types. We suggest that biotic interactions and dispersal limitation may play additional roles explaining species richness and turnover (Carstensen et al. 2018; Vasconcellos et al. 2020; Mattos et al. 2021; Monteiro et al. 2021). Importantly, the heterogeneity of vegetation types within the landscape allows high regional species turnover, while local richness was largely determined by graminoid species.

Old tropical mountains must be considered in the present scenario of climate change and anthropogenic impacts on biodiversity (Vačkář et al. 2012; Fernandes et al. 2020; Pörtner et al. 2021), which are leading to shifts in the environmental ranges of species and life-forms, impacting the overall mountain biodiversity (Zu et al. 2021). We argue that conservation needs to be taken at large scale, accounting for the diverse responses of life-forms to the environment, to ensure effective practices. We highlight the urgent need to account for the dominant and highly diverse grassy component for any conservation, management, and restoration measure. Also, we support the plea for conserving the entire elevation gradient (Fernandes et al. 2018, 2020) and a large variety of habitats and landscapes (Monteiro et al. 2020; Araújo et al. 2022) to ensure proper conservation of all plant life-forms and include spatially-restricted and endemic species, which would, otherwise, be lost to multiple anthropogenic threats.

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## Author Contribution

PPL and LPCM conceptualized the study, LPCM provided supervision and acquired funding, MGCC, ASS, SLS and JSM collected the data, PPL and VAK provided formal analysis and figures, all authors wrote the original draft and revisions of the manuscript and PPL edited the final manuscript.

## Ethics Declaration

**Data Availability:** Data is available at Zenodo, upon <https://doi.org/10.5281/zenodo.6994853>. The data presented in this study are available on request from the corresponding author.

**Conflict of Interest:** The authors declare no conflict of interest.

## Electronic supplementary material

Supplementary material (Appendixes 1-2) is available in the online version of this article at <https://doi.org/10.1007/s11629-022-7838-z>.

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