Plant phylogenetic diversity of tropical mountaintop rocky grasslands: local and regional constraints

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Abstract Mountains are interesting systems for studying patterns of diversity distribution and the role of environmental filters and competition on community assembly. According to the phylogenetic niche conservatism theory, the co-occurrence of closely related species might indicate that environmental filters are more important than competition when structuring communities in time and space. We investigated the patterns of phylogenetic diversity and the influence of environmental filters in the Brazilian rocky grasslands and tested the influence of phylogenetic niche conservatism. We placed 180 plots of 1 m^2 in five sites along an altitudinal gradient at the Cipó Mountains (Espinhaço Range, southeastern Brazil) and surveyed all vascular plant species and edaphic variables. We assessed the phylogenetic diversity of the communities by calculating the phylogenetic species variability and phylogenetic species richness. These measures were related to altitude and the edaphic variables through a principal component analysis and regressions. Phylogenetic species variability decreased towards higher altitudes and less fertile sites, whereas phylogenetic species richness increased. Thus, the number of species and the degree of phylogenetic clustering increased with increasing altitude, suggesting that the intensity of abiotic factors acting as environmental filters increased with altitude and could be constraining species in the community to a smaller number of clades.

Keywords Cerrado · Community assembly rules · Elevational gradient · Serra do Cipó · Mountain grasslands · Rupestrian grasslands

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Introduction

It has long been recognized that biological communities are structured along habitats (Lomolino 2001), which generally influences the species distribution. For example, species richness along latitudes and altitudes are probably the oldest known patterns of species distribution in the field of Ecology, a phenomenon studied by Alexander von Humboldt, Alfred Wallace, and Charles Darwin back in the 1800s

(Lomolino 2001). However, we still lack predictive power in understanding the evolutionary processes driving these patterns (Ricklefs 2004). Measuring biological diversity has also been a widely used approach for investigating communities, and a simple way to do that is by counting the number of species (Magurran 2004). More recently, biological diversity has been quantified by estimating the phylogenetic diversity of a community, a measure which incorporates the evolutionary history of a species and can be calculated using the current molecular and analytical tools for generating phylogenies (Webb et al. 2002).

Evolutionary history has been extensively used in the fields of community ecology, macroecology, and conservation biology (Webb et al. 2002; Parra et al. 2010). Nowadays, it is easier to study the evolutionary relationships of species due to many different methods to build megaphylogenies for a variety of taxonomic groups and to analyze phylogenetic data (Smith et al. 2009; Leibold et al. 2010; Beaulieu et al. 2012). In this sense, new metrics and indices have arisen in the past few decades (Tucker et al. 2017), such as Faith's phylogenetic diversity (Faith 1992), mean pairwise distance (Clarke and Warwick 1998; Webb et al. 2002), and net relatedness index (Webb 2000). Helmus et al. (2007a) proposed two metrics to estimate phylogenetic diversity: phylogenetic species variability (PSV) and phylogenetic species richness (PSR). These measures are intuitive because they account only for the variance of a neutral trait shared by all species in the community, thereby providing the evolutionary relatedness among species in an easy statistical approach (Helmus et al. 2007a).

Ecological communities are assemblages of co-occurring species and are mainly structured and ruled by evolutionary processes, which can occur at different temporal and spatial scales (Parra et al. 2010). Density-dependent interactions, such as competition, and abiotic factors, such as environmental filtering, act more at local scales, whereas extinction, speciation, and trait evolution act more regionally and for longer periods (Cavender-Bares et al. 2009). When we consider that assemblages of co-occurring species are predicted by their interactions and by the environment, we assume the concept of niche, the idea that species have specific environment requirements and constraints leading to their survival and relationships with other species (Hutchinson 1957). Niches tend to be conserved over time, and phylogenetically related species tend to be ecologically similar, which is known as "phylogenetic niche conservatism" (Losos 2008). Niche conservatism postulates that ecological differentiation between related species occurs less frequently than it would be expected if ecological diversification had occurred without evolutionary constraints (Losos 2008).

Environmental gradients are good models for assessing changes in community composition and structure and the evolutionary processes driving patterns of species diversity. Altitudinal gradients, as latitudinal ones, present change in temperature as a primary factor acting on the patterns of biodiversity (Mittelbach et al. 2007) and allow us to study changes in diversity at a smaller scale. In southeastern Brazil, the Espinhaço Range is one of the largest mountain chains and is among the most ancient landscapes on Earth (Schaefer et al. 2016; Silveira et al. 2016), being particularly suitable for this kind of study. In this mountainous landscape, the co-occurrence of different vegetation types is defined at local scales by edaphic factors, such as nutrient content, soil depth, and rockiness (Oliveira et al. 2015; Stradic et al. 2015, 2018; Schaefer et al. 2016). At regional scales, however, they are defined by changes in altitude-related factors, such as temperature, precipitation, wind speed, and drainage (Giulietti et al. 1987; Fernandes 2016; Shefer et al. 2016; Silveira et al. 2019). The higher the altitude, the harsher the environment and, therefore, the higher the intensity of abiotic factors acting as environmental filters, which can restrain the species of a community to a smaller number of clades (Fernandes 2016; Silveira et al. 2016; Abrahão et al. 2018).

Many studies have addressed the relationship between altitude and patterns of species diversity. Whereas some quantitative studies showed that diversity may decrease with increasing altitude (Terborgh 1977), others found a pattern called the "mid-domain effect" (Rahbek 1995), resulting from a unimodal curve in species richness (Kromer et al. 2005; Samson et al. 2006). Qian et al. (2014), analyzed the phylogenetic diversity of plant communities along an altitudinal gradient and showed that communities were more phylogenetically clustered at higher altitudes and more dispersed at lower altitudes, in contrast to the general published findings (Bryant et al. 2008). Here, we investigated the local patterns of phylogenetic diversity and the influence of edaphic factors as

key environmental filters along an altitudinal gradient in the Cipó Mountains. Our study is the first to include grasses and sedges in addition to other plant life forms characteristic of the rocky grasslands. Previous findings in altitudinal gradients (Rahbek 1995; McCain and Grytnes 2010; Smith et al. 2014) stated a uniform decreasing trend in species diversity along elevation or, in other times, a mid-domain pattern. Because of that, we expected that phylogenetic diversity of vascular flora—as estimated by the phylogenetic species variability and richness (Helmus et al. 2007a)—would decrease with increasing altitude due to the increasing intensity of environmental filters (Zhang et al. 2016).

Methods

Study area

The study was conducted in the Cipó Mountains, the local designation of the mountains belonging to the southern portion of the Espinhaço Range (19° 10′–20′ S and 43° 30′–40′ W), Minas Gerais State, southeastern Brazil (Fig. 1). The area comprises de Serra do Cipó National Park and its buffer zone, Morro da Pedreira Environmental Protection Area. Soils at the Cipó Mountains are usually very shallow, acidic, with low nutrient content and high aluminum toxicity, over quartzite and sandstone substrates (Negreiros et al. 2013; Stradic et al. 2018). Regional climate is classified as Cwa according to Köppen (1931), with cold, dry winters and warm, wet summers. Minimum monthly temperatures varied from 10 to 19 °C, while maximum monthly temperatures vary from 25 to 30 °C; mean annual rainfall is 1313 mm (Abrahão et al. 2018).

The landscape is strongly eroded and has evolved under extreme weathering and prolonged tectonic stability (Silveira et al. 2016; Schaefer et al. 2016). Mountaintops are covered by a vegetation complex that holds a high diversity of species (1590 species locally in the Cipó mountains) and a high level of endemism (e.g., 70% rate for the Velloziaceae in the Minas Gerais portion of Espinhaço Range, see Mello-Silva 1989). There is also great variation of vegetation types (5), including the so-called "campo rupestre"—also known as rupestrian grassland, or rocky grassland (Fernandes 2016; Silveira et al. 2016, 2019). The

cerrado predominates at altitudes lower than 900 m, and the rocky grassland dominates in altitudes higher than 1000 m; these two types are separated by a transition zone at around 900 m (Fernandes 2016). Some sedimentary rocks from the Espinhaço Range are dated from the Precambrian (Alkmin 2012) and, because of that, the rocky grassland has been considered an "old, climatically buffered, infertile landscape" (Silveira et al. 2016), a concept that describes ancient communities with high levels of species richness, climate stability, and infertile soils (Hopper 2009). The Cipó Mountains harbors at least 1590 angiosperm species (Silveira et al. 2016), presenting one of highest levels of endemism in the Espinhaço Range (Echternacht et al. 2011; Colli-Silva et al. 2019).

Sampling design

At the study area, we assigned five study sites distributed in an altitudinal range from 800 to 1400 m as follows: (1) "Rio Cipó", 821 masl, with predominance of cerrado; (2) "Cedro", 1101 masl; (3) "Pedra do Elefante", 1255 masl; (4) "Quadrante 16", 1303 masl with predominance of rocky grassland; and (5) "Alto Palácio", 1420 masl, with predominance of high altitude grassland (see Rocha et al. 2016 for descriptions). The sites represent a gradient of altitude-related variables estimated by the local weather stations at each site (Fernandes 2016): temperature decreases while insolation, and relative humidity increase with altitude. During 2016, four 270-m-long transects were established at each site; along each site, we systematically set up nine 1 m^2 plots, every 30 m (Fig. 1), summing 36 plots per site and a total of 180 plots in the area. Geographical coordinates were recorded, altitude and slope of each plot were measured, and all vascular plant species within each 1 m^2 plot were sampled. The superficial soil samples were collected in the four corners of each plot. The soil samples were analyzed at the Federal University of Lavras, for measures of pH, N, P, K, Mg^{2+}, Ca^{2+}, Al^{3+}, sum of bases, base saturation, aluminum saturation, cation exchange capacity, and the proportions of sand, silt, and clay (Arruda et al. 2014). We identified the plant species using identification keys (Mamede 1987; Wanderley 2011; Silva-Luz et al. 2012; Borges and Pirani 2013; Rando et al. 2013; Pscheidt 2015), comparing the vouchers with the
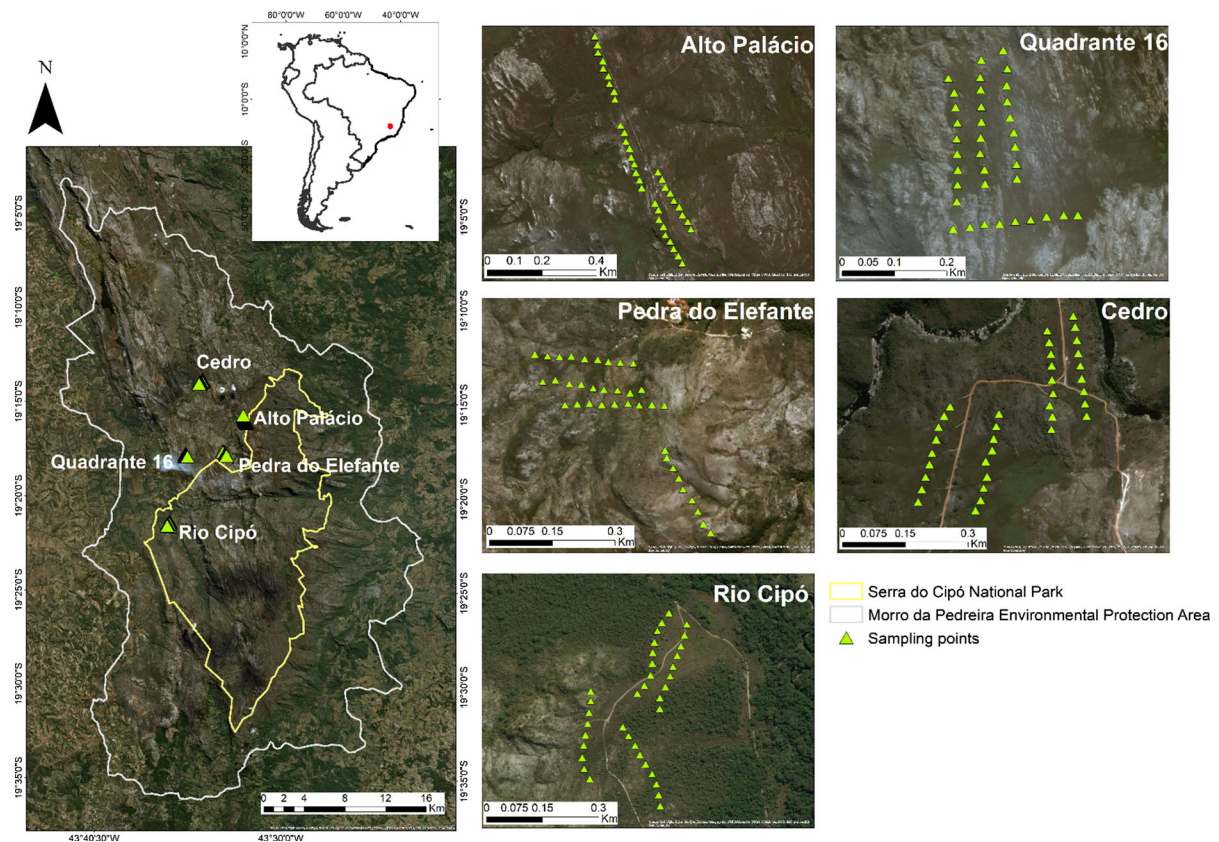
Fig. 1 Location of the five study sites along the altitudinal gradient of the Cipó Mountains (Serra do Cipó National Park and the Morro da Pedreira Environmental Protection Area), Espinhaço range, Minas Gerais State, southeastern Brazil. Alto Palácio—1420 m; Quadrante 16—1303 m; Pedra do Elefante—1255 m; Cedro—1101 m; Rio Cipó—821 m

reference collections, and with the help of taxonomists. Vouchers for the reproductive samples collected were lodged at the Herbarium Rioclarense (HRCB) of the São Paulo State University.

Statistical analysis

We checked species names on Plantminer (Carvalho et al. 2010) to look for synonyms and, then, built the phylogenetic tree with PhyloMaker (Qian and Jin 2016). We calculated two metrics of phylogenetic diversity (Helmus et al. 2007a, b): phylogenetic species variability (PSV) and phylogenetic species richness (PSR). PSV is independent of the species number and quantifies how the phylogenetic relatedness decreases the variance of some non-specified neutral trait shared by all species in the samples (Helmus et al. 2007a, b), representing the mean phylogenetic difference among the taxa in a community (Tucker et al. 2017). PSR considers this phylogenetic difference among taxa but includes the number of species, so it is simply the PSV multiplied by the number of species (Helmus et al. 2007a, b). PSR represents richness accounting for how much of biodiversity is added to the community considering more phylogenetically distinct species (Helmus et al. 2007a, b). These two metrics have the advantage of providing an integrated approach, with well-defined statistical properties (Helmus et al. 2007a, b). In addition, they allow an easy evaluation of the specific contributions to the different aspects of phylogenetic structure and facilitate the integration of phylogenetic information and strategies to biodiversity conservation (Helmus et al. 2007a, b).

Data were analyzed using Pearson's correlation analyses to select environmental variables that were not correlated to each other ($R < |0.7|$). Selected variables included the following: altitude, slope, pH,

N, P, K, Al^{3+}, sum of bases, base saturation, and the proportions of sand, silt, and clay. Akaike's Information Criterion (AIC) was used a priori to select the best model of variables. Our main hypothesis was that both phylogenetic richness and variability would decrease with increasing altitude—an expected pattern considering the strong pressure of environmental filtering in the area. To investigate this hypothesis, a principal component analysis was generated, followed by regression models that fit the indices of PSV and PSR into both axes of the PCA. Analysis were carried out in R (R Development Core Team 2018) and maps were built in ArcGIS (ESRI 2017).

Results

We surveyed 438 plant species, comprising 62 angiosperm families (Appendix 1 in Supplementary material). The most abundant families were Poaceae (103 species), Asteraceae (41), Xyridaceae (35), Cyperaceae (31), Eriocaulaceae (23), Melastomataceae (21), Fabaceae (19), and Velloziaceae (15) (see Table 1). Mean PSV was 0.70 in Rio Cipó (821 m), 0.57 in Cedro (1101 m), 0.65 in Pedra do Elefante (1255 m), 0.63 in Quadrante 16 (1303 m), and 0.60 in Alto Palácio (1420 masl). Mean PSR was 7.45 in Rio Cipó, 8.01 in Cedro, 12.11 in Pedra do Elefante, 11.03 in Quadrante 16, and 11.65 in Alto Palácio (Fig. 2). While the relationships are weak, PSV decreased significantly with increasing altitude ($P < 0.001$, $R^2_{adj} = 0.04$) and PSR increased with increasing altitude ($P < 0.001$, $R^2_{adj} = 0.17$).

The first component of the PCA ordination explained 37.7% of the variation and was positively related with altitude (Fig. 3, Table 2). The second component explained an additional 24.5% and was negatively related with soil fertility (Fig. 3, Table 2). Regression coefficients against PSV (Fig. 4, Table 3) presented a significant relationship ($R^2_{adj} = 0.118$, $P < 0.0001$) with PC1 ($P < 0.001$) but not with PC2 ($P < 1$). Regression coefficients against PSR (Fig. 4, Table 3) presented a significant relationship ($R^2_{adj} = 0.212$, $P < 0.0001$) with both PC1 ($P < 0.001$) and PC2 ($P < 0.001$).

Discussion

Our sample effort surveyed 438 species, representing well the diversity of plant species from the Cipó Mountains and the Espinhaço Range, comprising approximately 30% of the known Cipó flora (Giulietti et al. 1987; Pirani et al. 2003; Silveira et al. 2016). The total number of sampled species was, however, 63.5% higher than the 278 species sampled in a previous systematic survey at the same area and study sites (Mota et al. 2018), because all life forms sampling included graminoid species, the dominant life forms across rocky grasslands, and not just larger herbs and woody plants. The richest families we sampled—Poaceae (103 species), Asteraceae (41), Xyridaceae (35), Cyperaceae (31), and Eriocaulaceae (23)—were different from the study that did not sample graminoids, which found Asteraceae (43), Melastomataceae (34), Fabaceae (29), Eriocaulaceae, and Velloziaceae (21 species each) (Mota et al. 2018). Therefore, our all-inclusive survey demonstrated that the most species rich family on rocky grasslands are grasses, sedges, and other herbaceous plants. Poaceae

Table 1 Specifications for all five sampled sites at Cipó Mountains, Espinhaço Range, Southeastern Brazil, including altitude, slope averages, geographical coordinates, number of species and families, and growth forms

Site	Rio Cipó	Cedro	Pedra do Elefante	Quadrante 16	Alto Palácio
Altitude (m)	821	1101	1255	1303	1420
X (utm)	646,232	649,461	651,819	647,995	653,791
Y (utm)	7,858,989	7,872,971	7,866,048	7,865,950	7,869,121
Slope	− 6.12	− 7.03	− 18.20	− 6.14	− 7.78
Species	145	135	183	143	132
Families	40	34	36	36	27
Grass	40	35	37	32	29
Herb	27	52	84	74	80
Shrub	48	38	55	36	21
Tree	30	10	7	1	2
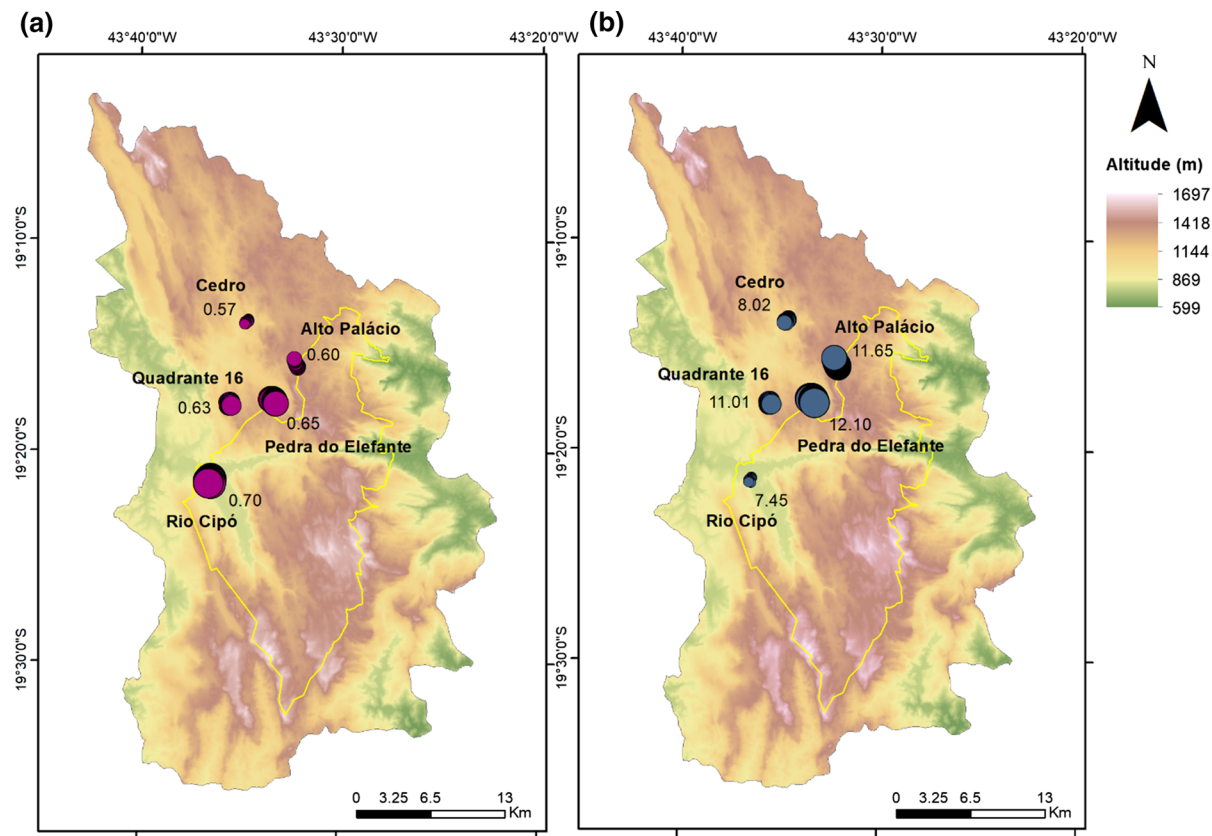
Fig. 2 Altitudinal maps showing mean values of **a** phylogenetic species variability and **b** phylogenetic species richness at the Cipó Mountains, southeastern Brazil. (1) Rio Cipó—821 m; (2) Cedro—1101 m; (3) Pedra do Elefante—1255 m; (4) Quadrante 16—1303 m; (5) Alto Palácio—1420 m

accounted for more than the double the species than the second richest family, Asteraceae. That is the expected result for a grassland-dominated landscape. Previous surveys on stone and sandy grasslands also highlight monocots as the dominant families (Stradic et al. 2015, 2018).

The altitudinal gradient in Cipó Mountains is convenient for studying changes in community assembly, mainly because climate and soil have a direct effect on how the mosaics of microhabitats are shaped and how the different vegetation physiognomies are distributed (Stradic et al. 2015; Silveira et al. 2016, 2019). The Espinhaço Range also accounts for a wide latitudinal and altitudinal variation, providing habitat heterogeneity and isolation among vegetation islands (Giulietti et al. 1987; Silveira et al. 2016) or provinces (Colli-Silva et al. 2019), influencing its high floristic richness. In this study, phylogenetic diversity was linked to environmental

constraints, such as nutrients (nitrogen, phosphorus, potassium, and aluminum), levels of sand, silt, and clay, pH and slope. PSV, which accounts for the relatedness among species and for pure phylogenetic signal (Helmus et al. 2007a, b), decreased with both axes of the principal component analysis. The first component was positively related with altitude, and therefore phylogenetic species variability decreased with increasing altitude. The second component showed a fertility gradient (less fertile sites with higher scores), thus PSV decreased towards infertile sites. On the other hand, PSR increased along PC1 and PC2 axes. Phylogenetic species richness, in this way, will be higher in more elevated and less fertile areas of the mountains. Our suggestion for this finding is the presence of phylogenetic niche conservatism, considering the decreasing pattern of phylogenetic species variability and assuming that traits are conserved for lineages in rocky grassland (Miazaki et al. 2015;

Fig. 3 Principal component analysis on the 12 selected environmental variables (arrows) collected along the altitudinal gradient of the Cipó Mountains, southeastern Brazil. The first component explained 37.7% and was mostly related with altitude. The second component explained an additional 24.5% of the variation was mostly a fertility gradient, with more fertile presenting negative scores
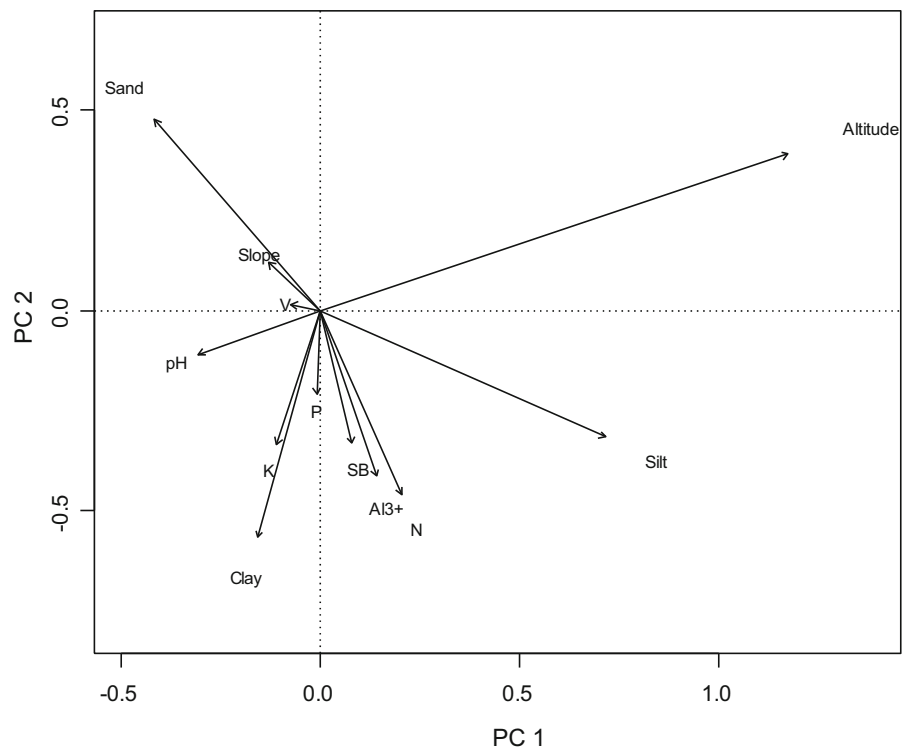

Table 2 Proportions of explanation on the two most explanatory ordination axes of the PCA with environmental variables

	PC1	PC2
Proportion explained	0.38	0.25
Altitude	1.38	0.46
Slope	− 0.15	0.14
N	0.24	− 0.54
P	− 0.01	− 0.25
K	− 0.13	− 0.40
pH	− 0.36	− 0.13
Al3+	0.17	− 0.49
SB	0.09	− 0.39
V	− 0.09	0.02
Sand	− 0.49	0.56
Silt	0.84	− 0.37
Clay	− 0.18	− 0.67

Pugliesi and Rapini 2015). We argue that severe environments with strong environmental filtering—expected to happen in more elevated areas—can constrain lineages that could potentially colonize them. However, the pattern found for phylogenetic species richness—increasing towards high elevations with less fertile sites—suggests that a higher number of species in these selected clades occur in an aggregated conformation in these particular sites.

Some studies have already found evidence to support phylogenetic clustering and niche conservatism in rocky grasslands (Miazaki et al. 2015; Pugliesi and Rapini 2015) and in high locations (Machac et al. 2011; Qian et al. 2014; Zhang et al. 2016). Here, although we cannot confirm niche conservatism, we argue in favor of it and the harsh environmental filtering. Although altitudinal gradients are expected to have a decreasing or a mid-peak pattern in species richness (Rahbek 1995; McCain and Grytnes 2010; Smith et al. 2014), we found that incorporating phylogenetic information changes this scenario; in our case, to the opposite pattern, increasing the species richness within conserved clades. What is known about the evolution of the rocky grassland flora was corroborated by our results, which supported niche conservatism and older lineages evolving in situ (Miazaki et al. 2015). Gondwanan families, for example, play an important role in the composition
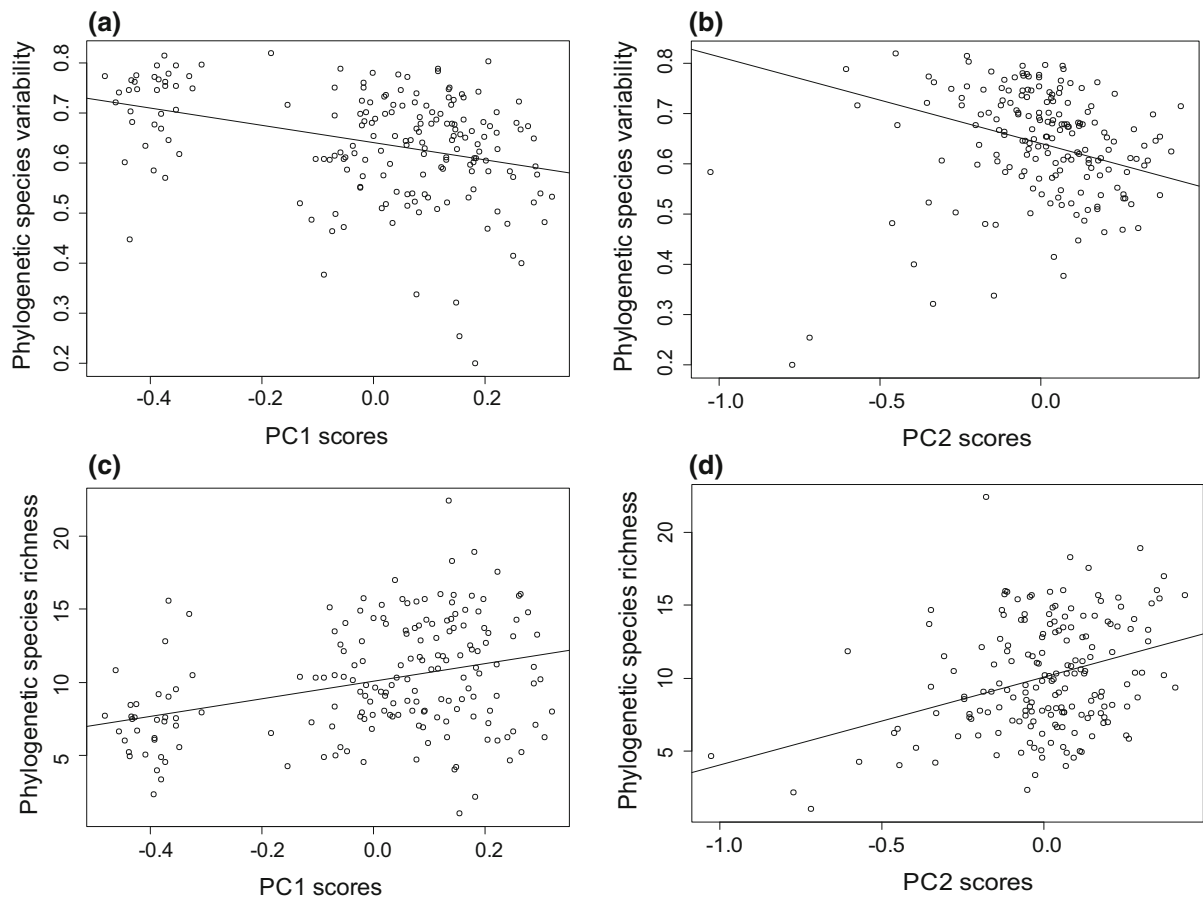
Fig. 4 Phylogenetic species variability in relation to the PCA scores from axis 1 (**a**) and axis 2 (**b**) and phylogenetic species richness in relation to the PCA scores from axis 1 (**c**) and axis 2 (**d**) along the altitudinal gradient of the Cipó Mountains, southeastern Brazil

Table 3 Regression coefficients for both PSV and PSR against the first two most explanatory axes of the PCA

	PSR	PSV
R^2	0.22	0.12
Adjusted R^2	0.21	0.11
F-Statistic	25.20	11.85
P value	< 0.01	< 0.01
PC1 axis		
Estimate	6.013	− 0.172
Std. error	1.167	0.035
P value	< 0.01	< 0.01
PC2 axis		
Estimate	5.701	0.003
Std. error	1.167	0.035
P value	< 0.01	0.93

of the Cipó flora and are thought to have diversified in situ there (Zappi et al. 2017). Moreover, the rocky grassland seems to be older than the cerrado in mountaintops (Simon et al. 2009; Antonelli et al. 2010), and we argue that these mountaintops could also behave floristically as an island, being currently isolated from other sources of dispersal and therefore presenting a more phylogenetic clustered pattern, a matter that deserves further investigation.

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