



Evolutionary history of *campo rupestre*: an approach for conservation of woody plant communities

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Abstract

The *campo rupestre* sensu lato is among the most species-rich vegetation in the world, harbouring a high proportion of endemic species. We aimed to identify the processes that could generate a high level of phylogenetic diversity (PD) in *campo rupestre* for woody species and point out biodiversity hotspot areas which may provide additional information for conservation planning. We compiled a database of 2049 woody species from 185 community inventories. We calculated the evolutionary history using species richness (SR), PD, mean pairwise phylogenetic distance between species (MPD), the mean nearest taxon distance (MNTD) and their equivalents standardised (ses.PDss, ses.MPD, ses.MNTD), evolutionary distinctiveness (ED), and biogeographically weighted evolutionary distinctiveness (BED). Cloud dwarf-forests had the highest SR, PD, MPD and ses.MPD and lowest MNTD, while rupestrian cerrado presented the highest ses.PD and ses.MNTD. All areas are important for conservation, but the intersections between the hotspots should receive special attention in future conservation actions. The grids identified as hotspots by three or more metrics were localized mainly in Espinhaço Range in Minas Gerais State and a further expansion of protected areas is required. Moreover, the intersections between the hotspots obtained by mean ED and ses.PD are concentrated in the rocky dwarf forest and rupestrian cerrado, with considerable conservation gaps. The degree of protection of *campo rupestre* was low with unprotected areas comprising 56% of the species. Our results show an urgent need for increasing protected areas of *campo rupestre* in order to avoid the loss of valuable, endemic species with unique evolutionary history.

Keywords Evolutionary distinctiveness · Rupestrian ecosystems · Species richness · Phylogenetic diversity · Rocky montane

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Introduction

The *campo rupestre* sensu lato has outstanding species richness and endemism and is among the most species-rich vegetation in the world (Fernandes et al. 2014; Silveira et al. 2016; Morellato and Silveira 2018). Approximately 40% of its species are endemic with varying degrees of rarity and life strategies (BFG 2015). The concept proposed by Silveira et al. (2016) defines *campo rupestre* sensu lato (*campo rupestre*) as a montane, grassy-shrubby, fire-prone vegetation mosaic with rocky outcrops of quartzite, sandstone or ironstone (i.e., banded ironstone formation, such as itabirites and cuirasses locally known as *canga*) along with sandy, stony, and waterlogged grasslands. Patches of transitional vegetation such as cerrado, gallery forests, and relictual hilltop forests (forest island or *capões*) are also within the *campo rupestre*. The *campo rupestre* core area stretches along the highlands of eastern Brazil (Hughes et al. 2013; Silveira et al. 2016; Neves et al. 2018), but disjunction areas also occur along several mountain ranges in central-western Brazil (Zappi et al. 2011; Mews et al. 2014) and the Amazon Forest (Silveira et al. 2016). Because of the high number of species with narrow distributions and the uneven floristic data that exist for the *campo rupestre*, each area is unique and potentially important for conservation (Rapini et al. 2002; Ribeiro et al. 2012; Zappi et al. 2017; Morellato and Silveira 2018; Mucina 2018).

Species diversity and patterns of endemism of *campo rupestre* have been severely affected by a strong human impact that has been intensifying in recent years, resulting in growing numbers of extinction and threatened species (see Fernandes et al. 2018); the importance of these species continues to increase for biodiversity preservation and scientific studies. An important and probably most effective way of protecting biodiversity is establishing protected areas. By setting up areas free from serious human disturbance, protection areas aim to ensure that biodiversity is well protected at all levels, including genes, species, phylogeny, and function. However, few protected areas have been created to protect this ecosystem (Silveira et al. 2016), and it is common that species and sites in need of protection fall outside the coverage of conservation areas (Oliveira et al. 2017).

The importance of *campo rupestre* has been emphasized for planning global conservation of biodiversity because of its singularity in terms of biodiversity, endemism, and threats (Jacobi et al. 2007; Fernandes et al. 2014; Morellato and Silveira 2018). Thus, many studies have argued about the ecology, composition, and diversity of this megadiverse group of flora in recent years (Echternacht et al. 2011; Bitencourt and Rapini 2013; Le Stradic et al. 2015; Silveira et al. 2016; Morellato and Silveira 2018). Although these features are extremely important in identifying key biodiversity regions, they focus on only taxonomic diversity. However, basing conservation priorities on species richness (SR) may not be the best strategy to conserve the diversity of life, since it considers all species as equal and ignores unique evolutionary status (Faith et al. 2010).

A valuable strategy to measure the evolutionary history of conservation interest is to use phylogenetic diversity sensu stricto (PD). Areas of high importance for conservation, which were not identified by traditional metrics based on species richness alone, emerge clearly from analyses based on phylogenetic methods (Mishler et al. 2014). The PD metric is a simple and widely applied measure of biodiversity that attempts to capture the historical dimension of evolutionary processes that are responsible for present-day patterns of biodiversity, not only based on the topology of phylogenetic trees but also the length of their branches (Faith 1992).

Phylogenetic diversity and correlated metrics have wide applications in various fields and have been performed for biodiversity conservation applications, where the goal is preservation of evolutionary history and feature diversity (Rodrigues and Gaston 2002; Ferrer et al. 2007; Forest et al. 2007; Devictor et al. 2010; Zappi et al. 2017). Other indices have been developed that combine both evolutionary and spatial features to elucidate the distribution patterns of biodiversity and identify hotspots (Soutullo et al. 2005; Isaac et al. 2007; Rosauer et al. 2009; Cadotte and Davies 2010; Cadotte et al. 2010), for example evolutionary distinctiveness (ED) (Isaac et al. 2007) and biogeographically weighted evolutionary distinctiveness (BED) (Cadotte and Davies 2010). Evolutionary distinctiveness enables us to prioritise species according to their phylogenetic isolation and may capture rare features important for ecosystem services (Redding et al. 2010). Therefore, groups of species with high ED scores may have increased functional importance (Cadotte et al. 2008; Redding et al. 2010). Thus, it is possible to assume that species characterised by high ED scores (evolutionarily isolated species) are species potentially more distinct genetically than moderate- or low-ranked species, and there is less redundancy in the genetic information they contain (Redding et al. 2010). Further modifications to the ED approach have been proposed, allowing it to also include abundance information to generate a metric of abundance-weighted ED that can be used to prioritise populations, species, habitats, and biogeographical regions (Cadotte and Davies 2010; Collen et al. 2011).

Biodiversity hotspot (areas of high diversity and/or endemism) assessments and gap analyses are urgently required to enhance the efficiency of the nature reserve network in Brazil and to provide valuable insights that might improve its management, especially for the conservation of rupestrian woody vegetation. Proponents of the concept suggest that focusing conservation efforts on biodiversity hotspots is the most efficient way to use limited resources to protect the most or rarest species (Myers et al. 2000; Myers 2003). In a recent study, Zappi et al. (2017) analysed the floristic and phylogenetic diversity in *campo rupestre* across Espinhaço Range. These authors found significant differences in floristic diversity and phylogenetic structure across a range of study sites encompassing open vegetation and forest on quartzite and on ironstone substrates, commonly termed canga. However, our study approaches a comprehensive data on woody species distribution, covering other rupestrian environments in different parts of the continent. Attempts to address this knowledge gap could be of importance for effective conservation policies and ecosystem management. Then, we focus on analyses of the evolutionary diversity of rupestrian woody plant communities across Brazil, measuring phylogenetic diversity and other commonly employed metrics of phylogenetic diversity and evolutionary distinctiveness. Consequently, maximising the preservation of areas with high values for PD and ED will also tend to maximise the preservation of feature diversity (Cadotte et al. 2010; Redding et al. 2010) and give a richer understanding of the processes that influence community assembly (Webb et al. 2002; Cavender-Bares et al. 2009) of rupestrian woody plant communities.

We aimed to identify the processes that could generate a high level of phylogenetic diversity in *campo rupestre*. The knowledge of the biodiversity of *campo rupestre* and the distribution range of species will improve our comprehension of the risks of phylogenetic diversity loss and adding information about local threats would enable us to refine the definition of *campo rupestre* hotspots. Our aims were (i) to evaluate the importance of abiotic factors in shaping rupestrian woody plant communities, (ii) to analyse phylogenetic diversity and evolutionary distinctiveness across *campo rupestre*, (iii) to identify the effectiveness of protected areas in conserving these hotspots, and (iv) to assess conservation gaps in *campo rupestre*. We aim to provide a solid support for promoting conservation of rupestrian woody plant biodiversity that can be used as a biological layer from which priority areas can be identified to

drive practices for political, social, and economic considerations in this rare and neglected ecosystem.

Materials and methods

Study area

Our study area was the rupestrian woody plant communities of Brazil. We evaluated 2049 species from 185 sites and 23,957 species records within a latitude range of 25°10'S to 03°20'S and longitude range of 63°41'W to 37°20'W (Fig. 1). Our data cover two thermic zones (tropical and equatorial) distributed across four biomes (Atlantic Forest, Amazon Forest, Caatinga, and Cerrado). The 185 sites occur in four different vegetation types, 76 in rupestrian cerrado, 42 in rupestrian grassland, 40 in cloud dwarf-forest, and 27 in rocky dwarf-forest.

The *campo rupestre* sensu stricto (see Silveira et al. 2016) (here referred as rupestrian grasslands) are old-growth grassland (i.e., ancient ecosystems characterised by high herbaceous species richness, high endemism, and unique species compositions; Vasconcelos 2011). The woody species are scattered in rupestrian landscape or in capões (grouping of woody species). They establish on quartzite, sandstone, or ironstone (i.e., banded iron formations, such as itabirites in the case of cangas) (Fernandes 2016).

The rupestrian cerrado represents an open to shrubby rupestrian grassland, in which many woody species of cerrado sensu stricto (savanna) are found on deeper soils (Ribeiro and Walter 2008; Pinto et al. 2009). In the steep slopes and escarpments along the plateau borders, shallow soils under strong erosion are covered by unusual savanna formation with a rupestrian character (Schaefer et al. 2016a, b).

The cloud dwarf-forest is a forest rich in epiphytes usually located at altitudes higher than 1000 m on deep soils (Schaefer et al. 2016a). These dwarf forests are transitional with shrubby candeias (*Eremanthus* sp.) and soils with better water retention (Schaefer et al. 2016b). Soils are rich in organic matter at the surfaces, but are very poor in nutrients (Bertoncello et al. 2011). However, the rocky dwarf-forest (rocky forest) is a forest type found in areas under stress conditions promoted locally by shallow, sandy and generally mineral-poor characteristics (Oliveira-Filho 2017). The sites are found mainly within the Cerrado biome, in northern (Tocantins state), western (Mato Grosso state) and northeastern (Piauí state) Brazil (Oliveira-Filho 2017).

The climatic regime for all areas is seasonally dry (Alvares et al. 2013), and the leaf flush varies among deciduous, semideciduous and evergreen (found above 1000 m of altitude in the Atlantic Forest; Oliveira-Filho 2015). The mean annual temperature varies from 14 to 26 °C, and the mean annual precipitation ranges from 701 to 2432 mm.

Dataset

We extracted a floristic dataset from the NeoTropTree (NTT) database (Oliveira-Filho 2017), described as rupestrian vegetation. The NTT consists of checklists of woody, free-standing (i.e., lianas excluded) plant species, compiled for geo-referenced sites, extending from southern Florida (U.S.A.) and Mexico to Patagonia. The NTT currently holds 7485 sites/checklists; 20,642 woody plant species; and 920,129 occurrence records. NTT site is defined by a single vegetation type contained within a circular area with a 5-km radius.

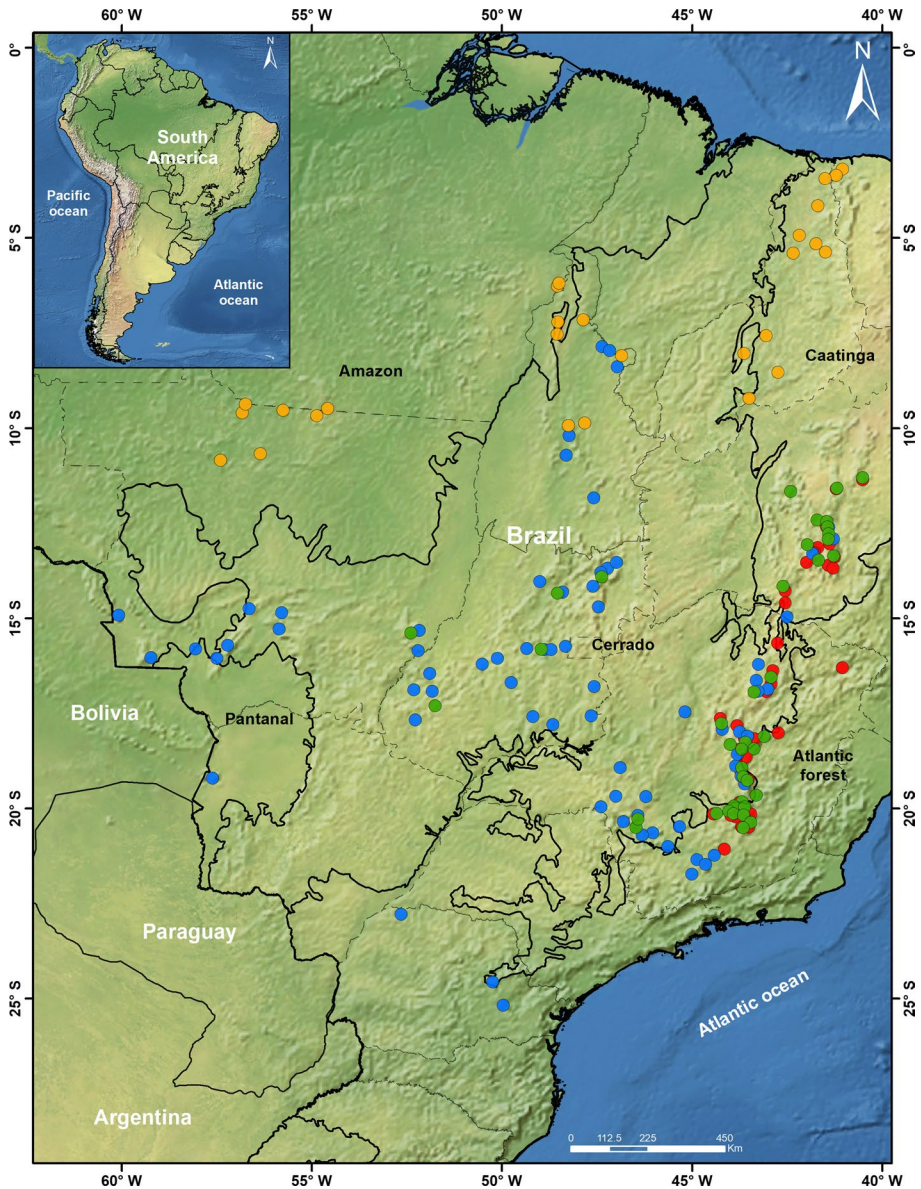


Fig. 1 Geographic distribution of the rupestrian vegetation in South America extracted from NeotropTree database and used in this study. The circles correspond to the vegetation type, cloud dwarf-forest: green circles, rupestrian grassland: red circles, rupestrian cerrado: blue circles, rocky forest: orange circles. Dashed lines represent Brazilian state borders. (Color figure online)

Occurrence records without an indicator or evidence of vegetation type, or sites with very incomplete species lists, are not included in NTT.

The NTT database also contains geodaphic and climatic variables for each site. These variables include: 11 BIOCLIM variables (Hijmans et al. 2005); potential

evapotranspiration (mm) and aridity index (Zomer et al. 2008); mean duration (days) and severity (days) of both water deficit and water excess periods; days of frost; surface rockiness (% surface); soil texture class (% volume) of size fraction (sand); salinity class (ECe in dS·m⁻¹); total saturation of bases (%) (soil fertility); water storage soil (Harmonized World Soil Database v1.2; available at <http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-databasev12/en/>); soil drainage classes (Santos et al. 2013); and hyperseasonality index (produced by the combination of soil drainage classes, mean annual precipitation, and indices of water deficit and excess).

Analysis of phylogenetic diversity

A phylogenetic tree of the whole species pool was generated using Phylomatic in Phylocom 4.2 (Webb et al. 2008) and the megatree R20160415.new (Gastauer and Meira-Neto 2017), based primarily on the APG IV phylogenetic classification of angiosperms (Angiosperm Phylogeny Group 2016). Given this stochasticity, the strong effect of tree ferns and gymnosperms on phylogenetic diversity metrics (they are subtended by very long phylogenetic branches), and the inexpressive richness of these groups, we excluded them from phylogenetic diversity calculations.

We calculated the evolutionary history present in communities using six metrics. (i) The most widely used phylogenetic metric is Faith's phylogenetic diversity (PD, Faith 1992), which is defined as the sum of the branch lengths of a phylogenetic tree connecting all species in the target assemblage. (ii) We also calculated the mean pairwise phylogenetic distance (MPD) between species in each vegetation types (cloud dwarf-forest, cerrado rupestrian, rocky dwarf-forest, and rupestrian grassland; Webb 2000; Webb et al. 2002) and (iii) the mean nearest taxon distance (MNTD; Webb 2000; Webb et al. 2002), which is the mean phylogenetic distance from each taxon to its closest relative in the community. To remove the influence of SR, we calculated the (iv) standardised effect size (ses) based on a null model for each community (Swenson 2014). These standardisations were accomplished by randomly drawing the same number of species from the phylogeny as present in the community; repeating 10,000 times; calculating PD, MPD, and MNTD for each randomisation; taking the difference between the observed values of PD, MPD, and MNTD and the mean of the random values; and dividing these differences by the standard deviation across the randomisations. The ses.MPD and ses.MNTD are equivalent to -1 times the net relatedness index (NRI) and the nearest taxon index (NTI), respectively (Webb et al. 2002). Positive ses values indicate phylogenetic overdispersion, whereas negative values indicate clustering (Webb et al. 2002).

We also extracted evolutionary distinctiveness scores (ED) from the phylogenies to describe species uniqueness (Isaac et al. 2007). Evolutionary distinctiveness is a measure of how much unique evolutionary history a species contributes to a phylogenetic tree. Species with no extant close relatives have high values of ED, whereas species with closely related extant species have low values. A community with high ED thus has more evolutionarily unique species (Edwards et al. 2017). Some additional weighted indices have been proposed, and these bring important extra information to help predict, understand, and avoid loss of evolutionary history (Veron et al. 2016). Biogeographically weighted evolutionary distinctiveness (BED) (Cadotte and Davies 2010) allows us to identify places where phylogenetic diversity may be highly concentrated and weights diversity as a function of range size and evolutionary distinctiveness (sensu Isaac et al. 2007) such that phylogenetic branch lengths are inversely weighted in proportion to the descendant species'

number of populations or range sizes. Thus, species with high evolutionary distinctiveness and greater rarity receive more weight (Rosauer et al. 2009; Cadotte and Davies 2010). Higher weights are assigned to more geographically restricted species because species with small ranges, on average, have a higher probability of extinction than their more widely distributed congeners (Gaston 2003; Jones et al. 2003). Such range-weighted metrics are also beginning to be used for assessments of biological diversity. We utilized the BED_T as the summation of the BED values of all species in a site; thus, sites with species that are narrowly distributed will have higher BED_T than sites with widely distributed species.

Identifying biodiversity hotspots

We compared the maps using six metrics (SR, PD, ses.PD, ED, proportion high ED10% and BED) to identify locations with high diversity. Any given 50 km × 50 km grid cell was marked as a hotspot if the value for a given index was in the top (20%) of its range. We produced maps of the overlapping between the hotspots in order to illustrate the grid cells with multi-metric hotspots. For each metric, we calculated the observed proportion of hotspots that were protected.

Finally, to identify the degree of biodiversity protection throughout the *campo rupestre*, we calculated the percentage of IUCN threatened species and the proportion of hotspot sites by SR, PD, ED, and BED inside and outside protected areas (PA). We conducted an assessment of the conservation status of *campo rupestre* by overlaying the distribution of our 185 sites on to the coverage of protected areas across Brazil. We used conservation units from the Cadastro Nacional de Unidades de Conservação (Ministério do Meio Ambiente – Brazil, www.mapas.mma.gov.br).

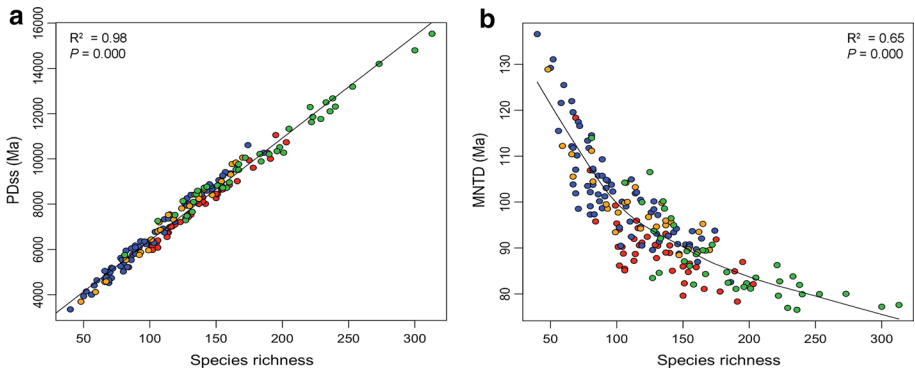
Data assessment and analysis

Values for PD, MPD, MNTD, ses.PD, ses.MPD, and ses.MNTD were compared between the four vegetation types (cloud dwarf-forest, rupestrian cerrado, rocky dwarf-forest, and rupestrian grassland) using F-tests and Tukey HSD. The species accumulation curve was performed according to Hsieh and Chao (2016), where the hill numbers constitute a family of diversity indexes that incorporate relative abundance and phylogenetic diversity. From this analysis, it is possible to compare the data of different communities in time and space, since the samples are standardised to the same size (number of individuals). The curves are generated with 95% confidence intervals obtained by the bootstrap method, which facilitates the comparison of several communities of extrapolated samples. For accumulation curves of phylogenetic diversity, we used the iNEXTPD package (Hsieh and Chao 2016) in R Statistical Environment (R Development Core Team 2017).

We constructed linear models, using generalised least squares (GLS) method to test the relationship between the phylogenetic metrics and climatic and soil variables. We assessed correlations amongst explanatory variables, and for each statistical model, we included the uncorrelated variables that had the most explanatory power. We included latitude and longitude variables as proxies for climatic variation that may not have been captured by the measured climatic and soil variables; this allowed us to account for spatial autocorrelation. We ensured that all variance inflation factors (VIFs) were less than five for each explanatory variable (Quinn and Keough 2002). We used the Akaike information criterion (AIC) to compare models. All analyses were conducted in the R 3.2.3 Statistical Environment (R Core Team 2017; available at <http://www.r-project.org/>) using ‘picante’ (Kembel et al.

Table 1 Sampling and tree community across rupestrian vegetation in Brazil, showing values of species richness (SR)

Vegetation type	No. of sites	Number of angio-sperm species per site
Rupestrian grassland	42	709 (69–203)
Rupestrian cerrado	76	632 (40–186)
Cloud dwarf forest	40	1138 (81–313)
Rocky dwarf forest	27	812 (48–170)

**Fig. 2** Relationship between (a) phylogenetic diversity sensu stricto and species richness, and between (b) mean nearest taxon distance and species richness

2015), ‘vegan’ (Oksanen et al. 2016), ‘car’ (Fox et al. 2014), and ‘nlme’ (Pinheiro et al. 2016) packages. We generated maps of diversity patterns using ArcGIS 10.0 (ESRI, Redlands, CA, USA).

Results

Cloud dwarf-forest had the highest SR, with 1138 woody plant species, whereas the lowest SR was found in the rupestrian cerrado (632). Rupestrian grassland and rocky dwarf-forest showed intermediate values of SR (709 and 812, respectively; Table 1). Across all sites, SR strongly positively correlated with PD ($r^2=0.98$, $P<0.001$; Fig. 2a), whereas MNTD had a negative correlation ($r^2=0.77$, $P<0.001$; Fig. 2b).

We observe similar patterns for phylogenetic diversity sensu stricto PD as we found for SR. The highest values were found for communities in cloud dwarf-forest (10,037 Ma), while the lowest values were found for communities in rupestrian cerrado (6522 Ma). The intermediate values were found in rocky dwarf forest (7813 Ma) and rupestrian grassland (7459 Ma; Fig. 3a), as observed in the rarefaction curve (Fig. S1). The MNTD showed an opposite result to that found for PD and SR, as expected when there are more species of the same clades. The highest value was found for the rupestrian cerrado communities (102 Ma), while the cloud dwarf-forest had the lowest value (87 Ma; Fig. 3b). For the standardised metrics (ses.PD and ses.MNTD), the highest values were also found in the rupestrian cerrado (1.13 and 0.256, respectively; Fig. 3c, d), and the lowest values were

found in rupestrian grassland (−3.11 and −2.38, respectively). Mean pairwise distance (MPD) and its standardised equivalent (ses.MPD) were strongly correlated with each other ($r=0.93$, $P<0.000$; Fig. S2). Values of MPD and ses.MPD were significantly higher in cloud dwarf-forest than in other vegetation types (Fig. 3e).

The best model for all metrics was the full model, including soil and climatic variables (Table 2). For all metrics except SR, the pure climatic model explained the data better than a model with just soil data. The best climatic model for SR included the same climatic variables as the model for PD (SR value was strongly positively correlated with PD) (Fig. 2; Table 2).

Data on protected areas

We found that important areas for rupestrian woody plant conservation had different spatial patterns for the phylogenetic diversity and correlated metrics (Fig. 4). Species richness and PD had similar patterns of distribution (Fig. 4a, b). Grids where occurs predominantly rocky dwarf-forest and rupestrian cerrado showed the highest ses.PD and mean ED values (Fig. 4c, d). In contrast, when considering the proportion of top 10% high-ED species in each grid cell, top ED species are most prevalent on the Espinhaço Range (Fig. 4e). There is a general trend for areas with higher species richness to also contain more top 10% ED species (Fig. 4a, e). The BED metric is more unevenly dispersed, with high values in Espinhaço Range, central-western Brazil and the Amazon Forest (Fig. 4f).

All of the areas identified as hotspots by three or more metrics were in south of the Espinhaço Range in Minas Gerais, including the region of the Iron Quadrangle and Serra do Cipó, and other regions as Serra da Canastra and part of the Chapada Diamantina in northern Espinhaço. The greatest overlap between pairs of metrics were for mean ED and ses.PD in rocky dwarf forest and cerrado rupestrian (Fig. 5). However, there were no cells identified as hotspots by all five metrics.

The degree of protection of *campo rupestre* was low and uneven across the four vegetation types. It was possible to verify that areas located in rupestrian cerrado and rocky dwarf-forest deserve more effective conservation efforts in comparison with other vegetation types (Figs. S3, 5). Unprotected areas comprise 56% of the woody species.

The hotspots area and the protected area show a low level of coincidence (Figs. 5, 6). Both ED and BED rupestrian woody plant hotspots were under-protected, with only a few hotspots protected. Numerous species with high ED and BED scores were not found in any protected area. For rupestrian woody plants, 25 (83.33%) and 24 species (80%) from the top 30 BED and ED species, respectively, were not found in any protected area.

Discussion

We found that different metrics of diversity identified different hotspots areas in the *campo rupestre*, which may provide additional information for conservation planning. These hotspots areas that are high conservation priorities in *campo rupestre* can be used to inform conservation actions to expand the current network of protected areas. We also emphasized that the soil and climatic conditions are very different between areas of rupestrian vegetation and have a strong effect on the distribution of plant species richness and phylogenetic diversity of rupestrian woody plant communities.

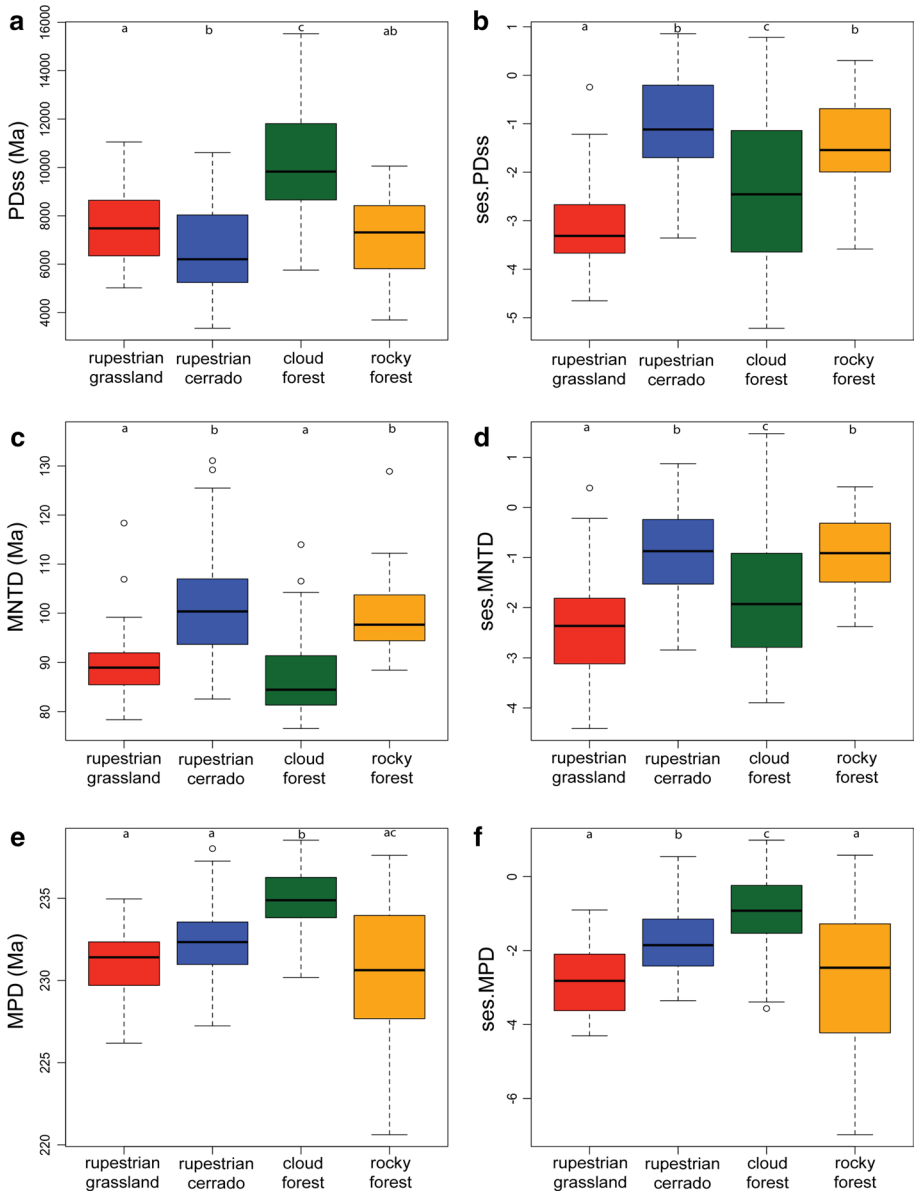


Fig. 3 Variation in phylogenetic diversity (PD), the mean pairwise phylogenetic distance between species (MPD), the mean nearest taxon distance (MNTD), and their equivalents standardised for species richness (ses.PDss, ses.MPD, ses.MNTD). Letters in boxplots indicate significant differences among mean values (Tukey's HSD; $P < 0.05$)

Our results suggest soil (e.g., rockiness) as an important environmental filter since it is the best explanatory variable for variation in SR and PD. Sites of *campo rupestre* with highest phylogenetic diversity sensu stricto (PD) were found within the cloud dwarf-forest. One explanation might be related to the particular environmental and ecological conditions

Table 2 Delta Akaike information criterion (AIC) values for different models to explain variation in species richness and phylogenetic diversity metrics of woody plants in ruprestrian vegetation

Modelos	SR	sesPD	sesMPD	sesMNTD
Just climate, no soil	- 68.82	- 36.76	- 29.7	- 23.49
Just soil, no climate	- 24.50	- 77.90	- 56.52	- 40.3
Climate and Soil	0	0	0	0
Variables included	GrassCover/Rockiness/ PrecDryP/WaterDefDur/ TempAnn	Altit/CloudItcp/PrecSeas/ PrecDryP/WaterExcDur/Rocki- ness	PrecAnn/CloudItc/WaterDefSev/Grass- Cover/RnkdTBS/IflamIndex/RnkdSand	TempAnn/PrecSeas/WaterExc- Dur/RnkdDrainage/SoilWater- Storage

All delta AIC values are scaled with respect to the best model for a given metric. Rockiness; GrassCover grass coverage, PrecDryP precipitation of driest month, WaterDefDur water excess duration; TempAnn: annual mean temperature; Altr: altitude, CloudItcp cloud interception, WaterDefSev water deficit Severity, PrecSeas precipitation seasonality, PrecAnn annual precipitation, RnkdSand ranked sandiness; RnkdDrainag ranked drainag

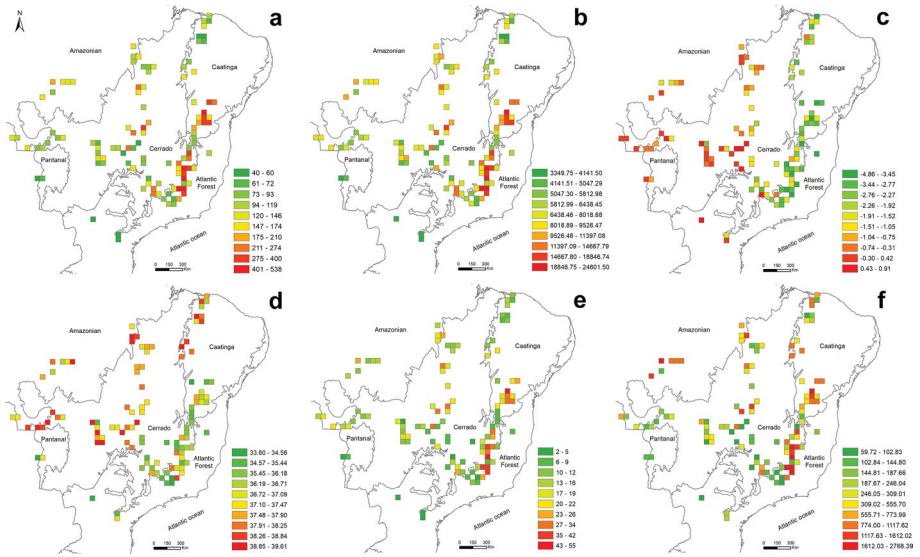


Fig. 4 Spatial distribution of tree biodiversity components across 50×50 km equal area grids; **a** species richness, **b** phylogenetic diversity, **c** ses.PD, **d** average Evolutionary Distinctiveness, **e** proportions give the prevalence of top 10% species in a grid, **f** biogeographically weighted evolutionary distinctiveness. Black lines represent the limits of Brazilian Biomes

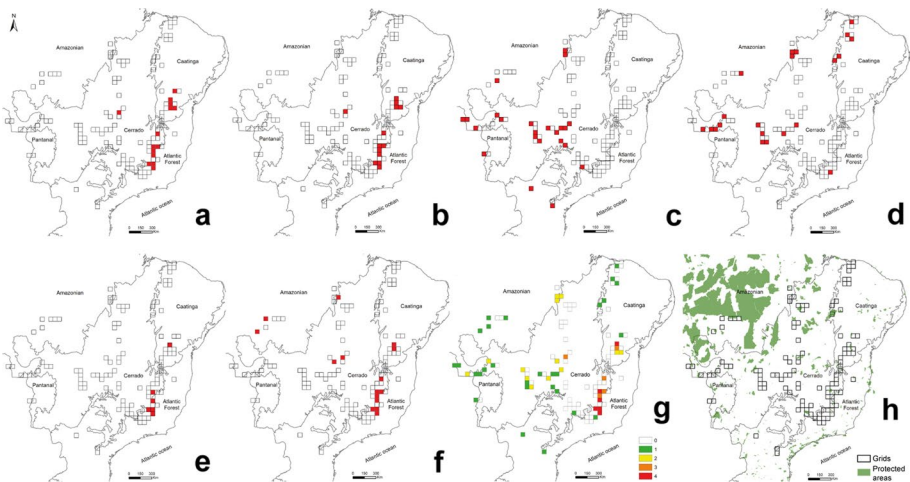


Fig. 5 Geographic distribution of hotspots identified by **a** species richness, **b** phylogenetic diversity, **c** ses.PD, **d** average Evolutionary Distinctiveness, **e** Proportions give the prevalence of top 10% species in a grid, **f** Biogeographically weighted evolutionary distinctiveness and **g** overlaps of hotspots among the diversity metrics for *campo rupestre* **h** areas in green are Brazilian protected area while black lines represent the limits of Brazilian Biomes. (Color figure online)

of cloud dwarf-forest, which are communities located in areas with cloud cover for most of the year and a lower index of rockiness that may be floristically influenced by adjacent Atlantic forest due to spatial and environmental proximity (Neves et al. 2018; Bueno

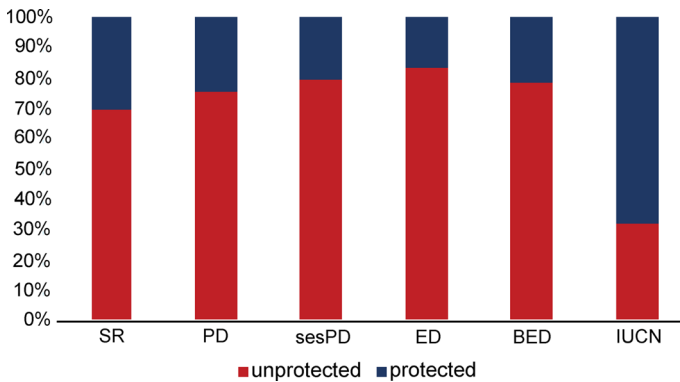


Fig. 6 Proportion of protection for each hotspot: species richness (SR), phylogenetic diversity (PD), ses. PD, evolutionary distinctiveness (ED), biogeographically weighted evolutionary distinctiveness (BED) and IUCN species inside and outside of protected areas

et al. unpublished data), increasing the phylogenetic diversity. However, lower MNTD values were found in cloud dwarf-forest, correlating negatively with SR and PD. We suggest that much of the high species diversity values found in cloud dwarf-forest may be due to recently radiated large genera such as *Guatteria*, (Erkens et al. 2007), *Trichilia* (Koenen et al. 2015), and *Inga* (Richardson et al. 2001). Therefore, low MNTD would be explained by the presence of short phylogenetic branches separating the nearest taxa in these diverse communities (Coronado et al. 2015).

Variation in environmental conditions across the geographically disjunct distribution of *campo rupestre* also seems to be the main factor leading to variation of ses. PD, ses.MNTD, and ses.MPD in woody plant communities. The pattern of reduction in ses.PD with increasing altitude may be related to variation in abiotic factors, such as lower temperatures and shallower soils as well as soil water storage, which hinders the establishment of species (Zhang et al. 2016). The highest ses.PD and ses.MNTD values found in the rupestrian cerrado woody plant community may be explained by the accumulation of lineages over many millions of years, which comprises a mosaic of species of multiple biogeographic origins (Simon et al. 2009). These highest values also may be favoured by a wide altitudinal. Rupestrian cerrado exhibits an altitudinal distribution between the two forest formations (cloud dwarf-forest and rocky dwarf-forest) and rupestrian grassland, thereby providing a connection zone to woody species in the altitudinal gradient in *campo rupestre* and sharing species with all the vegetation types of the *campo rupestre* (Bueno et al. unpublished data). Rocky dwarf-forest also shows high ses.PD and ses.MNTD values. We suggest that higher values are attributed to the spread distribution (Amazon and Cerrado biome) may be influenced by other communities. The lowest values of ses.PD and ses.MNTD were found in potentially more limiting environments, as rupestrian grassland, with highest rockiness and more restricted distribution. These lowest values found in rupestrian grassland is unsurprising given their lower woody species richness. Rupestrian grassland is characterised by high herbaceous species richness (Alves et al. 2010; Le Stradic et al. 2015; Mota et al. 2018), indicated that future studies of phylogenetic diversity with herbaceous strata across *campo rupestre* may help contribute to the identification of new hotspots areas. In addition, it is important to highlight which rupestrian grassland and cloud dwarf forest core area

stretches along Espinhaço Range and their occurrence on iron-rich substrates of enormous mining interest means that they are amongst the most threatened vegetation types in Brazil (Jacobi et al. 2007; Monteiro et al. 2018).

Mean pairwise distance (MPD) and its standardized equivalent (ses.MPD) are strongly correlated with each other, suggesting that each habitat has similar MPD to that expected given the number of species. Both MPD and ses.MPD are strongly influenced by branch lengths at the deepest nodes of the phylogeny, and as a result, these metrics are often strongly driven by how evenly taxa are divided amongst major clades (Swenson 2014). The higher MPD in cloud dwarf-forest suggests that the woody species recorded are distributed across a wider range of clades than those recorded in other vegetation types. In addition, the fact that ses.MNTD is lower in cloud dwarf-forest than in rupestrian cerrado and rocky dwarf-forest suggests that there is a broader representation of clades in forest habitats, but with many closely related species coexisting.

While communities in the cloud dwarf-forest have the greatest tree SR and PD in the Espinhaço Range (core area of *campo rupestre*), the rupestrian cerrado and rocky dwarf-forest show much higher phylogenetic diversity than expected given their species richness (ses.PD), suggesting that the disjunct areas in *campo rupestre* also have same value for conservation. Therefore, without the randomisation approach applied here, high cumulative score areas would simply be a reflection of high species richness areas (Safi et al. 2013). Higher ses.PD values found in rupestrian cerrado reflects accumulated lineage diversity with many deep phylogenetic branches for communities relative to their SR (Swenson 2009; Rezende et al. 2017); thus, PD and ses.PD may provide the most straightforward, interpretable means to evaluate lineage diversity in communities (Coronado et al. 2015).

We also identified hotspots using evolutionary distinctiveness (ED) and biogeographically weighted evolutionary distinctiveness (BED), which would also be useful for *campo rupestre* conservation planning. Grids where occurs predominantly rocky dwarf-forest and rupestrian cerrado showed the highest mean ED values. Relict species tend to have higher ED scores, implying that they are more phylogenetically specialised than those that radiated recently. In contrast, when considering the proportion of top 10% high-ED species in each grid cell, top ED species are most prevalent on the Espinhaço Range. Regions with high current prevalence of top ED species are those where evolutionarily distinct species have originated, or immigrated to, and remained; these may be considered as “cradles” and “museums” of diversity (Jetz et al. 2014). These regions with high concentrations of range-restricted species, such as mountains (e.g., Espinhaço range), have generally been purported to represent refugia that indicate long-term climatic stability and where we might expect to see ancient or relictual lineages (Fjeldsa and Lovett 1997; Sandell et al. 2011; Bueno et al. 2017). Even if such sites are not species richness hotspots, they may require nature reserves and funds because of their importance in maintaining future evolutionary potentials and local ecosystem services (Quan et al. 2017).

Preferentially conserving the most distinct (highest ED) species leads to more of the tree of life persisting into the future and proportional PD gain increases, as fewer species are given protection (Jetz et al. 2014). Species with small range sizes, compared with those that are widely distributed, are probably much more vulnerable, since their habitats may vanish with global climate change (Cadotte and Davies 2010). These regions therefore represent an invaluable resource for the conservation of *campo rupestre*.

Biogeographically weighted evolutionary distinctiveness (Cadotte and Davies 2010) weights diversity as a function of range size and evolutionary distinctiveness (sensu Isaac et al. 2007), such that phylogenetic branch lengths are inversely weighted in proportion to the descendant species' number of populations or range sizes. Thus, species with high

evolutionary distinctiveness and greater rarity receive more weight (Rosauer et al. 2009; Cadotte and Davies 2010). Higher weights are assigned to more geographically restricted species because species with small ranges, on average, have a higher probability of extinction than their more widely distributed congeners (Gaston 2003; Jones et al. 2003). Moreover, because of their small ranges and their evolutionary distinctness, they are highly relevant for conservation (Delic et al. 2017). Rare species represent a large proportion of unique feature diversity which will potentially help to maintain ecosystems that are resilient to threats, such as climate change (Mouillot et al. 2013). By capturing rarity and evolutionary history, BED species may thus be key species for the preservation of option values (Veron et al. 2016). Where conservation resources are limited, ED and BED are useful means for understanding biogeographic patterns and subsequent setting of biodiversity conservation priorities (Cadotte and Davies 2010; Huang et al. 2011).

We must emphasize that it is necessary to define a clear and agreed objective before choosing relevant metrics for a specific problem (Xu et al. 2017). The intersections between the hotspots obtained by all indices are very important for biodiversity protection because all the values of the indices were highest in these hotspots (Xu et al. 2017); as obvious start would therefore be to focus resources on these zones of overlap (Cadotte and Davies 2016). However, no area was identified as a hotspot by all metrics. The grids identified as hotspots by three or more metrics (mainly SR, PD, BED and prop. ED 10%) were in south of the Espinhaço Range in Minas Gerais, including the region of the Iron Quadrangle and Serra do Cipó, and the Chapada Diamantina in northern Espinhaço, and thus these areas should be prioritised in future conservation actions. However, hotspots that are only identified by one or several indicators are also extremely important, because different indices emphasize different aspects, including species richness, geographic range and phylogeny (Huang et al. 2011). Grids with high mean ED woody plant species and ses.PD are concentrated in the rocky dwarf forest and rupestrian cerrado located mainly in central Brazil, however, the coverage of nature reserves is low, with larger gap areas and without protected areas. Thus, such areas also require attention in conservation planning.

Each of the metrics used for the woody plant community in *campo rupestre* represents a different aspect of biodiversity. Despite their wide appeal and clearly articulated importance, hotspots are unlikely to provide a panacea for the current biodiversity crisis, because there is no single metric that can capture all aspects of diversity that we might value (Cadotte and Davies 2016). Moreover, our indices are only a few of the vast number of diversity metrics that could be applied to our data (e.g., Gotelli and Colwell 2001; Rosauer et al. 2009; Schleuter et al. 2010; Anderson and Crist 2011; Cadotte and Davies 2016). For example, we have identified critical regions or hotspots for *campo rupestre*, but we did not identify hotspot for threatened species. Monteiro et al. (2018) applied systematic conservation planning to indicate places with greatest conservation values necessary to secure the proper protection of threatened plant species within the southern Espinhaço Range. The degradation of these habitats, overexploitation of natural resources (e.g., mining) and climate change are the most significant of natural threats to biodiversity in the region, causing extensive damage to ecosystems, fauna and flora.

Brazilian PAs, however, are apparently not protecting most endemic species and lineages (Oliveira et al. 2017). Recently, Oliveira et al. (2017) found that aside from the Amazon, all Brazilian biomes have a PA coverage well below the 17% recommended by the Convention of Biological Diversity, thus reinforcing the need for new PAs. Currently protected areas performed poorly in terms of protecting species, phylogenetic diversity, and also in protecting threatened species, especially when we consider rupestrian cerrado and rocky dwarf-forest with larger gap areas and without protected areas in Brazil. This is

particularly worrisome given that endemic species and lineages are more susceptible to extinction in the face of degradation of habitat and climate change.

Conclusion

We identified areas of high phylogenetic diversity of woody plant communities in *campo rupestre* across Brazil to drive conservation areas that optimise the preservation of the evolutionary history of this vegetation. Our results provide a wide snapshot of priorities for action and highlight gaps in our knowledge of *campo rupestre* conservation.

Highest PD values were mainly found in cloud dwarf-forest, located in the Espinhaço Range, that were poorly covered by protected areas. Rupestrian cerrado exhibited the highest ses.PD, suggesting that these communities may hold higher lineage diversities than expected (given their species richness) and deserve simultaneous conservation attention. Our finding of lower ses.PD values in the rupestrian grassland communities, characterised by high herbaceous species richness, indicated that future studies of phylogenetic diversity with herbaceous strata across *campo rupestre* may help contribute to the identification of new hotspots areas. Yet because of the threats, endemism, and evolutionary distinctiveness of the species already present in our data, the hotspots we identified are priority areas for conservation. We also emphasised that conservation strategies need to pay greater attention to ED and BED of species in order to prevent the potential loss of large amounts of evolutionary history among plant classes. Although recent studies evidence the importance of evolutionary history and identify species with conservation priority, PD levels remain uncorrelated with levels of conservation attention (Sitas et al. 2009; Collen et al. 2011). Indeed, 83.33% of the top 30 ranked species in our BED woody plant list are currently receiving little or no conservation attention.

All areas are important for conservation, but the intersections between the hotspots should receive special attention in future conservation actions. The grids identified as hotspots by three or more metrics were localized mainly in the south of the Espinhaço Range in Minas Gerais State and a further expansion of protected areas is required. Such actions would potentially preserve unprotected unique evolutionary diversity in the Espinhaço Range which may have a high risk of local extinction and rapid degradation of ecosystem functions due higher mining pressure and require urgent attention. Moreover, the intersections between the hotspots obtained by mean ED and ses.PD are concentrated in the rocky dwarf forest and rupestrian cerrado, with considerable conservation gaps.

There is an urgency to develop coherent conservation strategies for these regions to protect what remains, but more importantly to ensure sustainable ecosystem services. Consequently, we suggest that the effectiveness of the established nature reserves should be improved and new protected areas should be delineated in the conservation gap areas for *campo rupestre*. Thus, would be possible to avoid a scenario where these areas lose too much of their unique evolutionary history not found anywhere else in the world.

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