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Lack of floristic identity in *campos rupestres* – a hyperdiverse mosaic of rocky montane savannas in South America

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HIGHLIGHTS

- *Campos rupestres* do not represent a single floristic group;

- Influence from surrounding *cerrados* drives compositional differentiation in *campos rupestres*;

- Environmental conditions can predict the differentiation amongst *campo rupestre* floristic groups;

- Conservation units fail to protect important parts of the *campo rupestre* floristic space;

- *campos rupestres* and their surrounding lowland *cerrados* merit simultaneous conservation attention.

Abstract

The rocky montane savannas of South America, known as *campos rupestres* in Brazil, where they largely occur, represent a megadiverse habitat housing c.15% of the Brazilian vascular flora in less than 1% of the Brazilian territory. Amongst other factors, the remarkable plant diversity in *campos rupestres* has been attributed to its occurrence as many isolated patches and to floristic influences from surrounding habitats, including lowland woody savannas (*cerrado*), Atlantic rain forests, seasonally dry woodlands and Amazonian rain forests. However, no study has assessed the degree to which the putative floristic influence from surrounding habitats drives compositional variation in *campos rupestres*. Here, we used a dataset on the composition of South American woody plant communities (> 4,000 community surveys, with > 100 representing *campos rupestres*), combined with environmental data, with the

aim of characterising and explaining compositional variation of the *campos rupestres* woody flora. Our results showed that all *campos rupestres*, including the sites occurring in Amazonian ironstone formations, are more similar to *cerrado* woody savannas than to any other South American vegetation formations covered in our dataset. Also, multiple *campo rupestre* floristic groups may be recognized based on distinct species composition and environmental conditions, primarily related to substrate and climate. We stress the importance of considering this floristic heterogeneity in conservation, management and research planning.

Keywords: *campos rupestres*, *Espinhaço* range, cangas, floristic composition, environmental heterogeneity, cluster analysis.

1. Introduction

The rocky montane savannas of South America, known as *campos rupestres* in Brazil, where they largely occur, are found on quartzite, sandstone and ironstone formations, mostly above 900m (a.s.l.) and up to 2,033m (Giulietti et al., 1997; Fernandes et al., 2014; Silveira et al., 2016). Its core area is spread along the highlands of eastern Brazil (Giulietti et al., 1997; Hughes et al., 2013; Silveira et al., 2016). Disjunct areas also occur along mountain ranges in central-western Brazil (Frisby and Hind, 2014; Mews et al., 2014; Silveira et al., 2016), eastern Bolivia (Saravia, 2008) and in the Amazon forest (Silveira et al., 2016). The *campos rupestres* are a growing focus of attention because they have been recently proposed as one of the world's old climatically-buffered

infertile landscapes (OCBILs, e.g., the *fynbos* of the Cape Floristic Region; Silveira et al., 2016).

In Brazil, the *campos rupestres* contain c.5,000 vascular plant species (Reflora, 2016), corresponding to a remarkable c.15% of the Brazilian vascular flora in less than 1% of the Brazilian territory (Fernandes et al., 2014; Silveira et al., 2016). Amongst other factors, this outstanding floristic diversity in *campos rupestres* – a pattern common to OCBILs (Hopper et al., 2009) – has been attributed to its high levels of local endemism (Hensold, 1988; Echternacht et al., 2011a) as well as to the geographically disjunct distribution of *campo rupestre* sites and, hence, the associated floristic influence from distinct habitats (Giulietti et al., 1997), namely *cerrado* woody savannas, Atlantic rain forests, seasonally dry woodlands and Amazonian rain forests. However, to our knowledge, no study has assessed the degree to which this alleged floristic influence from surrounding habitats drives compositional differentiation of *campos rupestres*.

Attempts to address this knowledge gap could be of importance for effective conservation strategies. If the floristic variation of *campos rupestres* is high, with multiple distinct floristic groups, future conservation assessments could highlight, for instance, that a large number of separate conservation areas are needed to fully protect *campos rupestres* diversity. Here we go a step further in data refinement and analysis by using a large dataset on the composition of South American woody plant communities (> 4,000 community surveys, with > 100 representing *campos rupestres*), combined with environmental data, in order to elucidate the spatial floristic patterns of *campos rupestres*. We address the following hypotheses stemming from the literature

(Giulietti et al., 1997; Echternacht et al., 2011b): (h_1) multiple *campo rupestre* floristic groups may be recognized based on distinct species composition; (h_2) community composition differentiation amongst *campo rupestre* floristic groups can be predicted by variation in environmental conditions.

2. Material and Methods

2.1. Study area

The South American rocky montane savannas (henceforth *campo rupestre* for a single site, and *campos rupestres* for multiple sites) cover c.65,000 km^2 (Fernandes et al., 2014) and occur primarily on quartzite and sandstone formations in the highlands (mostly > 900 m a.s.l) of eastern Brazil as well as in scattered mountain ranges in central-western Brazil (Frisby and Hind, 2014; Mews et al., 2014, Silveira et al., 2016). These highlands border three primary vegetation 'Domains' (IBGE, 1993; Ab'Sáber, 2003): the Atlantic Domain to the east and south (known as *Mata Atlântica* in Brazil), the Caatinga Domain to the north and the Cerrado Domain to the west (see Giulietti et al., 1997; Hughes et al., 2013; Silveira et al., 2016). The prevailing land cover of these bordering Domains are rain forest in the *Mata* Atlântica, semi-arid thorn woodlands in the Caatinga and woody savannas in the Cerrado. C*ampos rupestres* are also found in ironstone formations of south-eastern and central-western Brazil, eastern Bolivia and the south-eastern Amazon Forest (known as *cangas* in Brazil; Jacobi and Carmo, 2011; Silveira et al., 2016). *Campo rupestre* landscapes also comprise patches of transitional vegetation (e.g.,

parkland savanas, riverine forests), but here we adopt the *sensu stricto* definition of *campos rupestres*, which comprises only the grassy-shrubby savannas on quartzite, sandstone or ironstone rock outcrops (Alves et al., 2014). Many *campo rupestre* sites comprised in this contribution were not included in previous studies (Fernandes et al., 2014; Silveira et al., 2016), especially those found in quartzite and sandstone outcrops across the Goiás state (central-western Brazil; Mews et al., 2014) and the ironstone-associated *campos rupestres* found in the Mato Grosso do Sul state, near the Brazil-Bolivia border (Neves and Damasceno-Junior, 2011). Mountaintop grasslands (*campos de altitude*), which are found nearer to the Atlantic coast (Ribeiro et al., 2007), were not included in this contribution because their flora is distinct and more closely related to that of the *páramos* in the Andes (Safford, 2007).

2.2. Dataset

We extracted the dataset from the NeoTropTree (NTT) database (http://prof.icb.ufmg.br/treeatlan), which consists of checklists of woody, freestanding (i.e., lianas excluded) plant species, compiled for geo-referenced sites, extending from southern Florida (U.S.A.) and Mexico to Patagonia. NTT currently holds 5,126 sites/checklists, 14,878 woody plant species and 920,129 occurrence records. A site/checklist in NTT is defined by a single vegetation type, following the classification system proposed by Oliveira-Filho (2015), contained in a circular area with a 10-km diameter. Where two or more vegetation types co-occur in one 10-km area, there may be two geographically overlapping sites in the NTT database, each for a distinct vegetation type.

The data were originally compiled from an extensive survey of published and unpublished literature (e.g., PhD theses), particularly those comprising floristic surveys and forest inventories. Moreover, new species occurrence records obtained from major herbaria and taxonomic monographs have been added to the checklists when they come from within the 10-km diameter of the original NTT site, and within the same vegetation type. All species and their occurrence records were checked regarding current taxonomic and geographical circumscriptions, as defined by the team of specialists responsible for the online project *Flora do Brasil* (available at http://floradobrasil.jbrj.gov.br/). The compilation of NTT avoided, therefore, the inclusion of occurrence records with doubtful identification, location or vegetation type. It also excluded checklists with very low species richness (< 20 species), because this is often due to low sampling/collecting efforts, which results in poor descriptive power.

The dataset extracted from NTT consisted of 4,637 South American woody plant community surveys, of which 115 were *campos rupestres* from eastern and central western Brazil, south-eastern Brazilian Amazon and eastern Bolivia. The full species matrix contained presence/absence data for 11,954 woody plant species, with a total of 883,258 presences, and the *campos rupestres* species matrix contained presence/absence data for 1,055 woody plant species, with a total of 12,801 presences.

The NTT database also includes 24 environmental variables for all sites, obtained from multiple sources. Elevation (m above sea level) at the site centre, obtained from WorldClim 1.4 (Hijmans et al., 2005), was used as an integrative environmental variable. Climatic variables consisted of isothermality, maximum temperature of warmest month, mean annual temperature, mean annual

precipitation, mean daily temperature range, minimum temperature of coldest month, precipitation of driest month, precipitation of wettest month, precipitation seasonality, temperature annual range and temperature seasonality, obtained from WorldClim 1.4 data layers (Hijmans et al., 2005); cloud interception (mm) and frost frequency (days), obtained from modelling known values as response variables (data obtained from 135 and 57 Brazilian Meteorological Stations measuring frost frequency and cloud interception, respectively), and elevation, latitude and the aforementioned WorldClim layers as predicting variables; duration (days) and severity (mm) of water deficit, produced by interpolating 5-day intervals of monthly temperatures and precipitation (WorldClim 1.4; Hijmans et al., 2005) to be plotted in, and then extracted from, Walter's Climate Diagrams (Walter, 1985); and two additional variables, potential evapotranspiration (mm) and an aridity index (annual precipitation/potential evapotranspiration), derived by Zomer et al. (2007, 2008) from WorldClim data.

Six variables were substrated-related: grass coverage (%), obtained by direct observation of the site surface via Google Earth[©] images in five 100×100m areas, one at the central coordinates of the NTT site and four at 2.5 km away from it and towards the NE, SW, NW and SE; soil coarseness (% sand), soil fertility (% base saturation) soil salinity (ds/m) and surface rockiness (% exposed rock), obtained from the Harmonized World Soil Database v 1.2 (available at http://www.fao.org/soils-portal/soil-survey) and then ranked by mid-class percentage (raw figures were unrealistic due to local soil heterogeneity); and soil drainage classes, obtained following EMBRAPA's protocol (Santos et al., 2013), which combines soil type, texture and depth with land forms.

2.3. Analyses of community composition

We used Simpson distance as the dissimilarity metric and unweighted paired groups as the linkage method in a hierarchical clustering analysis (McCune and Grace, 2002). We built 1000 clusters, with each cluster being built after randomising the row order in the species composition matrix (species per site), following the procedure proposed by Dapporto et al. (2013). The final cluster is assembled following the majority consensus rule: if a given group is represented in at least 50% of the trees built using a given set of samples, that group is represented in the final consensus tree (Omland et al., 2008). This analysis was conducted using the recluster package (Dapporto et al., 2015) in the R Statistical Environment (R Development Core Team, 2016).

We assessed the overall patterns of floristic identity in *campos rupestres* by (i) analyzing species occupancy (i.e., with species incidences rather than abundances), and (ii) performing an ordination of *campo rupestre* woody plant communities (115 sites) by non-metric multidimensional scaling (NMDS) of their species composition (McCune and Grace, 2002) using Simpson distance as the dissimilarity metric. Following methods similar to those proposed by Kreft and Jetz (2010), the colours blue, green, yellow and red were assigned to the four corners of the two-dimensional ordination plot in clockwise order from the origin. NMDS scores were then mapped in geographic space by assigning a colour to each site according to its position in the two-dimensional ordination space. Beforehand, the ordination was rescaled to axes ranging from 0 to 1. Rescaling is possible with NMDS results since ordination axes as such have no meaning and only the relative position of points in ordination space matters. The NMDS

and the colour assignment were conducted in the statistical packages vegan (Oksanen *et al.*, 2016) and recluster (Dapporto et al., 2015), respectively, both in the R Statistical Environment (R Development Core Team, 2016).

We tested whether variation in environmental conditions can predict differentiation in *campos rupestres* community composition, and then visually explored the results by (i) plotting the NMDS scores in ordination and geographic space, and (ii) fitting the values of the most important environmental variables by generalized linear models (GLM) and generalized additive models (GAM), respectively. This routine follows methods similar to those proposed by Blanchet et al. (2008) and Legendre et al. (2012), which comprise (i) the exclusion of 261 singletons (species found at a single site), as they commonly increase the noise in most analyses without contributing information (Lepš and Šmilauer, 2003); (ii) the Hellinger transformation of the binary presence/absence data (Legendre and Gallagher, 2001), which reduces the weight of widespread species and their inherent effect in ordination analyses; (iii) the independent compilation of significant spatial and environmental variables through a forward selection method for redundancy analysis (RDA), after first checking that the respective global models were significant (Blanchet et al., 2008); (iv) an additional and progressive elimination of collinear variables based on their variance inflation factor (VIF) and ecological relevance, until maintaining only those with VIF < 10 (Quinn and Keough, 2002); and (v) variation partitioning of the community composition matrix with respect to the significant spatial and environmental variables. As spatial variables, we used principal coordinates of neighbour matrices (PCNMs; Borcard et al. 2004), which represent the spatial structure of the sampling units at multiple spatial

scales without considering any environmental variation (Borcard et al., 1992; Legendre et al., 2002; Borcard et al., 2004). We tested the overall significance of the environmental fraction (controlled for spatial autocorrelation) by applying ANOVA permutation tests (999 permutations) for RDA (Peres-Neto et al., 2006). The variable selection, variation partitioning and GLM/GAM analyses were conducted using the fields (Nychka et al., 2015), spacemakeR (Dray et al., 2010) and vegan (Oksanen et al., 2016) packages in the R Statistical Environment.

Finally, we conducted an assessment of the conservation status of *campos rupestres* by overlaying the distribution of our 115 sites on to the coverage of protected areas across South America. We used conservation units from the *Cadastro Nacional de Unidades de Conservação* (Ministério do Meio Ambiente - Brazil, www.mapas.mma.gov.br) and World Database on Protected Areas (IUCN & UNEP - WCMC, www.protectedplanet.net). All maps were designed using the package maptools (Lewin-Koh and Bivand, 2012) in the R Statistical Environment.

3. Results

3.1. Floristic patterns

The hierarchical clustering showed that *campos rupestres*, including the sites occuring in Amazonian ironstone formations, are more similar to *cerrado* woody savannas than to any of the other South American phytogeographical domains (Fig. 1). These c*ampo rupestre* sites share 95% of their woody plant species with other habitats in our community dataset, being 74% with Cerrado woody plant formations and 53% with other phytogeographical regions (i.e.,

Amazon, Atlantic Forest and Caatinga). *Campo rupestre* sites do not form a single cluster but are scattered within a broad *cerrado* cluster (Fig. 1). The assessment of species incidences revealed that 80% of species have relatively low occupancy across *campos rupestres* (dashed line in Fig. 2). The distribution of *campos rupestres* in the ordination space yielded by NMDS suggests a compositional segregation into four relatively distinct floristic units (Fig. 3), namely northern (blue spectrum), south-eastern (brown-yellow spectrum), north-eastearn (green spectrum) and central-western (red-purple spectrum) *campos rupestres*. Bolivian *campos rupestres* are floristically related to the central-western group (see similarity in Fig. 3b), and the foristic differentiation between eastern groups is comparatively more subtle.

The conservation status of *campo rupestre* sites is uneven across these four floristic groups (Fig. 4a). Many central-western *campos rupestres* are unprotected, while northern *campos rupestres* are better protected (Fig. 4a). The conservation assessment revealed that the current network of protected areas does not cover the entire floristic space of *campo rupestre* woody plant communities (Fig. 4b).

3.2. Environmental drivers of community turnover

The forward selection procedure retained six PCNMs for modelling variation in *campo rupestre* community composition (adjusted R^2 = 0.158, which is fairly close to the value for all 38 PCNMs without any selection, adjusted R^2 = 0.159). These selected spatial vectors are amongst the first PCNMs, which represent broad-scale, positive spatial autocorrelation. Regarding environmental variables, the forward selection retained 13 environmental

variables (adjusted R^2 = 0.271, which is near the value for all 24 environmental variables without any forward selection, adjusted R^2 = 0.304) for modelling variation in *campo rupestre* community composition (Table 1). Altitude, aridity index, isothermality, maximum temperature of hottest month, mean daily temperature range, minimum temperature of coldest month, potential evapotranspiration, precipitation of wettest month, salinity, temperature annual range, and water deficit duration and severity were the excluded environmental variables.

When partitioning the variation explained by the retained environmental and spatial predictors, we found that the environmental fraction explained 27% of the variation, 15% of which was independent of spatial autocorrelation ($P <$ 0.01). The environmental predictors could not account for 3% of the spatially structured variation ($P < 0.01$), and 70% of the variation remained unexplained. By fitting the values of the most important environmental variables in ordination and geographic space (Fig. 3a and b, respectively), we observed a strong east to west gradient related to decreasing surface rockiness (Fig. 3a-b), a proxy for soil water deficit, thus segregating eastern *campos rupestres* from northern and central-western *campos rupestres*. A south-east to north gradient was related to increasing mean annual temperature (MAT) and decreasing temperature seasonality (TempSeas), with northeastern and central-western *campos rupestres* occurring in intermediate MAT and TempSeas (Fig. 3a-b). Mean annual precipitation (MAP) was the third most important variable and was associated with the floristic differentiation of north-eastern from northern *campos rupestres*, with south-eastern and central-western occurring in intermediate MAP (Fig. 3b).

4. Discussion

4.1. Floristic identity of *campos rupestres*

The first hypothesis was clearly supported by our results. Multiple *campo rupestre* floristic groups may be recognized, based on distinct woody plant species composition. Instead of representing a single floristic group across South America, the *campos rupestres* form several separate groups within a wider *cerrado* savannas group. This is the first attempt to show the degree to which the geographically disjunct distribution of *campo rupestre* sites, and its associated environmental heterogeneity, is underpinning the outstanding floristic diversity in *campos rupestres*. Despite the fact that our dataset only comprises woody plants, we predict that subsequent studies focusing on herbs (a large component of *campos rupestres* floristic diversity) and/or animals will reinforce this claim; i.e., influence from surrouding habitats is an important factor shaping overall species composition in *campos rupestres*. Also, we hypothesize that the high level of local endemism found in the non-woody component of *campos rupestres* (Hensold, 1988; Mello-Silva, 1989; Echternacht et al., 2011a) leads to even greater floristic heterogeneity amongst *campos rupestres*; i.e., floristic dissimilarity amongst *campos rupestres* is even higher if considering the non-woody component.

Our results show that individual *campo rupestre* groups share more species with surrounding lowland *cerrados* than they do with other *campo rupestre* groups. On the other hand, the *campo rupestre* sites in southeastern and central-western Brazil represent a large and relatively cohesive floristic group of *campos rupestres* (larger red cluster in Fig. 1), in agreement with a

considerable degree of floristic similarity between *campos rupestres* from the *Espinhaço* range (southeastern Brazil) and the disjunct mountain ranges from central-western Brazil (Feres et al., 2009).

4.2. Environmental drivers of community turnover

The second hypothesis was also supported by our results. Community composition differentiation amongst *campo rupestre* floristic groups can be predicted by variation in environmental conditions. Our results show that northern *campos rupestres* occur in wet and warm environments with lower surface rockiness (i.e., low soil water deficit). The northeastern group occurs in the driest extreme of the precipitation space occupied by *campos rupestres*, whereas southeastern and central-western *campos rupestres* are found in intermediate, moist enviroments. The later two groups diverge over two other important gradients: the southeastern group occurs in environments with lower mean annual temperature, higher temperature and higher surface rockiness, while the central-western group has lower rockiness and intermediate mean annual temperature and temperature seasonality.

Variation in environmental conditions across the geographically disjunct distribution of *campos rupestres* seems to be the main factor leading to floristic divergence of *campo rupestre* woody plant communities. However, understanding species-environment relationships in *campo rupestre* woody plant communities is complex, as it partly depends on understanding the floristic relationships between *campos rupestres* and their surrounding lowland cerrados. On the one hand, the environmental gradients found across *campos rupestres* have given rise to a pattern of low species occupancy such that many

campo rupestre woody plant species inhabiting this gradient can be said to belong to only one of the four floristic groups. On the other hand, most of these species also occur in other habitats of our woody plant community database, suggesting that the environmental similarity between *campos rupestres* and the surrounding lowland *cerrados* has allowed a regular exchange of woody plant species between these two habitats. This is in agreement with a previous study showing that *campos rupestres* and lowland cerrados in Goiás state, a portion of our central-western group, differ in population structure of their woody plant species but not in composition (Mews et al., 2014). From an ecological perspective, *campos rupestres* and their surrounding lowland *cerrados* are likely to form a continuous metacommunity with spatial variation in woody plant population sizes being mainly driven by source-sink dynamics (Pulliam and Danielson 1991); i.e., species that are better adapted to lowland *cerrados* (source habitat for this species) are also found in campos rupestres (sink habitat for this species), though in smaller populations, since species better adapted to rocky substrate and shallower soils will prevail in population size.

4.3. Spatial structure

The *campo rupestre* floristic groups are largely geographic, thus suggesting that there may be a role for spatially structured dispersal limitation and historical biogeography in driving floristic differentiation. Nevertheless, our results indicate that environmental conditions are better predictors of community turnover (a proxy for niche-based dispersal limitation) than are geographical factors (i.e., community composition/differentiation of unsampled *campos rupestres* is better predicted based on environmental similarity than by

geographic proximity)*.* This is supported by the negligible unique variation attributed to positive spatial autocorrelation in *campos rupestres*, a proxy for a distance decay in community similarity (Nekola and White, 1999), and by the fact that it is more parsimonious to attribute the spatially structured environmental variation to niche-based controls (cf. Legendre et al., 2009; Neves et al., 2015). The niche-based dispersal limitation in *campos rupestres* is further supported by two other results: (i) the comparatively high compositional variation in southeastern Brazil is most likely to be associated with the role of environmental heterogeneity in underpinning the occurrence of three floristic groups, regardless of geographic proximity; and (ii) 95% of woody plant species in *campos rupestres* are also found in other habitats, but have restricted distributions across *campos rupestres*, likely because environmental conditions are more similar between *campos rupestres* and surrounding lowland *cerrados* than between geographically distant *campo rupestre* groups (spatially structured environmental variation).

4.4. Conservation implications

Threats to *campo rupestre* biodiversity are many, and include mining, unplanned urbanisation, high frequency of anthropogenic fire, uncontrolled harvesting of ornamental plants, eucalyptus plantations, selective logging and unplanned tourism (Giulietti et al., 1997; Jacobi et al., 2007, 2011; Fernandes et al., 2014; Silveira et al., 2016). Considering the pervasive nature of most of these threats, conservation strategies for *campos rupestres* need to be urgent and well-informed scientifically. We believe our findings fit the 'well-informing' criteria and are therefore of relevance for conservation planning. Here we show

that *campos rupestres* are in fact segregated into three or four compositionally distinct floristic units, which dictates that each group deserves separate conservation planning. In doing so, future assessments may call attention to the distribution of protected areas within each of these *campo rupestre* groups. Recent studies have shown that at smaller geographic scales (e.g., *Espinhaço* Range in eastern Brazil), several areas could be distinguished based on taxonomic and evolutionary uniquiness of plants (Echternacht et al., 2011b; Bitencourt and Rapini, 2013; Souza et al., 2013; Echternacht et al., 2014).

We also showed that *campo rupestre* floristic groups are unevenly protected and that geographical gaps in the distribution of conservation units result in a failure to protect important parts of the *campo rupestre* floristic space. More specifically, *campos* rupestres found at intermediate values of the floristic space summarized by the first NMDS axis are largely unprotected. These are *campos rupestres* occurring under intermediate mean annual precipitation (c.1,500 mm) in western Goiás state (central-western group) and southern Minas Gerais state (southeastern group). We also call attention to the *campos rupestres* found in Mato Grosso do Sul state, near the Bolivia border. These *campos rupestres*, occurring in the ironstone formations of the Urucum plateau, are largely unprotected, poorly studied and highly threatened by opencast mining (Neves and Damasceno-Junior, 2011).

An alternative, and important, route forward in conservation planning lies in addressing the evolutionary history of these *campo rupestre* groups. Previous studies indicate that plant lineages from multiple biogeographical origins have colonized *campos rupestres* many times over evolutionary history. For instance, some bromeliad (Versieux et al., 2012) and orchid species (Gustafsson et al.,

2010) found in *campos rupestres* seem to have an Atlantic rain forest origin (i.e., sister taxa are mainly found in Atlantic rain forests), while some legume species seem to have an origin in seasonally dry woodlands (Souza et al., 2013). In addition, others have stressed the idea that *campos rupestres* have acted as 'species pump' for the surrounding lowland habitats (Simon et al., 2009; Silveira et al., 2016). Either way, future studies intending to quantify these evolutionary shifts could shed light into the historical assembly of the *campo rupestre* flora and, potentially, emphasize the necessity of conservation strategies aiming to protect distinct *campo rupestre* groups along with associated surrounding habitats.

5. Conclusion

We found an overall lack of compositional identity across the *campos rupestres* woody flora, which is driven by their geographically disjunct distribution with its associated environmental heteregoneity and floristic influence from surrounding habitats. Therefore, we stress the necessity of considering such floristic and environmental heterogeneity in conservation, management and research planning and emphasize the need for multiple protected areas across the separate floristic groups of *campos rupestres*. Our findings also indicate that *campos rupestres* and their surrounding lowland *cerrados* exchange woody plant species regularly and, therefore, merit simultaneous conservation attention. Conservation units aiming to protect *campo rupestre* biodiversity should not be limited to *campo rupestre* areas. Rather, effective protected areas should function as ecological corridors connecting multiple *campos rupestres* through lowland *cerrados*. We predict

that future studies will confirm that lowland *cerrados* are linking geographically distant woody plant populations, thus improving ecological functionality of *campos rupestres*; such as pollen flow between *campo rupestre* sites.

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Figure 1. Hierarchical clustering for 4,637 South American woody plant communities based on their species composition. The dissimilarity measure and linkage methods used were Simpson and unweighted group average, respectively. The woody plant communities are discriminated by different colours: black, 621 *cerrado* woody savannas; red, 115 *campos rupestres*; gray, 3,901 other South American woody plant communities.

Figure 2. Rank occupancy of *campo rupestre* woody plant species. Each gray circle represents a *campo rupestres* species in our dataset. Darker shades of gray indicate overlapping circles (i.e., two or more species have similar occupancies). Circles below the dashed line occur in 20 or less *campo rupestres* sites (80% of the 1,055 species).

Figure 3. Ordination of 115 sites of *campo rupestre* inferred from non-metric multidimensional scaling (NMDS) of their woody plant species composition (a), and geographical variation of species composition and mean annual precipitation (b). NMDS scores were plotted in the ordination diagram after assigning a colour to each site according to its position in the two-dimensional ordination space (axes 1 x 2). Variation in surface rockiness, mean annual temperature and temperature seasonality were fitted in ordination space by generalized linear model. Colours of circles plotted across geographic space are identical to the colours of circles in the NMDS scatter plot. Variation in mean annual precipitation was fitted across geographic space by generalized additive model. Dashed lines in (b) represent Brazilian state borders. AF = Atlantic Forest Domain (white along the Atlantic coast); Am = Amazon (white in

northwestern South America); Ca = Caatinga (light gray); Ce = Cerrado Domain (dark gray).

Figure 4. Conservation assessment of *campo rupestre* woody plant communities. (a) Distribution of protected and unprotected *campos rupestres* in South America. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders. **(b)** Conservation status of the two-dimensional floristic space of *campo rupestre* woody plant communities. Circles represent the position of *campo rupestre* sites in ordination space inferred from non-metric multidimensional scaling (NMDS axes 1 x 2) and are identical to the position of *campos rupestres* in Fig. 3a. Variation in surface rockiness, mean annual temperature and temperature seasonality were fitted in ordination space by generalized linear model. Contours representing mean annual precipitation were fitted in ordination space by generalized additive model. Dashed lines in (a) represent Brazilian state borders.
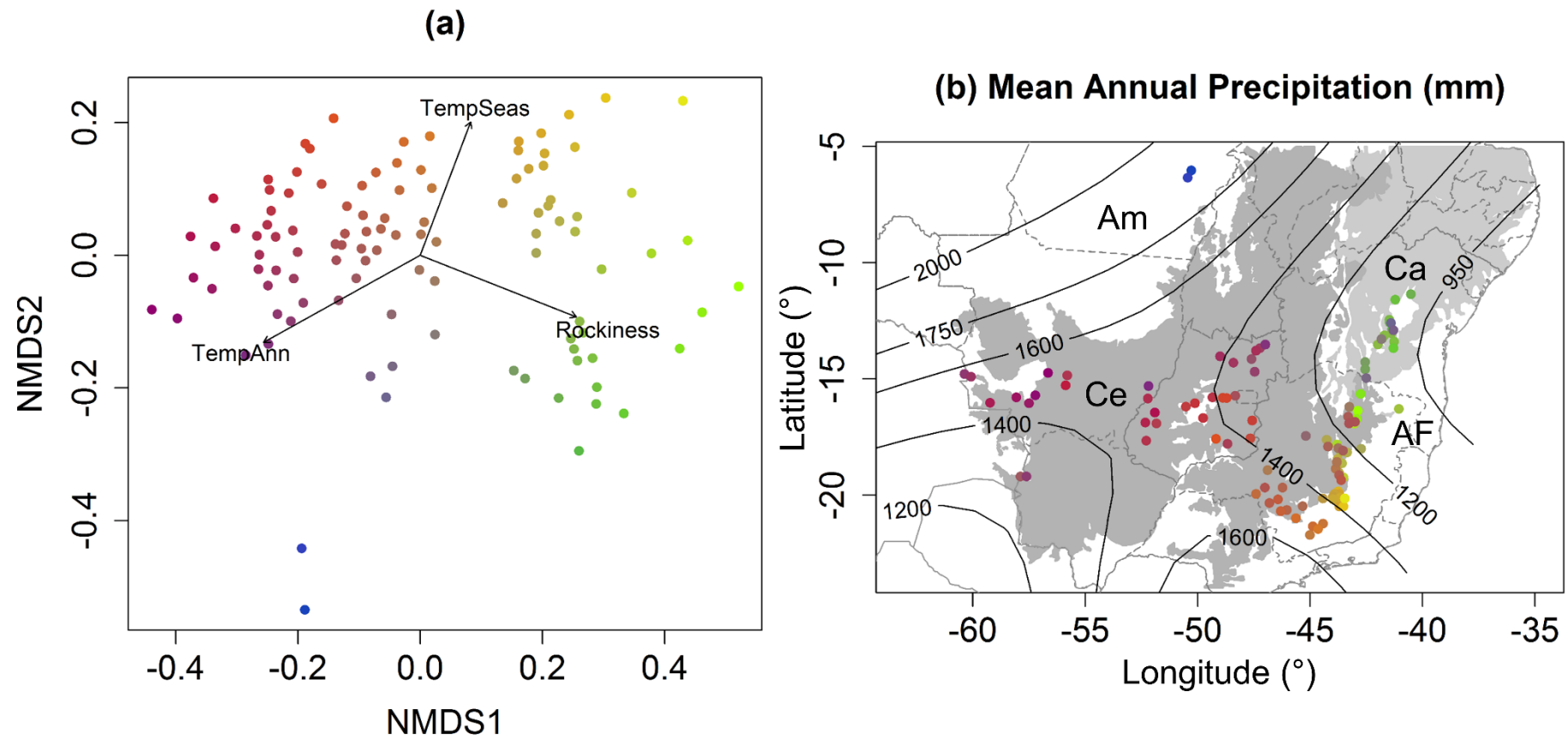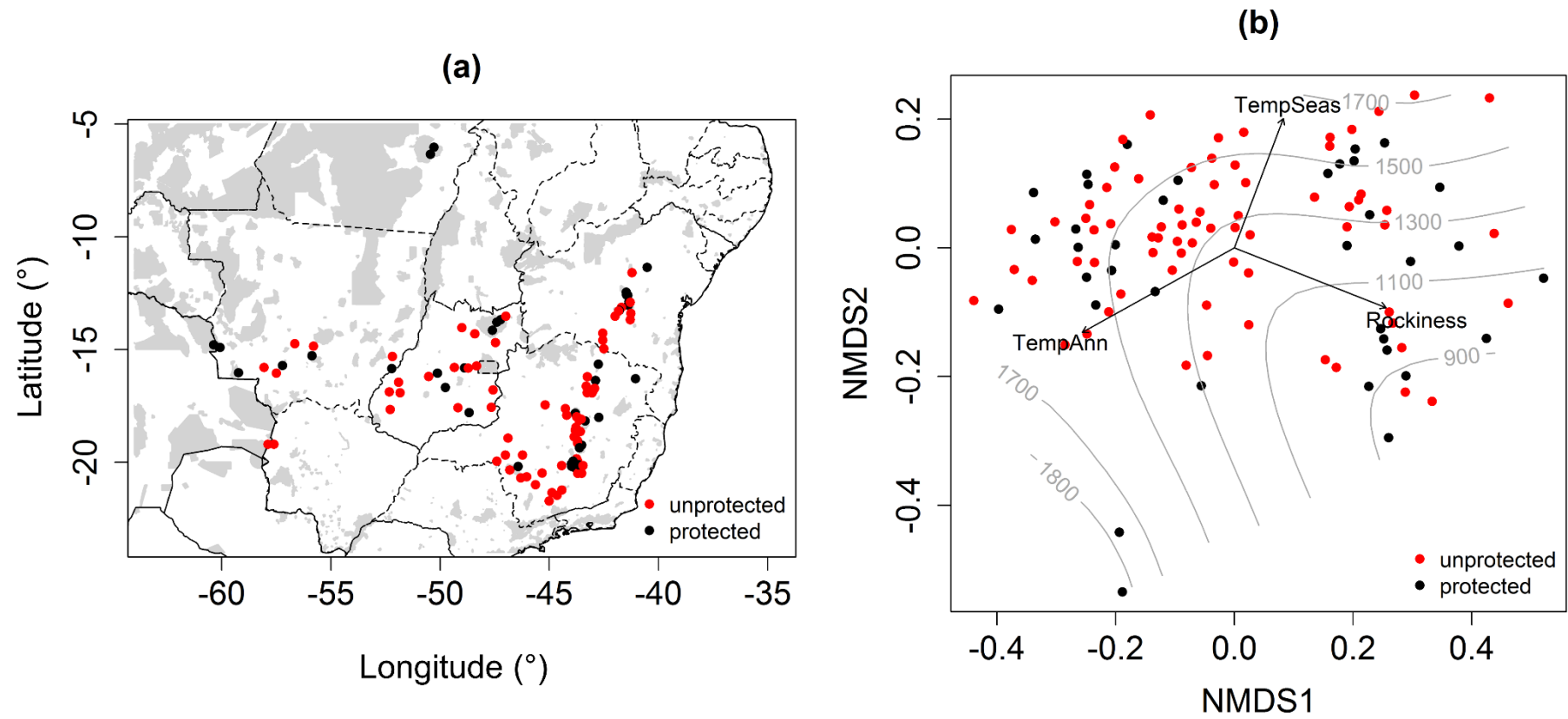
Figure 1

Figure 2

(a)

(b) Mean Annual Precipitation (mm)

Figure 3

(a)

(b)
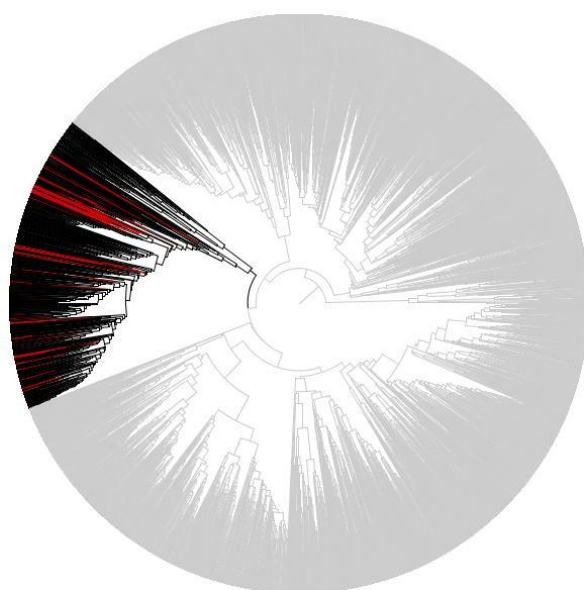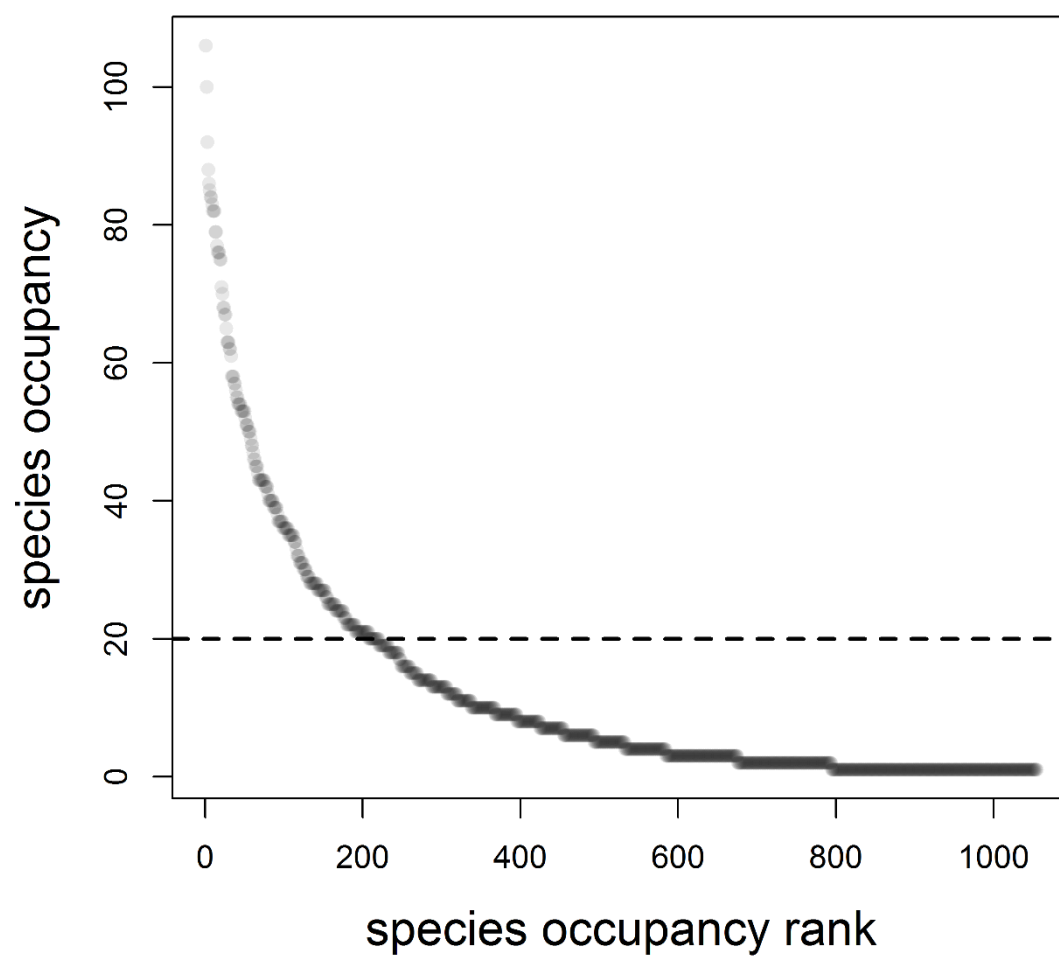
Figure 4

Table 1. Table 1 Variables selected for the study of environmental drivers of community turnover across *campos rupestres* of South America. The variables shown are ordered by the amount of explanation in species composition variation across the *campos rupestres*. Goodness-of-fit of the predictor variables were assessed through adjusted coefficients of determination, Akaike Information Criterion (AIC), F-values and significance tests (p-value). VIF, variance inflation factor, was obtained using the r-squared value of the regression of one variable against all other explanatory variables.

	cumulative adjusted R^2	AIC	F-value	p-value	VIF
Rockiness	0.12	-55.55	15.86	0.002	2.64
Mean annual temperature	0.15	-59.75	6.2	0.002	7.20
Mean annual precipitation	0.18	-63.03	5.22	0.002	1.69
Temperature seasonality	0.21	-65.07	3.93	0.002	3.77
Precipitation seasonality	0.22	-66.34	3.14	0.002	5.59
Grass coverage	0.23	-67.44	2.96	0.002	1.78
Soil drainage	0.24	-67.61	2.03	0.002	1.29
Soil fertility	0.25	-67.79	2.03	0.002	4.17
Days of frost	0.25	-67.71	1.77	0.002	1.29
Mean daily temperature range	0.26	-67.62	1.74	0.002	1.50
Precipitation of driest month	0.26	-67.45	1.65	0.002	6.21
Cloud interception	0.27	-67.2	1.57	0.002	4.42
Sandiness	0.27	-66.66	1.29	0.028	4.75