

PHYLOGENETIC DIVERSITY
PATTERNS REVEAL CONTRASTING
AND SPATIALLY DEPENDENT
EVOLUTIONARY HISTORIES IN A
HYPER-DIVERSE MONTANE
VEGETATION COMPLEX

Y A G O B A R R O S - S O U Z A

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Phylogenetic diversity patterns reveal contrasting and spatially dependent
evolutionary histories in a hyper-diverse montane vegetation complex

Padrões de diversidade filogenética revelam histórias evolutivas contrastantes e espacialmente dependentes em
um complexo vegetacional montanhoso hiper diverso

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Phylogenetic diversity patterns reveal contrasting and spatially dependent evolutionary histories in a hyper-diverse montane vegetation complex

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Abstract

Old, climatically buffered, infertile landscapes (OCBILs) comprise some of the world's most diverse floras. Such floras, according to OCBIL theory, are expected to favour the persistence of old lineages. Nevertheless, recent and fast diversification apparently played a major role in the evolutionary history of a Neotropical OCBIL, the *campos rupestres*. Here we aimed to elucidate the distribution of concurrent evolutionary processes by assessing fine spatial patterns of phylogenetic diversity and endemism in the *campos rupestres*. Based on predictions of the OCBIL theory and on the insular nature of this vegetation, we proposed that (1) patterns of phylogenetic overdispersion and paleo-endemism predominate, revealing a flora mainly composed by relatively old lineages. Furthermore, (2) both the taxonomic and the phylogenetic composition should be highly geographically structured if present and past barriers to dispersion have restricted spatial connections between different parts of the *campos rupestres*. To test those hypotheses, we calculated taxonomic and phylogenetic alpha and beta diversity metrics and conducted categorical analyses of neo- and paleo-endemism (CANAPE) for six *campos rupestres*' representative angiosperm groups. Our analyses were based on occurrence data gathered from herbaria databases and on recently published, well-sampled phylogenetic hypotheses. We defined grid cell's size according to redundancy values in order to maintain satisfactory sampling rates while preserving spatial resolution. We found that phylogenetic overdispersion predominates in the *campos rupestres* flora. However, this general pattern is permeated by both lineage- and site-specific phylogenetic clustering, suggesting that recent diversification events depend on particular

regional conditions and on the overall maintenance of old lineages across the *campos rupestres*. CANAPE shows that endemism patterns differ between regions, but paleoendemism is widespread and particularly prominent where phylogenetic overdispersion is more evident. Moreover, although taxonomic composition is highly geographically structured and seems to be influenced by different types of surrounding vegetation, phylogenetic composition indicates past spatial connections that might have been established by different processes. These results highlight the importance of considering the spatial component when investigating diversification patterns and suggest that the flora of old, climatically buffered, infertile landscapes might have been shaped by spatially dependent evolutionary processes.

Keywords— OCBIL; *campos rupestres*; Brazilian Central Plateau; *Serra da Canastra*; Espinhaço Range; phylogenetic diversity; CANAPE; beta diversity; phylobeta diversity

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1 Introduction

Old, climatically buffered, infertile landscapes (OCBILs) are scarcely distributed around the globe but comprise some of the world's most diverse floras (Berry and Riina, 2005; Born et al., 2007; Burbidge, 1960; Giuletta et al., 1997; Hopper and Gioia, 2004). These floras are inherently fragmented and often distributed within matrices of young, disturbed and fertile landscapes (Gallagher, 2016; Hopper, 2009; Hopper et al., 2016; McQuoid, 2014). Coupled with long-term climatic and geological stability and reduced dispersion capacity (Colville et al., 2020; Hopper, 2009), this insular nature favours high levels of species turnover and endemism (Bradshaw et al., 2015; Burgman, 1988; Cowling, 1990; Cowling and McDonald, 1998; Cowling et al., 1994; Gibson et al., 2017; Yates et al., 2019) and an elevated persistence of relict species and old lineages (Barbosa et al., 2015; Berry and Riina, 2005; Burbidge, 1960; Goldblatt and Manning, 2002; Hopper et al., 1999; Hopper and Gioia, 2004; Warren and Hawkins, 2006). Given their indisputable biological importance, OCBILs have received increased attention since Hopper (2009) first developed a framework for hypothesis testing in these areas. However, although considerable research effort has been devoted towards the Greater Cape Floristic Region (Allsopp et al., 2014), the Southwest Australian Floristic Region (Byrne et al., 2011; Cook et al., 2015; Groom and Lamont, 2015; Lambers et al., 2014) and the Pantepui of the Guyana Shield (Salerno et al., 2015, 2012), only recently the Brazilian *campos rupestres* have been recognised as an OCBIL (Hopper et al., 2016; Silveira et al., 2016).

The *campos rupestres* are a hyper-diverse montane vegetation complex that encompasses one of the most speciose and endemic floras in the tropics (Alves and Kolbek, 1994; BFG, 2015; Giuletta and Pirani, 1988; Giuletta et al., 1997). Despite corresponding to less than 1% of Brazil's terrestrial territory, they amount to approximately 15% of its vascular plant diversity (Fernandes et al., 2014; Giuletta et al., 1997; Rapini et al., 2008; Silveira et al., 2016). The *campos rupestres* occur on ancient quartzite, sandstone and ironstone formations (Alkmim, 2012; Alkmim and Marshak, 1998; Almeida-Abreu and Renger, 2017; Fernandes, 2016; Pedreira and De Waele, 2008) and are constituted by a mosaic of vegetation physiognomies that includes grasslands and rock-dwelling plant communities intermingled with a

few patches of gallery forests (for a detailed review, see Alves et al., 2014; Fernandes, 2016; Silveira et al., 2016). The Espinhaço Range, a mountain chain distributed along the Brazilian states of Minas Gerais and Bahia, concentrates most of this vegetation (Giulietti et al., 1997), but the *campos rupestres* also occur in other mountainous areas such as the Brazilian Central Plateau (Goiás) and the *Serra da Canastra* (western Minas Gerais; Figure 1; Silveira et al., 2016). These are all topographically heterogeneous regions located between 900 and over 2,000 m a.s.l. and often interrupted by lowland vegetation (Giulietti and Pirani, 1988; Giulietti et al., 1997; Silveira et al., 2016).

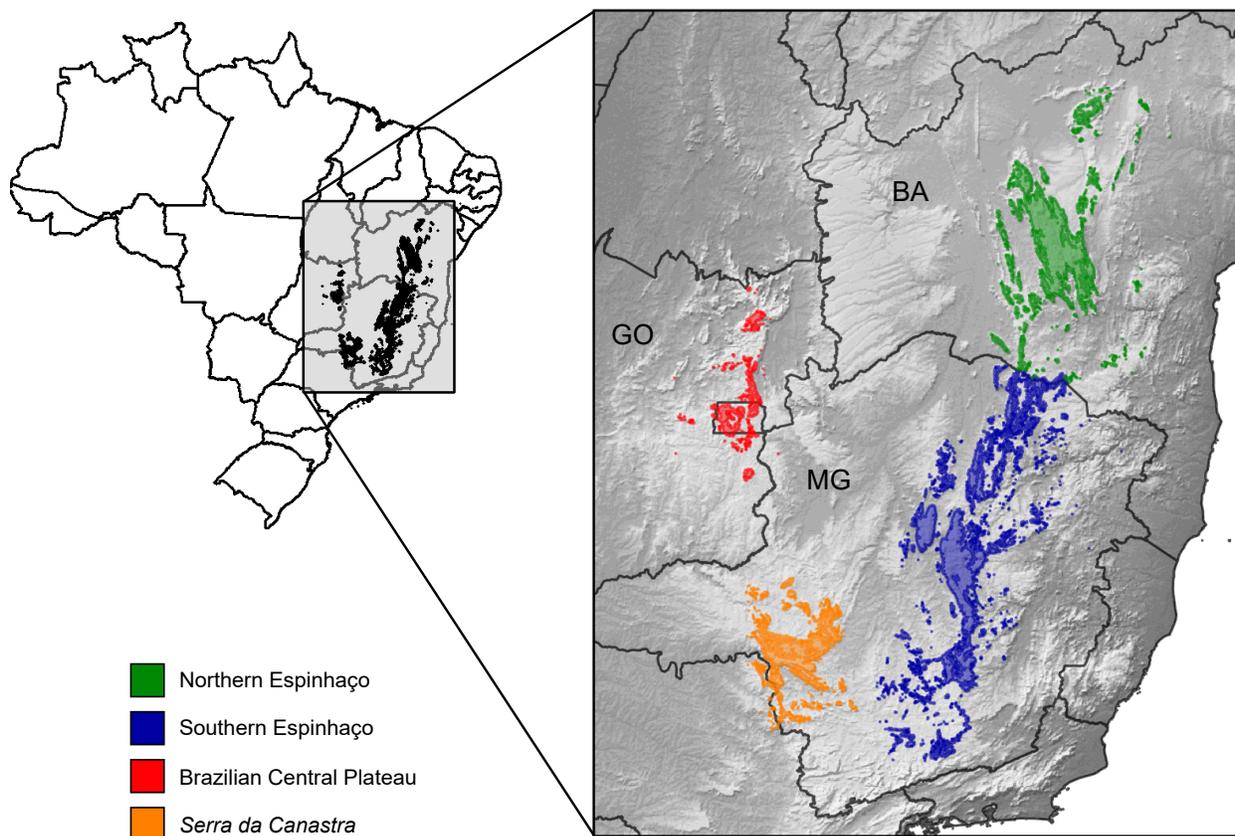


Figure 1: Main distribution of the *campos rupestres* within the Brazilian territory and across the states of Bahia (BA), Minas Gerais (MG) and Goiás (GO). This vegetation complex is concentrated in the Espinhaço Range, but also occurs in the Brazilian Central Plateau and the *Serra da Canastra*. Here we considered the *campos rupestres* as divided into four different sections: the Southern and Northern Espinhaço, the Brazilian Central Plateau and the *Serra da Canastra*. Adapted from Silveira et al. (2016).

Due to this highly discontinuous distribution, most *campos rupestres* species are spatially restricted (Conceição and Pirani, 2007; Echternacht et al., 2011, 2010; Giulietti and Pirani, 1988; Trovó et al., 2013) and/or occur as small, disjunct populations (Giulietti et al., 1997; Lousada et al., 2013). This has often been evoked to support the species-pump hypothesis,

which attempts to explain the exceptionally high diversity and endemism rates of the *campos rupestres* (Giulietti et al., 1997; Harley, 1988) and other island-like systems (e.g. Nevado et al., 2018; Schoville et al., 2012). According to this hypothesis, the range of montane populations isolated during interglacials would increase during periods of global glaciation. Given the recurrent climatic shifts that marked some periods such as the Tertiary and especially the Quaternary (Adams et al., 1999; Zachos et al., 2008), expansion-contraction cycles would promote irregular gene flow followed by an increase in local diversification favoured by isolation (Giulietti et al., 1997) and, in some cases, hybridisation (e.g. Antonelli et al., 2010). In effect, range expansions of *campos rupestres* populations might have been common during glaciations in the Pleistocene (Barbosa et al., 2015; Barres et al., 2019; Bonatelli et al., 2014; Collevatti et al., 2009), a period over which most speciation events presumably took place (Vasconcelos et al., 2020). Therefore, the species-pump hypothesis predicts that *campos rupestres* plant communities are mostly composed by recently diversified lineages with a narrow distribution (i.e. neo-endemics; Giulietti et al., 1997; Harley, 1988), a scenario in fact confirmed by some studies (e.g. Rando et al., 2016; Ribeiro et al., 2014; Souza et al., 2013; Trovó et al., 2013).

However, OCBIL theory predicts a predominance of old communities instead (Hopper, 2009; Hopper et al., 2016). As proposed for the Cape and the southwestern Australia (Cowling et al., 2014), long term climatic and topographical stability would have promoted the establishment of refugia, favouring the persistence of old clades and shaping contemporary hyper-diversity by supporting the accumulation of species. Indeed, although this prediction has been recently contested (Cortez et al., 2020), several evidences indicate that the *campos rupestres* harbour a substantial proportion of ancient lineages, some of which might have diversified as early as the Oligocene/Miocene (Alcantara et al., 2018; Antonelli et al., 2010; Gustafsson et al., 2010; Rapini et al., 2007; Zappi et al., 2017). This reveal an ancient origin for this vegetation complex and places the *campos rupestres* as the older open vegetation in the Neotropical region (Hughes et al., 2013). The putative simultaneous occurrence of old and recently diversified lineages led some authors to propose that the *campos rupestres* represent both museums (ancient refugia) and cradles (areas of recent diversification; e.g. Bitencourt and Rapini, 2013; Fiorini et al., 2019). Evidently, an one-size-fits-all explanation

to elucidate patterns of diversity is certainly inaccurate. Rather, complex and idiosyncratic evolutionary processes most likely have shaped the *campos rupestres* flora.

These processes probably have depended on the interaction between a number of intrinsic and extrinsic factors, such as ecophysiological requirements (see Fernandes, 2016) and distribution of abiotic conditions across space (e.g. Neves et al., 2018; Schaefer et al., 2016a,b). Nonetheless, even though space is an undeniably important component in evolution and biogeography (Crisp et al., 2011; Croizat, 1962; Nürk et al., 2019), little is known about the distribution of old and/or recently diversified lineages in the *campos rupestres* (however, see Bitencourt and Rapini, 2013). Because of the high levels of topographical, climatic and edaphic heterogeneity of this vegetation complex (Giulietti et al., 1997; Neves et al., 2018; Schaefer et al., 2016a,b), it is clear that acknowledging the spatial component of diversity patterns is of a paramount importance to better understand the *campos rupestres*' evolutionary history.

Spatial analyses of phylogenetic diversity and endemism are reliable approaches to address this issue (e.g. Forest et al., 2007; Heenan et al., 2017; Mishler et al., 2014; Scherson et al., 2017). Phylogenetic diversity (Faith, 1992) offers helpful insights into biogeographical processes shaping local communities (Webb et al., 2002), such as in situ diversification and persistence of deeply diverged lineages (e.g. Boyer et al., 2016; Divya et al., 2020). Likewise, the distinction between centres of neo- and paleo-endemism (e.g. Mishler et al., 2014) informs about the spatial distribution of both recently and deeply diverged lineages with a narrow geographic range. Although these methods indicate how different localised evolutionary processes are distributed across space, they do not capture spatial variation of phylogenetic composition (i.e. phylogenetic turnover). This may only be detected by phylo-beta diversity metrics (e.g. Lozupone and Knight, 2005), which, when considered in tandem with beta diversity (e.g. Jaccard, 1901), provides valuable information on past connections between areas and historical processes structuring communities (Graham and Fine, 2008).

Therefore, following recent research priorities for this hyper-diverse montane vegetation (Morellato and Silveira, 2018), we aimed to elucidate the distribution of concurrent evolutionary processes by assessing fine spatial patterns of phylogenetic diversity and endemism in the *campos rupestres*. These patterns are hereby investigated for six angiosperm groups

representative of this vegetation complex, and, thus, good models to infer general patterns for the whole flora. Based on OCBIL theory predictions, we expect that phylogenetic overdispersion and paleo-endemism will predominate if the persistence of old lineages is a widespread and dominant process in the *campos rupestres*. If this is not true and plant communities are mostly composed by recently diversified lineages, phylogenetic clustering and neo-endemism should prevail. Moreover, given the highly topographical, climatic and edaphic heterogeneity of the *campos rupestres*, we expect that both the taxonomic and the phylogenetic composition of this vegetation complex are highly geographically structured if past and present barriers to dispersion have restricted spatial connections between different mountains.

2 Methods

To answer our questions, we used six model groups for which published, well-sampled phylogenetic hypotheses are available, namely *Mimosa* L. (Leguminosae), *Diplusodon* Pohl (Lythraceae), *Comanthera* L.B. Sm. (Eriocaulaceae), Velloziaceae J. Agardh, Lychnophorinae Benth. (Asteraceae) and *Paepalanthus* Mart. (Eriocaulaceae). These groups are well-represented in the *campos rupestres*, their life forms range from herbs to trees and they comprise both monocots and eudicots. Therefore, we believe they were well suited for our analyses and adequate to infer general diversity patterns in the *campos rupestres*.

Because the *campos rupestres* are a complex assemblage of different vegetation physiognomies, patches of gallery forests and the *campos rupestres sensu stricto* (Silveira et al., 2016) are intertwined within the presumed *campos rupestres*' occurrence area. While this might have biased our results, we took especial care to choose only groups that are mostly restricted to grasslands and associated vegetation on rocky outcrops.

Our approach was divided into two parts: (1) data compilation and cleaning and (2) spatial analyses. Bellow we present workflows for each step, all of which was conducted in the R statistical computing environment (R Core Team, 2013).

2.1 Data compilation and cleaning

We retrieved occurrence data in the whole Brazilian territory for our model groups from two databases, specifically GBIF (GBIF.org, 2020) and speciesLink (CRIA, 2020). Occurrence data from these databases were then concatenated into a single data set for each group in order to facilitate posterior treatment. To reduce data dimensionality, we removed all variables but 15, which included information relevant for data cleaning and spatial analyses. These were: institution code, collection code, collection catalogue number, generic epithet, specific epithet, infraspecific epithet, original database name, names of determiners, record number, basis of record, collectors' names, federative unity of occurrence, municipality of occurrence, field notes, latitude and longitude. We also assigned each entry with an unique identifier number.

To clean our data, we followed the methods proposed by Magdalena et al. (2018), with some changes included. The cleaning procedure was divided into five steps: (1) defining a coordinate reference system; (2) standardising names of determiners, filtering by taxonomic specialists and checking for typos and taxonomic synonyms; (3) selecting and evaluating records with geographic coordinates; (4) identifying records without geographic coordinates; and (5) standardising names of geographic units and inferring geographic coordinates based on municipalities or field notes. These steps were preceded by a pre-refinement routine.

2.1.1 Pre-refinement

Although speciesLink and GBIF have independent data, they also share identical records that would be duplicated in the merged data set. In order to remove duplicated information, we kept only one copy of records whose values in the following attributes were identical: institution code, collection code and collection catalogue number. We did so because redundancy analysis (see below) relies on the ratio between richness and sampling. Also, a reduced number of records facilitate cleaning procedures.

Next, we removed records without identification at species level, without names of determiners or without vouchers (field observations). We also standardised federative unities names and kept only observations from federative unities covering the *campos rupestres* (i.e. Bahia, Minas Gerais, Goiás, Federal District, Mato Grosso, Paraíba and Pernambuco; Silveira

et al. 2016). We chose to maintain records with no information on federative unity of occurrence in order to avoid losing data with information on geographic coordinates, municipality of occurrence or field notes. These records would be cleaned in following steps.

2.1.2 Coordinate reference system

We established the World Geodetic System (WGS84) as our coordinate reference system. Considering that WGS84 is the reference frame used by the Global Positioning System (GPS), we found it appropriate when dealing with coordinates generated by a GPS receiver device, which is the case for occurrence data retrieved from GBIF and speciesLink.

2.1.3 Filtering by taxonomic specialists and checking for taxonomic synonyms

Taxonomically unreliable data is a source of bias in spatial diversity analyses (Goodwin et al., 2015). To avoid this issue, we filtered the data set by determiners' names, keeping only observations identified by taxonomic specialists. We defined a taxonomic specialist as an author of monographs, floras or taxonomic reviews on the family of the focal group. This step was preceded by a semi-automatic routine for standardisation of determiners' names based on Jaro-Winkler distances (Jaro, 1989). We manually checked determiners' names with a similarity of 70% or more with any of the taxonomic specialists names.

Also, to further improve the quality of our data, we checked for taxonomic synonyms and typos in species' names. We did this by generating a list with all species' names and manually evaluating them with the aid of Tropicos (Tropicos.org, 2020), The Plant List (The Plant List, 2020) and Reflora (Reflora, 2020). Synonyms were replaced by accepted names and typos were corrected. We removed records of species whose names were not found in any of the aforementioned platforms.

2.1.4 Evaluation and inference of geographic information

After removing taxonomic dubious data, we focused on cleaning geographic information. This procedure was divided into two steps. First, we evaluated coordinate quality, and then we inferred georeference data for records lacking or with invalid coordinates.

Authenticity of geographic information was assessed with the 'CoordinateCleaner' package (Zizka et al., 2019). Records fitting one or more of the following criteria were considered invalid: (1) identical or plain zero values for latitude and longitude; (2) points falling in oceans; (3) geographic isolation (not applied to species with less than seven records); and (4) proximity to biodiversity institutions. 'CoordinateCleaner' also flags records near the centroid of a country's capital by default, but we did not consider them invalid because the Brazilian capital is an area of interest.

In order to infer coordinates for records without or with invalid georeferences, we used data on municipality of occurrence or field notes. To do so, we first standardised these two attributes by removing accents and special characters and capitalising major words. We then extracted a list of municipalities in which the *campos rupestres* occur by overlapping the Brazilian municipalities (IBGE, 2019) with the distribution of the *campos rupestres* according to Silveira et al. (2016). Next, we standardised this list following the same routine as for municipalities and field notes, filtered our data set and inferred coordinates for each record based on the centroid of its municipality. For records without this information, we used field notes, as these often mention the municipalities in which the records occur. Finally, we removed all records, including those evaluated in previous steps, whose coordinates fell outside the *campos rupestres*' distribution, making it ready for the spatial analyses and ensuring a data set comprised only by species occurring within the area of interest.

2.2 Spatial analyses

In an attempt to understand the taxonomic and phylogenetic structure and composition of plant communities in the *campos rupestres*, we calculated richness and phylogenetic diversity (PD; Faith, 1992) and ran UPGMA analyses using Jaccard distance (Jaccard, 1901) and UniFrac (Lozupone and Knight, 2005). We also conducted categorical analyses of neo- and paleo-endemism (CANAPE; Mishler et al., 2014) to assess the distribution of neo- and paleo-endemic lineages.

Since most of our analyses rely on phylogenetic trees, we obtained the most recent phylogenetic hypothesis for each group (Alcantara et al., 2018; Andrino et al., 2020; Echternacht et al., 2014; Inglis and Cavalcanti, 2018; Loeuille et al., 2015; Simon et al., 2011). Trees were

pruned to include only species present in the distribution matrices. Similarly, we removed from these matrices species not present in the phylogenetic trees. This assured consistency between phylogenetic trees and distribution matrices, which is fundamental to run phylogeny-based analyses. Also, we scaled every tree by total tree length, making it possible to compare the results for different groups and with future studies. All analyses were conducted at species-level.

2.2.1 Spatial grids

The analyses of spatial patterns of diversity primarily depend on the establishment of a spatial grid cells' size. Although there is no way to objectively define the best resolution (Blackburn and Gaston, 2002), this step is fundamentally important, since grid resolution could affect the results of biogeographical studies (Rahbek, 2005; Willis and Whittaker, 2002). Thus, in order to select adequate grid cells' size, we used redundancy values, which assesses sampling effort by considering both richness and number of samples ($1 - [\text{richness}/(\text{number of samples})]$). A redundancy value close to one indicates good sampling; zero represents only one sample per taxa (Scherson et al., 2017).

Once we generated grid cells based on the distribution area of the *campos rupestres*, with sizes ranging from 0.1 per 0.1 DD to 5.0 per 5.0 DD, we calculated redundancy for all cells at different sizes and assessed the relationship between grid cells' size and redundancy (calculated as the median of all redundancy values at a given cell's size). Redundancy, although somehow arbitrary, aided us to find a good trade-off between grid cell' size and sampling. After choosing the best grid resolution, we removed grid cells that had only one sample per species, thus avoiding unreliable data. This eliminated cells located in federative unities in which the *campos rupestres* are less represented, such as Mato Grosso, Paraíba and Pernambuco.

2.2.2 Alpha diversity

We calculated two metrics of alpha diversity: species richness and PD (Faith, 1992). We also tested the commonly found correlation between them (Faith, 1992; Forest et al., 2007; Polasky et al., 2001; Rodrigues and Gaston, 2002; Scherson et al., 2017; Tôrres and Diniz-Filho, 2004)

with Spearman's correlation tests (Spearman, 1904). Using the 'picante' package (Kembel et al., 2010), we calculated PD for each group as the sum of branch lengths connecting a given set of species to the root of a phylogenetic tree (Faith, 1992).

Because PD is often correlated with richness, decoupling these two metrics provides a powerful tool to assess community phylogenetic structure and, thus, offers valuable insights into macroecological and biogeographical processes (Webb et al., 2002). We did this by running linear regression analyses in order to model the relationship between phylogenetic diversity and richness and then assessed the residuals of these models (PD \sim SR residuals). When higher or lower than zero, PD \sim SR residuals may indicate PD higher or lower than expected based on richness, respectively (Brown et al., 2020; Colville et al., 2020; Forest et al., 2007).

Also, to get a more comprehensive perspective on the spatial distribution patterns of richness, PD and PD \sim SR residuals, we combined data from all groups. Because the phylogenetic trees were scaled by total tree length, PD was comparable between results. Thus, we obtained total richness and PD by summing these metrics for all groups in each cell. We used these data to run a linear regression analysis and then assessed PD \sim SR residuals for all groups combined.

2.2.3 Beta and phylogenetic beta diversity metrics

In order to evaluate whether the plant communities in the *campos rupestres* are taxonomically and/or phylogenetically structured, we conducted UPGMA analyses for each group using dissimilarity matrices based on Jaccard distance (beta diversity; Jaccard 1901) and UniFrac (phylobeta diversity; Lozupone and Knight 2005). As with alpha diversity metrics, we also performed an UPGMA analysis based on Jaccard distance for all groups combined simply by merging our distribution matrices. This approach was not possible with UniFrac, however, since this metric relies on pairwise calculations based on phylogenetic trees.

The consensus dendrograms were each based on 1000 replicates, with a consensus criterion of 0.5. Defining a cutting level in a dendrogram in order to visualise meaningful groups is highly arbitrary, but we based our decision on fusion level values (Borcard et al., 2018) and attempted to maintain a consistent number of clusters between all groups. Prior to

conducting these analyses, we removed singletons (species whose occurrence is restricted to a single cell) in order to avoid data noise. Jaccard distance assesses the degree in which a given pair of communities are dissimilar to each other. Likewise, UniFrac gives the proportion of the phylogenetic tree which is not shared between two sites. These metrics provide values ranging from zero to one, with zero indicating complete similarity and one implying total dissimilarity. These analyses were conducted using the 'recluster' package (Dapporto et al., 2013).

We decided to use Jaccard distance and UniFrac to assess both present and past aspects of community assembling processes. While beta diversity provides useful information on the amount of taxonomic overlapping between sites, phylobeta diversity adds the dimension of evolutionary time into this context (Emerson and Gillespie, 2008; Graham and Fine, 2008; Wiens and Donoghue, 2004), providing useful knowledge on potential historical constraints.

2.2.4 CANAPE

The categorical analyses of neo- and paleo-endemism were conducted following the methods developed by Mishler et al. (2014), which involve prior calculation of PE (Rosauer et al., 2009) and RPE (Mishler et al., 2014). CANAPE consists of a two-step statistical process that identifies areas of statistically significant neo- or paleo-endemism. We based this process on a null model which randomises occurrence matrices while fixing richness and frequency of occurrence (999 replicates for each instance). PE and RPE were calculated with the 'PDcalc' package by D. Nipperess (under development). We ran CANAPE according to the algorithm hereinafter specified.

First, to evaluate if a given grid cell harbours statistically significant phylogenetic endemism, either actual or comparative PE (i.e. PE based on a tree with equal branch lengths) must be significantly high (one-tailed test, $\alpha = 0,05$). If this condition holds, then the grid cell is subsequently defined as one of the non-overlapping categories of endemism distinguished by CANAPE. If RPE is significantly low or high (two-tailed test, $\alpha = 0,05$), the grid is respectively defined as a neo-endemic or paleo-endemic site. Otherwise, if this condition does not hold but both actual and comparative PE are significantly high (one-tailed test, $\alpha = 0,05$), the grid is a centre of mixed endemism, a category which has neither a prevalence

of long, rare branches nor of short, rare ones, but a mix of both. A grid which is defined as such can be further categorised as a super endemic site if both actual and comparative PE are significantly high at a lower confidence interval ($\alpha = 0,01$). In this study, we found some cells for which the first condition held true (i.e. either actual or comparative PE were significantly high) but then did not fall in any of the categories CANAPE is able to distinguish. We defined those cells as harbouring an "uncertain" endemism type.

Because we did not consider occurrence data within adjacent areas, we recognise that a potential bias in our analyses is that they are only relative to the *campos rupestres*. While this could be problematic regarding analyses of endemism, CANAPE relies on the range of phylogenetic branches rather than that of terminals. Besides, the *campos rupestres* are known to harbour an exceedingly high proportion of endemics (Giulietti et al., 1997), most of which are restricted to small areas (e.g. Bitencourt and Rapini, 2013; Echternacht et al., 2011; Rapini, 2010; Trovó et al., 2013). Thus, we believe our data and analyses were robust enough to assess the distribution of different types of endemism within the *campos rupestres*' range. Nevertheless, including the surrounding vegetation in future studies will certainly improve knowledge on these patterns.

3 Results

3.1 Redundancy

Redundancy values for all groups steadily increase together with grid cells' size until reaching a plateau around 0.9 (Figure 2). However, a value of 0.9 for redundancy defines cells' sizes too large to recover variations in spatial patterns. Hence, aiming for a balance between resolution and redundancy, we chose to use cells of 0.6 per 0.6 decimal degrees (roughly 66 km per 66 km), whose redundancy values fluctuate between 0.6 and 0.8.

3.2 Richness and phylogenetic diversity

Richness in the *campos rupestres* is concentrated in the Southern Espinhaço, with some cells including as many as 160 species, and, to a lesser extent, in the Brazilian Central

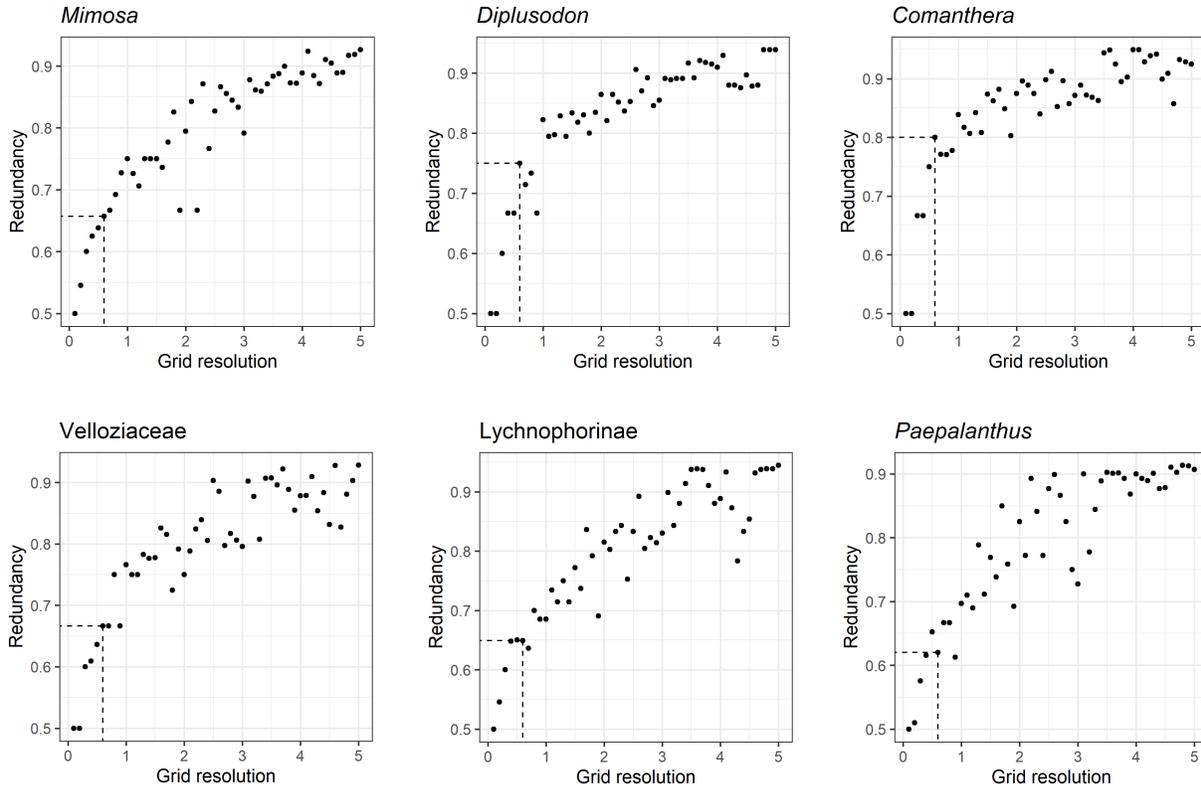


Figure 2: Median values of redundancy based on data of the respective focal group plotted against grid resolution in decimal degrees. The higher redundancy is, the better the sampling quality. Note that redundancy for all groups steadily increases alongside grid cells' size, reaching a plateau at around 0.9. Dashed lines indicate redundancy for the chosen grid resolution (0.6 per 0.6 decimal degrees).

Plateau (Figure 3). Particularly in the Central Plateau, richness peaks in the grid cell that includes the national capital. Although automated georeferencing around country capitals is a common error source in georeferenced databases (Zizka et al., 2019), removing those records to avoid bias could have a negative effect, underestimating analyses' results by ignoring *campos rupestres* that do occur in that grid cell. Thus, we decided to keep those records, particularly as our results are in accordance with taxonomic studies indicating high *Mimosa* and *Diplusodon* diversity in the Central Plateau (Barneby, 1991; Cavalcanti, 1995, 2007).

As expected (Faith, 1992; Forest et al., 2007; Polasky et al., 2001; Rodrigues and Gaston, 2002; Scherson et al., 2017; Tôrres and Diniz-Filho, 2004), richness and phylogenetic diversity are strongly and positively correlated (Figure 4). Thus, especially when considering all groups combined, the grid cells with the highest PD values are located in the Southern Espinhaço (Figure 5). However, assessing the residuals of the linear relationship between richness and PD reveals key insights into the phylogenetic structure of the *campos rupestres* communities.

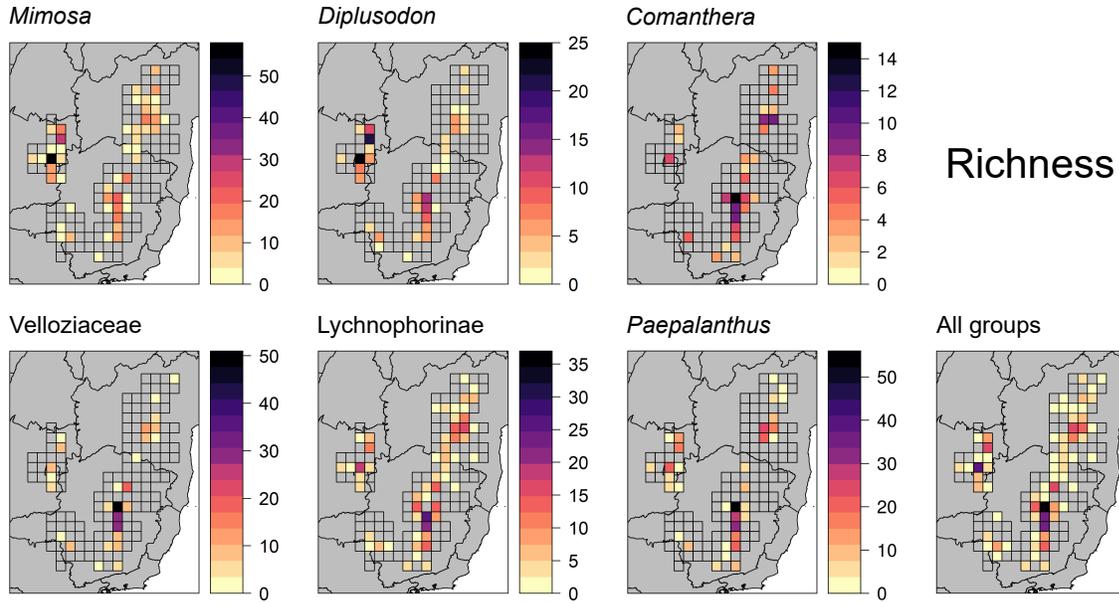


Figure 3: Spatial distribution of species richness of each focal group individually and of all groups combined across the *campos rupestres*. Transparent grid cells indicate absent data.

Although merging data from all groups is a good approach to identify general patterns, we exercised caution in analysing the spatial distribution of total $PD \sim SR$ residuals, as some groups contributed much less than others to the combined results (Figure 6).

Positive and negative residuals respectively indicate phylogenetic overdispersion and clustering (i.e. communities in which PD is higher or lower than expected based on richness). Distribution patterns of residuals differ between groups (Figure 7), but a predominance of phylogenetic overdispersion is clear in the Espinhaço Range and, to a lower extent, in the *Serra da Canastra*. This is remarkably evident in the Northern Espinhaço, which harbours the highest residuals. Although this is not clear when considering all groups combined, phylogenetic clustering is prominent for *Mimosa* and *Diplusodon* in the Brazilian Central Plateau, for *Comanthera* in the Southern Espinhaço, and for *Paepalanthus* across the Espinhaço Range. However, while the occurrence of phylogenetically overdispersed communities is widespread and relatively consistent between groups, patterns of phylogenetic clustering are spatially restricted and greatly varies depending on the focal group.

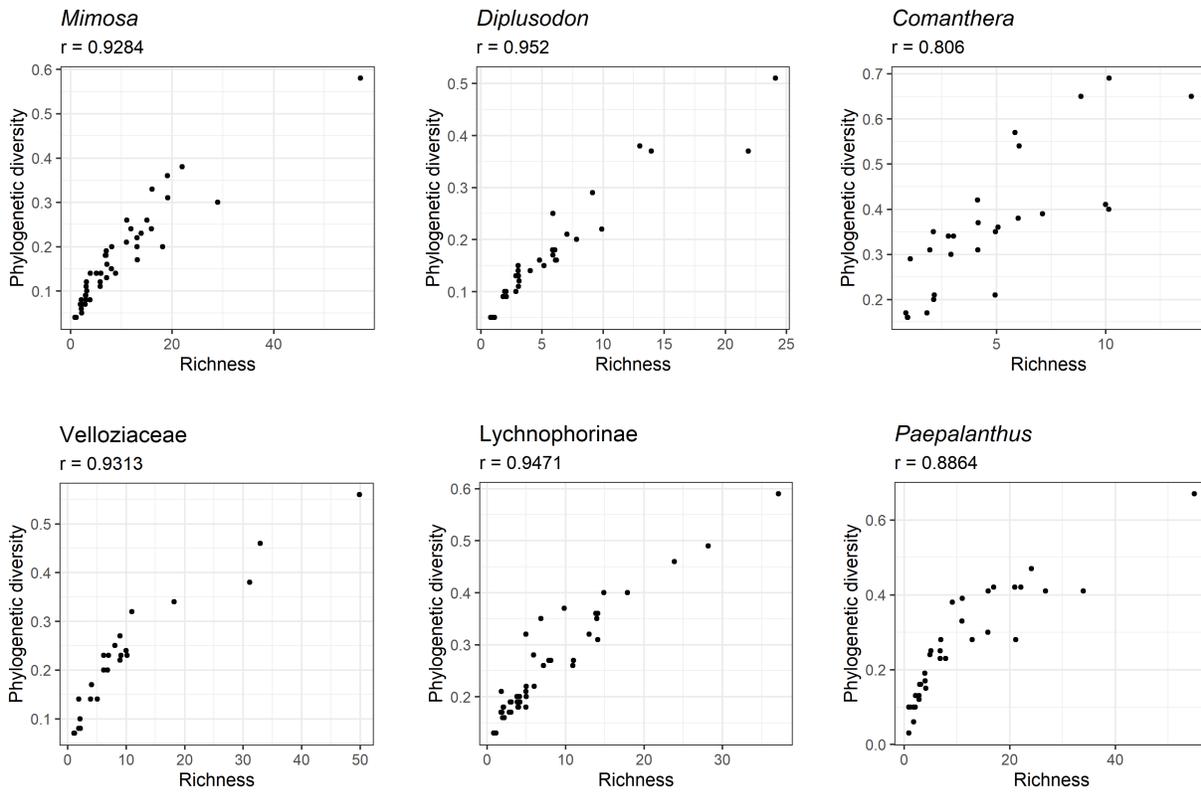


Figure 4: Relationship between phylogenetic diversity and species richness based on data of the respective focal group. Spearman's correlation coefficients (r) indicate a strong and positive correlation.

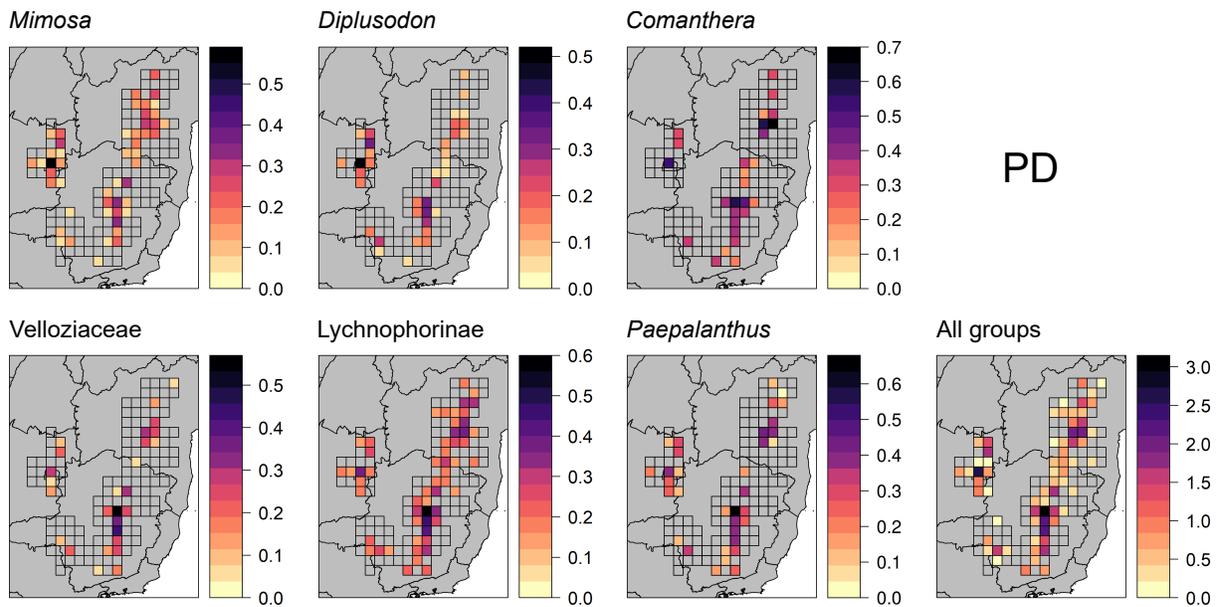


Figure 5: Spatial distribution of phylogenetic diversity across the *campos rupestres*. Transparent grid cells indicate absent data.

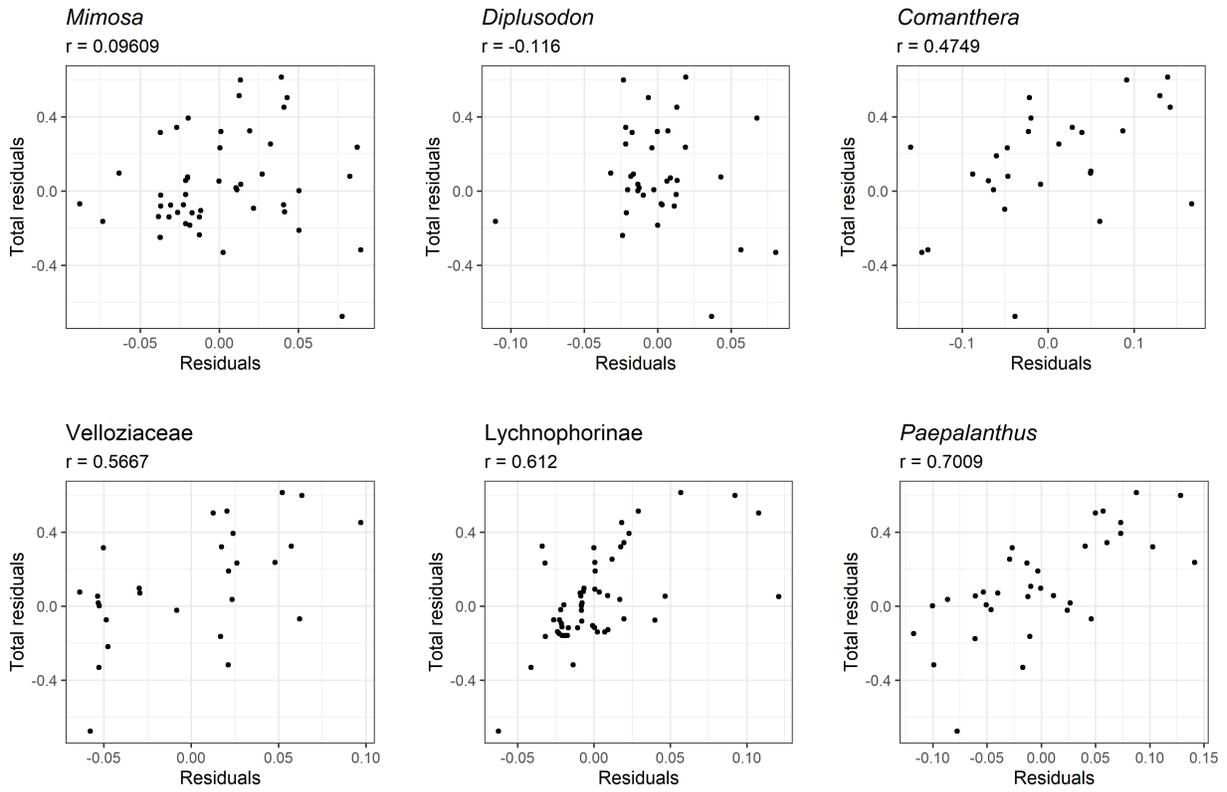


Figure 6: Relationship between PD ~ SR residuals of linear regressions using data from all groups combined (Total residuals) and data from the respective group (Residuals). There is a positive correlation between these two variables, except for *Mimosa* and *Diplusodon*. When considering these groups, Spearman's correlation coefficients (r) imply no correlation at all.

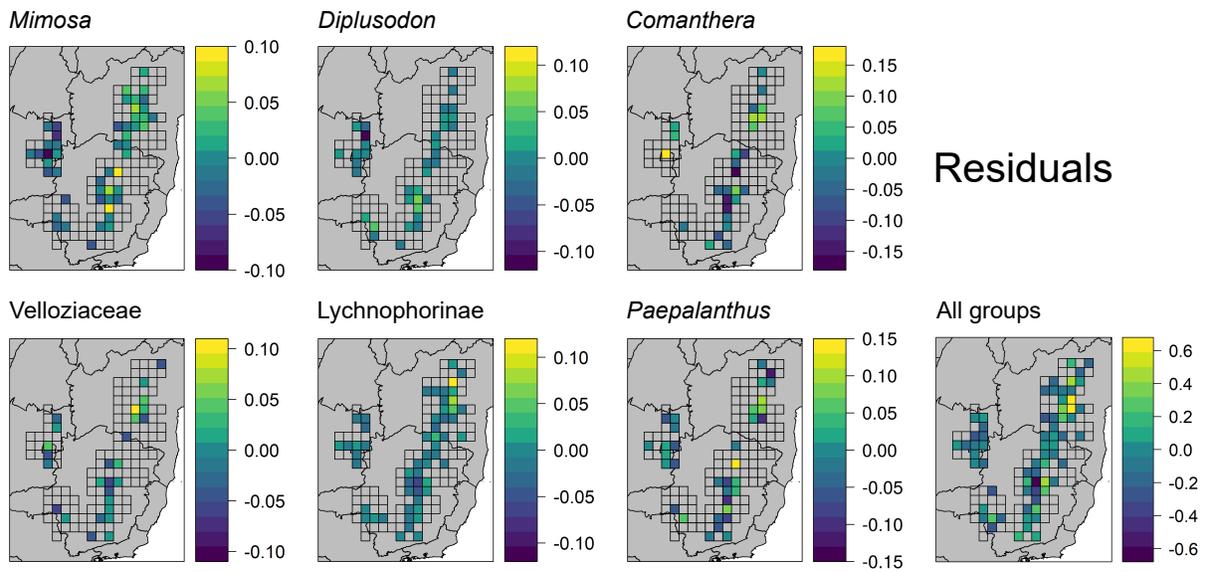


Figure 7: Spatial distribution of PD ~ SR residuals in the *campos rupestres*. Positive and negative residuals respectively indicate phylogenetic overdispersion and clustering (i.e. communities in which PD is higher or lower than expected based on richness). Transparent grid cells indicate absent data.

3.3 CANAPE

The categorical analyses of neo- and paleo-endemism inferred different patterns for each group (Figure 8). However, we identified a consistent spatial partitioning of endemism categories. The Northern Espinhaço mainly harbours paleo-endemic lineages (*Mimosa*, Velloziaceae and Lychnophorinae), although mixed endemism was inferred for *Comanthera*. The Southern Espinhaço, on the other hand, does not exhibit a predominance of any specific type of endemism, but includes all categories. The northern part of the Southern Espinhaço was inferred to display paleo-, super and mixed endemism (*Paepalanthus*, *Comanthera* and Velloziaceae), while its southern and central parts exhibits super and neo-endemism (*Paepalanthus* and *Comanthera*). Also, mixed endemism defines the *Serra da Canastra* (*Diplusodon* and Velloziaceae) and neo-, paleo- and super endemism characterise the Brazilian Central Plateau (*Mimosa*, *Diplusodon* and *Comanthera*). Thus, while paleo-endemic lineages predominate in the Northern Espinhaço, a mix of paleo- and neo-endemism is characteristic of other *campos rupestres* areas.

We believe CANAPE was not able to distinguish some endemic cells in *Comanthera* because of low statistical power. *Comanthera* is a small genus (Echternacht et al., 2014), and the number of species assessed in this work was further reduced so that the phylogenetic tree and the distribution matrix could match (see Methods). Thus, due to low variation, occurrence and phylogenetic data might not have been sufficient to reliably run the series of permutations on which CANAPE relies.

3.4 Jaccard distance and UniFrac

UPGMA analyses based on Jaccard distance and UniFrac showed different levels of geographic structuring in the taxonomic and phylogenetic composition of plant communities in the *campos rupestres* (Figure 9 and 10). Although it is not possible to merge all groups in order to run UniFrac (see Methods), the combined beta diversity results reveal that the Northern Espinhaço is the most contrasting area, while the Brazilian Central Plateau, the *Serra da Canastra* and the Southern Espinhaço share a floristic identity and, thus, compose a taxonomically cohesive area we henceforth refer to as the Central Plateau-Southern

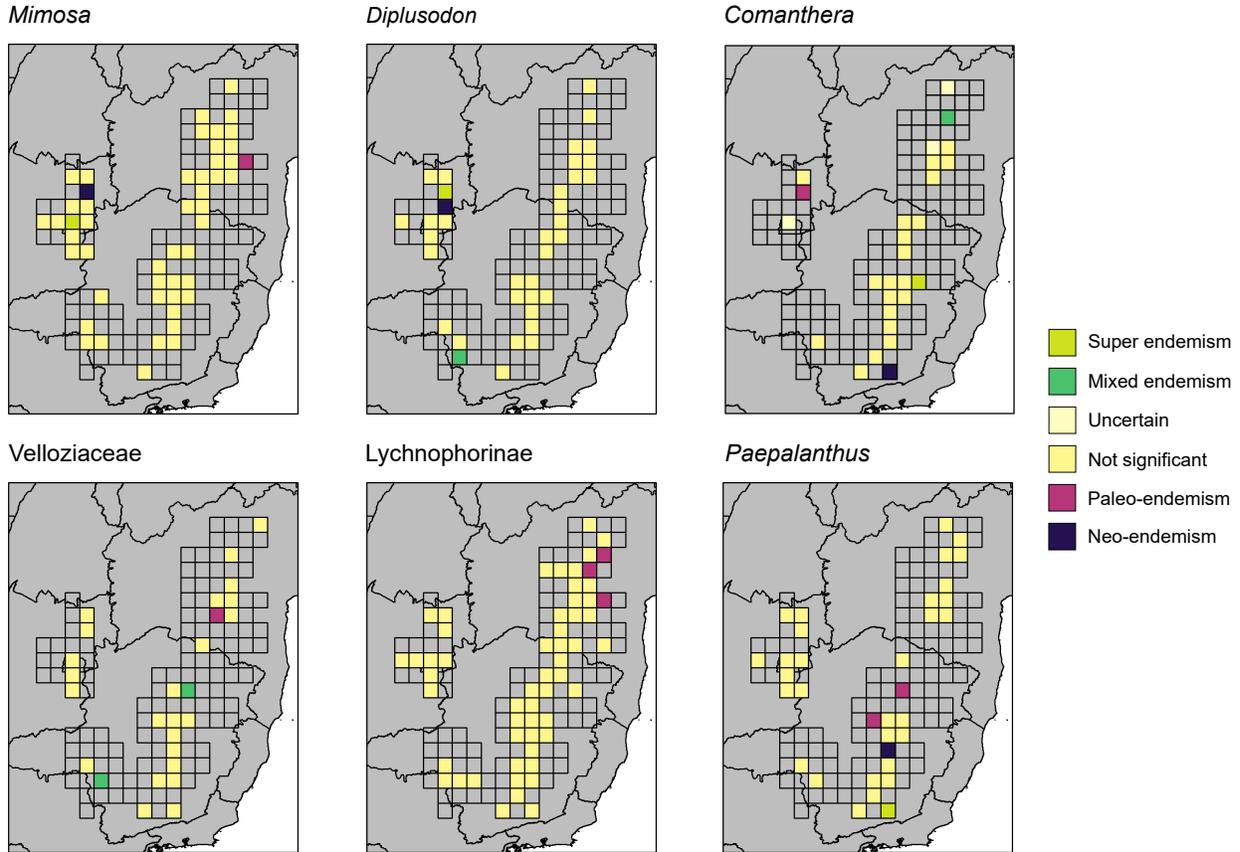


Figure 8: CANAPE results. Neo-endemic cells contain a predominance of short, rare phylogenetic branches; paleo-endemic cells contain a predominance of long, rare branches; and cells with mixed endemism contain a mixture of both. Mixed endemism can be further categorized as super endemism in a cell in which it is statistically significant at a lower confidence interval ($\alpha = 0.001$). Some cells in *Comanthera* passed the first statistical test that defines CANAPE, but then did not fall in any endemic category this analysis is able to distinguish. We defined those cells as harbouring an "uncertain" endemism type. Transparent grid cells indicate absent data.

Espinhaço.

The remarkable contrast between the floristic composition of the Northern Espinhaço and that of other *campos rupestres* is not only evident for all groups combined, but also when individually considering each taxa, attesting to the consistency of this pattern. The floristic cohesiveness between the Brazilian Central Plateau, the *Serra da Canastra* and the Northern Espinhaço is also very strong. Even in the few cases in which the Brazilian Central Plateau and/or the Southern Espinhaço appear as taxonomically unique (e.g. *Diplusodon* and *Paepalanthus*), these regions are nested into the Central Plateau-Southern Espinhaço arch.

Nonetheless, this hierarchically organised geographic structuring is displayed at a less sub-

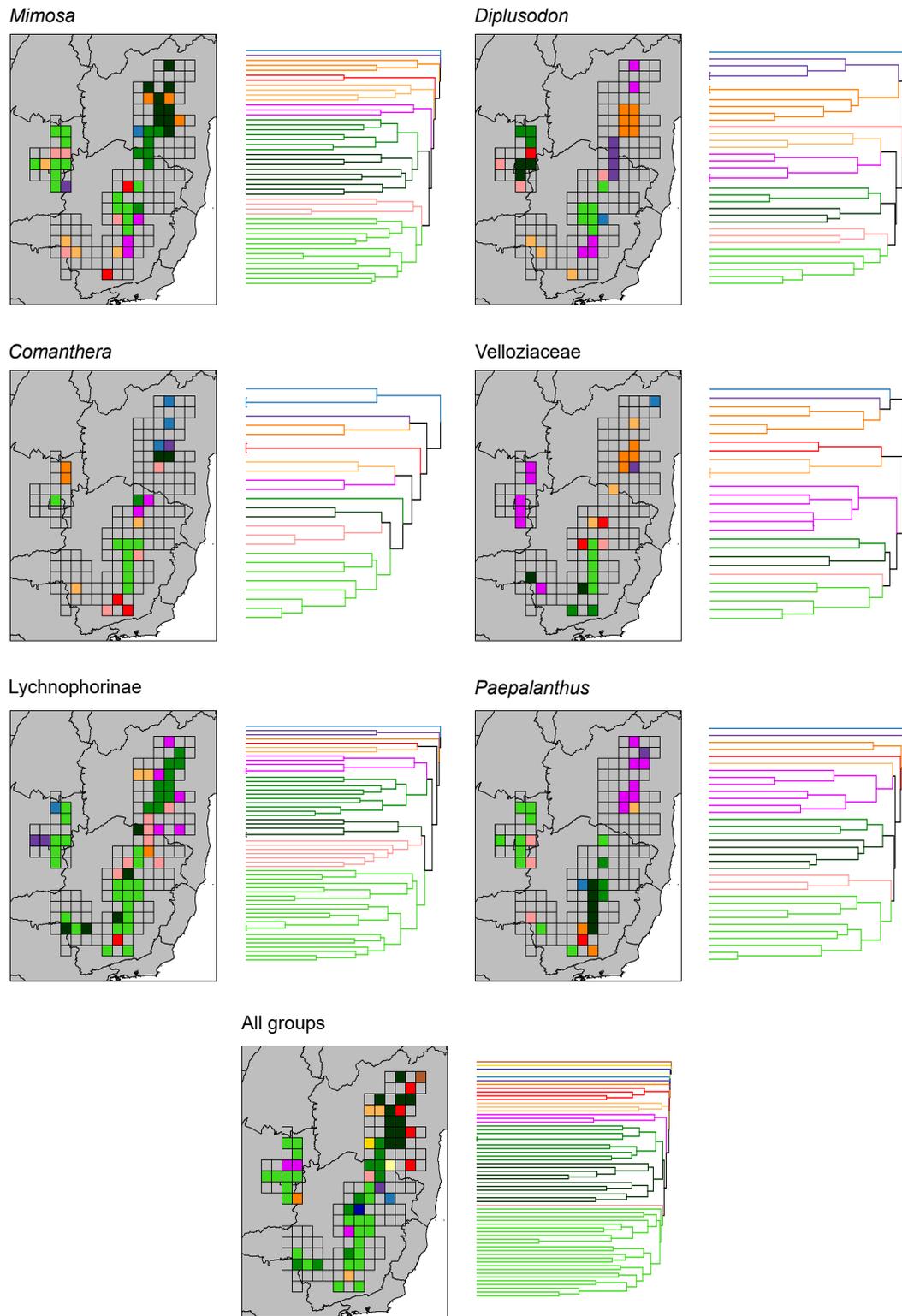


Figure 9: Hierarchical clustering of *campos rupestres* communities based on their taxonomic composition. Colours and cells in the map correspond to colours and terminals in the dendrogram, respectively. The closer the terminals are, more taxonomic identity the corresponding cells share. Transparent grid cells indicate absent data.

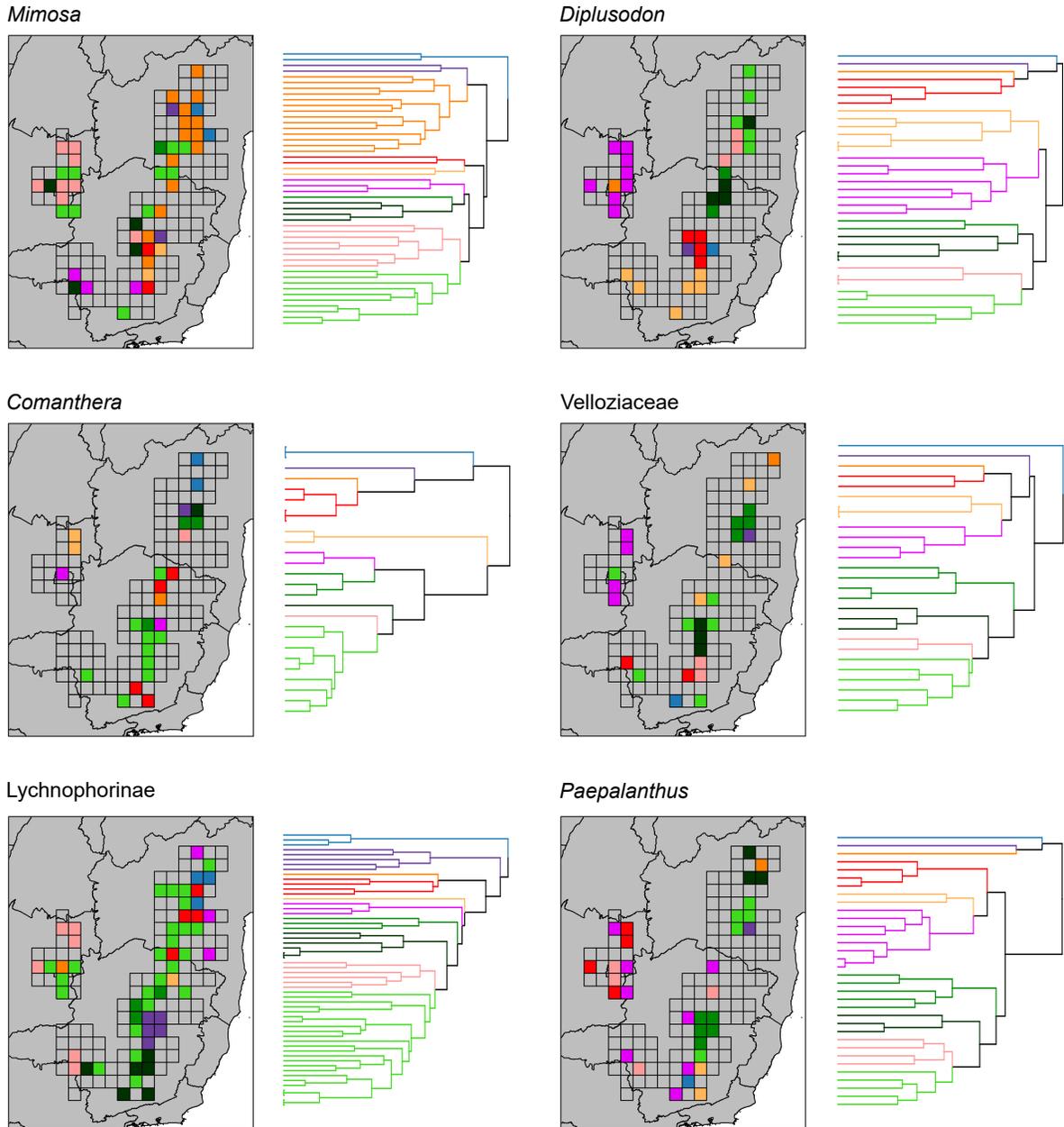


Figure 10: Hierarchical clustering of *campos rupestres* communities based on their phylogenetic composition. Colours and cells in the map correspond to colours and terminals in the dendrogram, respectively. The closer the terminals are, more phylogenetic identity the corresponding cells share. Transparent grid cells indicate absent data.

stantial degree when considering the phylogenetic composition of the *campos rupestres* flora, suggesting common lineages even between floristically distinct areas. Except for *Diplusodon*, taxonomic and phylogenetic composition are not coherent, even though they concur at first glance. For example, the Northern Espinhaço is evolutionary unique when considering the results for *Paepalanthus* and Velloziaceae, but most of this region is nested into widespread

clusters. However, even though in some cases, such as that of *Mimosa* and Lychnophorinae, the majority of the *campos rupestres* is connected by a single cluster, a few small and disjunct areas stand in marked contrast.

4 Discussion

Here we investigated spatial patterns of richness, phylogenetic diversity and endemism for the *campos rupestres* flora. We also assessed phylogenetic and taxonomic differences between communities using beta and phylobeta diversity metrics. Although some singularities suggest a complex assemblage of different evolutionary histories, we identified general patterns. Below we present these patterns and discuss processes that might have shaped them.

4.1 Richness, phylogenetic diversity and endemism

Richness and phylogenetic diversity are not evenly distributed in the *campos rupestres*, but concentrated in the Brazilian Central Plateau and the Southern Espinhaço. Nonetheless, decoupling these metrics from each other reveals different scenarios. PD~SR residuals for all groups combined depict a general predominance of phylogenetic overdispersion throughout the *campos rupestres*. This is particularly clear in the Northern Espinhaço, gradually becoming less evident towards the Southern Espinhaço and the *Serra da Canastra*. On the other hand, the Brazilian Central Plateau is composed by expected PD values only. We view this pattern with caution, as there may be a bias against groups whose communities are phylogenetically clustered in this region (see Figure 6). Regarding endemism patterns, the Northern Espinhaço is mainly defined by paleo-endemism, while the Southern Espinhaço, the *Serra da Canastra* and the Brazilian Central Plateau floras include a mixture of paleo- and neo-endemic lineages.

Widespread phylogenetic overdispersion agrees with OCBIL theory (Hopper, 2009), which predicts the persistence of old lineages in ancient, climatically buffered and infertile landscapes as the *campos rupestres* (Hopper, 2009; Hopper et al., 2016; Silveira et al., 2016). Particularly, the *campos rupestres* long-term climatic and topographical stability (Alkmim, 2012; Pedreira and De Waele, 2008; Silveira et al., 2016) might have led to the persistence of

relatively older (deeply diverged) lineages, leaving the phylogenetic overdispersion signature we found (Divya et al., 2020; Lososová et al., 2015). CANAPE reinforces this idea showing that endemics commonly belong to old lineages (paleo-endemism). This pattern is specially prominent in the Northern Espinhaço, where both paleo-endemism and phylogenetic overdispersion predominate.

Contrasting with the Northern Espinhaço, the Central Plateau-Southern Espinhaço arch includes more areas of phylogenetic clustering and a mix of paleo- and neo-endemism or even marked neo-endemism. This pattern is more clear in analyses of individual taxa, especially in the Brazilian Central Plateau, where neo-endemism for *Mimosa* and *Diplusodon* overlaps with phylogenetically clustered communities. These results show that the Central Plateau-Southern Espinhaço arch flora includes patches of younger (short branches) and closely related lineages (Divya et al., 2020; Honorio Coronado et al., 2015; Webb et al., 2002), as previously indicated by phylogenetic and diversification analyses (Bonatelli et al., 2014; Rando et al., 2016; Trovó et al., 2013; Vasconcelos et al., 2020). Recent diversification of the *campos rupestres* flora, especially during the Pleistocene (Vasconcelos et al., 2020), is commonly attributed to population expansion-contraction cycles during climatically unstable periods (Antonelli et al., 2010; Barbosa et al., 2012, 2015; Barres et al., 2019; Bonatelli et al., 2014; Giuliatti et al., 1997).

Due to the presence of both recent and old lineages, the different sections of the *campos rupestres* have been treated as museums (the Northern Espinhaço) or as cradles (the Southern Espinhaço) of lineages (Bitencourt and Rapini, 2013). However, our results indicate that more recent lineages, which abound in the Central Plateau-Southern Espinhaço arch, are in fact embedded in a widespread relatively older flora. These older lineages, maintained in climatically and topographically stable areas, as discussed above, were likely the raw material for the bursts of recent diversification inferred for the *campos rupestres* flora (Vasconcelos et al., 2020) and highlighted here. We have also shown that these recent events are in fact spatially restricted and lineage-dependent (Figures 7 and 8), a pattern that may be related to edaphic and ecophysiological features (Fernandes, 2016; Giuliatti et al., 1997; Oliveira et al., 2016; Schaefer et al., 2016b) and to the heterogeneous topography (Giuliatti et al., 1997) of the *campos rupestres*. Variations in the ecological conditions of corridors between formerly

disjunct areas (Safford, 2007), and in the degree of connectivity between different areas across time (Flantua et al., 2019) likely affected the dispersal and diversification of distinct lineages in different ways.

Different processes may have contributed to the formation of the *campos rupestres* flora (Rapini et al., 2020; Vasconcelos et al., 2020). However, given the climatic stability of the *campos rupestres*, processes other than ecological opportunity due to extinction (Vasconcelos et al., 2020) may be behind the bursts of diversification seen for this flora. Hybridisation, for example, is common in angiosperms (Rieseberg and Willis, 2007), often linked to macroevolutionary diversification events (Rieseberg, 1997; Rieseberg and Willis, 2007), and could generate the lineage and site specific patterns we uncovered here. Most of the species generated during these diversification events, however, saturate the local community beyond their carrying capacity and, thus, likely promote local extinction, particularly of themselves (McPeck, 2007). The role of such transient species in the *campos rupestres* flora is reinforced by the occurrence of phylogenetic clustering in species-rich sites shown here for individual taxa (McPeck, 2007), as well as by the overall high proportion of short branches seen for the Central Plateau–Southern Espinhaço arch (Cortez et al., 2020). Repetition of these localised birth and death events over time could produce the spatial patterns of phylogenetic diversity and endemism we found. Why local diversification is more common in the Central Plateau–Southern Espinhaço arch than in the Northern Espinhaço can be better explained by the beta and phylobeta diversity analyses we discuss below.

4.2 Taxonomic and phylogenetic composition

As expected for island-like systems (Carstensen et al., 2012; Chiang and Schaal, 2006; Garcia-Verdugo et al., 2010; Graham and Fine, 2008; Koscinski et al., 2008; Kubota et al., 2011; Papadopoulou et al., 2009), beta diversity clearly shows a hierarchically organised geographic structuring in the floristic composition. Taxonomically, the Southern Espinhaço and the Brazilian Central Plateau differ in their species composition. Nonetheless, they form a cohesive group together with the *Serra da Canastra* (the Central Plateau–Southern Espinhaço arch), particularly in contrast to the Northern Espinhaço. Phylobeta diversity showed that a few small and disjunct areas present an unique evolutionary identity. At a larger scale,

however, those results suggest that currently distinct floras may share a evolutionary history.

The floristic dissimilarity between the Northern Espinhaço and other *campos rupestres* sections has been previously stressed in different studies (Barbosa et al., 2012; Bitencourt and Rapini, 2013; Colli-Silva et al., 2019; Harley, 1988; Neves et al., 2018; Rapini, 2010; Ribeiro et al., 2012; Trovó et al., 2013). A possible explanation for this contrast is the role of the extensive lowland between the two portions of the Espinhaço Range as a barrier to migration (Bitencourt and Rapini, 2013; Giuletta et al., 1997; Harley, 1988; Rapini et al., 2008). However, even though *campos rupestres* species are known for their limited dispersal potential (Arruda et al., 2020; Conceição et al., 2016; Giuletta et al., 1997), changes in community composition across this vegetation may be better predicted by environmental conditions rather than geographic factors, such as distance (Neves et al., 2018). Indeed, our results on beta diversity coincide with differences in climatic, edaphic and topographical conditions along the *campos rupestres*. While the Northern Espinhaço is relatively less fragmented and located in the driest extreme of the Brazilian precipitation gradient, the Central Plateau-Southern Espinhaço arch lies in a relatively moister environment and is comprised by highly disjunct areas with higher surface rockiness (Bitencourt and Rapini, 2013; Neves et al., 2018).

In addition, given its remarkable influence on the *campos rupestres* woody flora (Neves et al., 2018), the surrounding vegetation might also have contributed to shape the patterns we found. Unlike the Central Plateau-Southern Espinhaço arch, which is chiefly embedded in a savanna-like vegetation (the *cerrado*), the Northern Espinhaço is predominantly surrounded by a massive seasonally dry tropical forest, the *caatinga* (Neves et al., 2018). Due to similar environmental conditions (Bitencourt and Rapini, 2013; Neves et al., 2018), exaptations (*sensu* Gould and Vrba, 1982) might have enabled lineages from different surrounding vegetations to invade the *campos rupestres* (Rapini et al., 2020). A lineage in *Calliandra* Benth. (Leguminosae), for example, originated in the *caatinga* and radiated into a speciose and endemic clade in the Northern Espinhaço (Souza et al., 2013). Thus, by periodically receiving lineages from the different surrounding vegetations (Neves et al., 2018), *campos rupestres* communities would eventually differentiate into distinct floristic groups.

This relationship might also have affected the evolutionary processes that presumably

shaped the *campos rupestres* (see section 4.1). Because the *caatinga* is also an ancient and climatically stable habitat (Queiroz et al., 2017; Simon et al., 2009; Werneck et al., 2011), a higher proportion of paleo-endemic and deeply diverged lineages are expected to colonise the Northern Espinhaço. On the other hand, events of recent diversification in the Central Plateau-Southern Espinhaço arch would be facilitated by the profound effects that Pleistocene climatic fluctuations had on the *cerrado* (Alves and Kolbek, 1994; Behling, 2002; Pirani et al., 1994; Rapini et al., 2020; Safford, 2007; Werneck et al., 2012). However, the Northern Espinhaço and the Central Plateau-Southern Espinhaço arch are not completely evolutionary independent, as they also share widespread lineages. Whether these lineages spread over the *campos rupestres* by past dispersal, or by niche shifts to the surrounding vegetation (Rapini et al., 2020), is still debatable. Nonetheless, the taxonomic contrast between the Northern Espinhaço and the Central Plateau-Southern Espinhaço arch might have been shaped by the degree each of these regions interacted with the surrounding vegetation. Phylobeta diversity analyses incorporating a broader data set may help to elucidate the historical connections between the *campos rupestres*, the *cerrado* and the *caatinga* floras.

5 Conclusion

As a recently recognised OCBIL, the hyper-diverse *campos rupestres* have been receiving increased global attention (e.g. Cortez et al., 2020; Hopper et al., 2016; Morellato and Silveira, 2018). The evolution of plant communities in this vegetation complex has been intensively debated and different models were proposed to explain its remarkable rates of diversity and endemism (Hopper, 2009; Rapini et al., 2020; Vasconcelos et al., 2020). However, although evolution is strongly dependent on space, few studies brought attention to the spatial distribution of phylogenetic diversity and endemism patterns in the *campos rupestres*. Here we aimed to clarify conflicting evidences for distinct evolutionary processes by combining spatial and phylogenetic data.

We show that the *campos rupestres* are split into two large areas of cohesive floristic diversity: the Northern Espinhaço and the Central Plateau-Southern Espinhaço arch, which spans the Brazilian Central Plateau, the *Serra da Canastra* and the Southern Espinhaço. Although

past connections between disjunct areas might have been facilitated by the surrounding vegetations, the contrast between these regions is reinforced by patterns of phylogenetic diversity and endemism. While phylogenetic overdispersion and paleo-endemism are dominant in the Northern Espinhaço, phylogenetic clustering and neo-endemism are mostly restricted to the Central Plateau-Southern Espinhaço arch. This is not only in agreement with patterns of floristic composition, but also with the distribution of environmental conditions and surrounding vegetations, which might have played an important role in the assembly of the *campos rupestres* flora. Thus, although the *campos rupestres* evolution was likely complex and diverse (Rapini et al., 2020; Vasconcelos et al., 2020), we showed it to be geographically partitioned both in macro and local scales.

Overall, this species-rich, highly endemic vegetation complex is mainly composed by museums, some of which may harbour cradles of recently diversified lineages. Therefore, our spatial approach reconciles the apparent contradiction between OCBIL theory and evidences for recent and fast diversification in the *campos rupestres*. The combined effects of both ancient and recent diversification have been discussed not only for the *campos rupestres* (Bittencourt and Rapini, 2013; Bonatelli et al., 2014; Hughes et al., 2013; Silveira et al., 2016; Simon et al., 2009; Souza et al., 2013; Trovó et al., 2013), but also for other OCBILs such as the Greater Cape Floristic Region (Cowling et al., 2014; Linder, 2008). Nonetheless, our work is the first to demonstrate that recent diversification events in the *campos rupestres* are both taxa- and site-dependent and may rely on the overall maintenance of relatively older lineages. These findings emphasise the importance of considering the spatial component when investigating diversification patterns and suggest that the flora of old, climatically buffered, infertile landscapes might have been shaped by idiosyncratic, spatially dependent evolutionary processes.

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