UNIVERSIDADE FEDERAL DE MINAS GERAIS

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre

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Daniela Melo Garcia De Oliveira

BIOGEOGRAPHY AND COMMUNITY ASSEMBLY OF *CAMPOS RUPESTRES*

Belo Horizonte

2022

Daniela Melo Garcia De Oliveira

BIOGEOGRAPHY AND COMMUNITY ASSEMBLY OF *CAMPOS RUPESTRES*

Versão Final

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre do Departamento de Biologia Geral do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Ecologia.

Área de Concentração: Macroecologia

Orientador: Prof. Dr. Danilo Rafael Mesquita Neves

Belo Horizonte

2022

043 Oliveira, Daniela Melo Garcia de.
Biogeography and community assembly of campos rupestres [manuscrito] / Daniela Melo Garcia de Oliveira. – 2022.
50 f. : il. ; 29,5 cm.

Orientador: Prof. Dr. Danilo Rafael Mesquita Neves.
Dissertação (mestrado) – Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas. Programa de Pós-Graduação em Ecologia Conservação e Manejo da Vida Silvestre.

1. Ecologia. 2. Campo Cerrado. 3. Biogeografia. 4. Metacomunidades. I. Neves, Danilo Rafael Mesquita. II. Universidade Federal de Minas Gerais. Instituto de Ciências Biológicas. III. Título.

CDU: 502.7

Ficha catalográfica elaborada pela bibliotecária Fabiane Cristielle M. Reis - CRB: 6/2680

UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

Ata da Defesa de Dissertação

Nº 433
Entrada: 2020/1

Daniela Melo Garcia de Oliveira

No dia 22 de agosto de 2022, às 14:00 horas, por videoconferência, teve lugar a defesa de dissertação de mestrado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) mestrando(a) Daniela Melo Garcia de Oliveira, intitulada: **"Biogeography and community assembly of campos rupestres"**. Abrindo a sessão, o(a) orientador(a) e Presidente da Comissão, Doutor(a) Danilo Rafael Mesquita Neves , após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Geraldo Alves Damasceno Júnior (UFMS), Márcia Cristina Mendes Marques (UFPR) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

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INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

FOLHA DE APROVAÇÃO

"Biogeography and community assembly of campos rupestres"

DANIELA MELO GARCIA DE OLIVEIRA

Dissertação de Mestrado defendida e aprovada, no dia **22 de agosto de 2022**, pela Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais constituída pelos seguintes professores:

Doutor(a) Geraldo Alves Damasceno Júnior
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Documento assinado eletronicamente por **Marcia Cristina Mendes Marques**, **Usuário Externo**, em 24/08/2022, às 12:09, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

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AGRADECIMENTOS

Mestrado, puerpério e pandemia. Esses três grandes processos calharam de acontecer simultaneamente na minha vida e talvez por isso seja difícil para mim escrever agradecimentos. Não porque eu não tenho a quem agradecer, muito pelo contrário tenho e muitas pessoas a quem devo a finalização deste trabalho, mas o fato é que agradecimentos são carregados de alegria e um enorme alívio de dever cumprido, sentimentos esses que não carrego comigo. Mas, "para não dizer que eu não falei de flores" segue aqui a minha eterna gratidão aos que nunca soltaram minha mão.

Em primeiro lugar, gostaria de agradecer ao meu orientador Dr. Danilo Rafael Mesquita Neves, que viabilizou de todas as formas possíveis a realização desse trabalho. O Goiás é aquele tipo de pessoa que tenta sempre dar o melhor de si em todos os sentidos, e isso faz dele um excelente cientista e um orientador humano e compreensível! Muito obrigada pelos ensinamentos ecológicos, de análises no R, por sempre colocar mensagens motivadoras ao final dos recados e e-mails trocados, pela compreensão com prazos mesmo com uma agenda cheia. Fazer parte do seu laboratório foi extremamente enriquecedor para minha caminhada na biologia, antes todos os laboratórios acadêmicos tivessem um ambiente prazeroso e colaborativo como o Macroecology Lab. Mesmo distante fisicamente você fez tudo isso ser possível. Valeu demais!

Aproveito para agradecer todos os integrantes do laboratório com quem criei laços via slack! Uma menção especial a Leila, por socorrer inúmeras vezes com o R e pela paciência ao explicar e prontidão para ajudar! Muitíssimo obrigada, Leila, grande parte do que aprendi ao longo do mestrado foi você quem me ensinou!

Gostaria de agradecer também a Luuuu (Luisa Azevedo), por ser tão natureza na minha vida. Obrigada Lu, por ter caminhado juntinho comigo nesses dois anos e meio, mesmo isoladas fisicamente, nunca estivemos tão próximas. É até difícil descrever a importância que você tem para conclusão desse mestrado, porque você foi muitas vezes meus braços, pernas e cabeça. Obrigada por compartilhar os perrengues, tristezas e frustações, mas sempre manter tudo floreado e o mais leve possível.

A minha família, minha rede de apoio, vovô Miso, vovó Dea, vovó Julia e tia Lulu sem o amor e apoio incondicional de vocês com a Flor NADA disso teria ficado pronto, nada mesmo. Obrigada por terem dedicado muito do tempo livre de vocês para me ajudar. Eu amo muito vocês!

A minha rede de apoio virtual, todos os amigos da biologia, os amigos há muito tempo e as amigas do AA que sempre escutaram todas as minhas reclamações com muito apoio e compreensão. Um agradecimento especial a Dudinha, Quel e Belle por serem extremamente presentes na vida da Flor mesmo de longe, vocês são as madrinhas do coração, e são as amigas que sei que poderei contar para tudo nessa vida. As Biomoms pelas infinitas trocas de vivências e apoio.

Gostaria de agradecer a CAPES pela bolsa, sem esse auxílio ficaria (e ficará) inviável seguir carreira científica.

Por último preciso agradecer ao meu companheiro Lucas, que me ajudou do início ao fim desse mestrado, desde os estudos para realizar a prova, até a formatação da dissertação. Obrigada por compartilhar a vida todinha comigo, principalmente a carga danada que é ser pais de um serzinho absolutamente extraordinário. À Flor, minha filha, o ser extraordinário que, apesar de ter tornado essa caminhada infinitamente mais difícil, me mostrou o que realmente importa nessa vida, me arrancou os sorrisos mais verdadeiros nos momentos de dor mais profunda.

“*Uma posição no mundo acadêmico tampouco é um caminho para se tornar mais realizada ou criativa. Na ausência de um movimento forte de mulheres, o trabalho na academia pode ser sufocante, porque você deve atingir padrões que você não tem o poder de determinar e, logo, você começa a falar um idioma que não é o seu.”*

(Trecho do livro: O Ponto Zero da Revolução, Silvia Federici)

RESUMO

Objetivo: Campos rupestres são paisagens antigas com afloramentos rochosos na América do Sul, ocupando principalmente áreas montanhosas acima de 900 m de altitude até 2033 m. Com objetivo de elucidar estratégias eficazes de conservação para este ecossistema, nos exploramos a identidade florística dos campos rupestres e testamos se a variação nas condições climáticas e edáficas limitam a distribuição de espécies de plantas dentro de cada um dos grupos florísticos campos rupestres.

Localização: Campos rupestres brasileiros abrangendo a Cadeia do Espinhaço (de Minas Gerais-MG até a Bahia-BA), Quadrilátero Ferrífero (Minas Gerais-MG), Serra dos Carajás (Pará-PA) e o maciço do Urucum em Corumbá (Mato Grosso do Sul-MS)

Taxon: Angiospermas

Métodos: Compilamos um banco de dados com 98 levantamentos florísticos georreferenciados em campos rupestres espalhados pelos principais biomas tropicais da América do Sul, compreendendo 5.182 espécies de angiospermas. Usamos uma análise de partição *k-means* para avaliar a identidade florística entre as comunidades vegetais dos campos rupestres e, em seguida, usamos análises de redundância para avaliar se o principal gradiente de variação florística dentro de cada grupo está associado à variação nos fatores ambientais (clima e solo) e espaciais. Além disso, para avaliar a estrutura da comunidade para cada um dos grupos, usamos a abordagem de metacomunidades.

Resultados: Nossos resultados suportam seis grupos florísticos distintos, ou metacomunidades de campos rupestres, com uma clara segregação entre canga e quartzito. As condições climáticas e edáficas atuam em escalas espaciais distintas moldando a variação na composição da comunidade de cada metacomunidade. Finalmente, a variação na composição da comunidade é consistentemente estruturada pela substituição de espécies ao longo de gradientes ambientais.

Principais conclusões: Ressaltamos a importância de estratégias de conservação que considerem áreas de proteção em vários pontos distintos ao longo dos gradientes ambientais de cada metacomunidade de campo rupestre. Além disso, sugerimos o abandono do termo campo rupestre sensu lato (ou seja, quartzito e canga agrupados) e que as medidas de compensação levem em consideração grupos biogeográficos dentro de cada geomorfologia.

Palavras-chave: campos rupestres, biogeografia, assembleia de comunidade

ABSTRACT

Aim: *Campos rupestres* are rocky montane old-growth grasslands in South America, mostly occupying montane areas above 900 m a.s.l. and up to 2033 m. To address effective conservation strategies for these hyperdiverse, yet threatened ecosystems, our aim was to explore the floristic identity of *campos rupestres*, and to test whether variation on climatic and edaphic conditions limit the distribution of plant species within floristic groups of *campos rupestres*.

Location: The *campo rupestre* s.l. vegetation in Brazil, comprising the *Espinhaço* Range (Minas Gerais-MG and Bahia-BA), Iron Quadrangle (Minas Gerais-MG), *Serra dos Carajás* (Pará-PA) and the Urucum Plateau in *Corumbá* (Mato Grosso do Sul-MS).

Taxon: Angiosperms

Methods: We compiled a database with 98 geo-referenced floristic surveys in *campos rupestres* scattered across major tropical biomes of South America, comprising 5,182 species of angiosperms. We used k-means partitioning analyses to define the optimal number of floristic clusters among *campo rupestre* plant communities, and then used redundancy analyses to evaluate whether the major gradient of floristic variation within each group are associated with variation in environmental (climate and soil) and spatial factors. Furthermore, we tested whether the overall importance of species replacement for the assembly of campos rupestres' metacommunities.

Results: Our results support six distinct floristic groups, or metacommunities of *campos rupestres*, with a clear segregation between ironstone and quartzite outcrops. Climatic and edaphic conditions act at distinct spatial scales shaping variation in community composition of each metacommunity. Finally, variation in community composition is consistently structured by species turnover along environmental gradients.

Main conclusions: We stress the importance of conservation strategies that consider protection areas spanning several distinct points along the environmental gradients of each *campo rupestre* metacommunity. Moreover, we suggest dropping the term *campo rupestre* sensu lato (i.e., quartzite and *canga* lumped together) and that compensation measures should take into account biogeographical groups within each geomorphology.

Keywords: *campo rupestres,* biogeography, community assembly

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1. INTRODUCTION

Campos rupestres are rocky montane old-growth grasslands in South America, mostly occupying montane areas above 900 m a.s.l. and up to 2033 m (Fernandes, 2016; Pirani & Giulietti, 1988; Silveira et al., 2016). Its marked dominance of monocots, and recurrent morphological convergences between phylogenetically distant plant taxa gives the impression of a uniform landscape (Giulietti et al., 1987). On a finer scale, however, this ecosystem ranges from grasslands and savannas on steep, rocky slopes and hilltops, to forest islands (Rapini et al., 2008).

Due to its high topographic heterogeneity, *campos rupestres* exhibits a diverse array of microclimates and edaphic niches (Campos et al., 2018; Carmo & Jacobi, 2016; Liu et al., 2018), which leads to an outstanding plant diversity and endemism (Fernandes et al., 2020; Silveira et al., 2016). Although this region covers less than 1% of the Brazilian territory, it hosts nearly 15% of the national flora (Silveira et al., 2016). Furthermore, nearly 40% of its species are narrow endemics (ca. 2,000 species), many of which are threatened with extinction (Martinelli & Moraes, 2013).

Moreover, *campos rupestres* have been experiencing one of the most intense land use alterations among all Brazilian ecosystems (Fernandes, 2016; Pena et al., 2017; Sonter et al., 2014), but while the highest levels of plant biodiversity in *campos rupestres* is found in grassland communities, most conservation efforts are focused on the surrounding forests (Veldman et al., 2015). Open vegetation habitats in *campos rupestres* not only are the major centers of endemism, but also play a critical role in ecosystem connectivity and environmental services related to human wellbeing, such as water provision (Fernandes, 2016; Hopper et al., 2016; Veldman et al., 2015).

To address effective conservation strategies in any ecosystem, it is critical to understand biodiversity patterns across multiple spatial scales and investigate how environmental and spatial factors shape such patterns. These have been important topics in ecology for decades (Scheiner & Willig, 2005; Terborgh, 1971; Whittaker, 1956, 1975), and scientists developed multiple theoretical approaches to tackle them in the context of biogeography (Brown, 2014; Von Humboldt, 1807; Von Humboldt & Bonpland, 2009) and community assembly (Leibold & Mikkelson, 2002).

Natural communities can be interpreted in both local and regional scale. At the local scale, communities are distinct entities that, combined, form a metacommunity. Hence, a metacommunity represents the regional scale, which is connected by several localities through dispersal, and therefore comprises more than one scale simultaneously (Leibold & Chase, 2018). The metacommunity concept has received increasing attention from researchers, helping them to envision a different perspective of how regional processes contribute to ecological properties in local communities (de la Sancha et al., 2014; Giovâni et al., 2021; Heino et al., 2015, 2017; Henriques-Silva et al., 2013). Through a theoretical approach for understanding biodiversity patterns and its variations, it recognizes that environmental and spatial factors, as well as dispersal processes and biotic interactions are the major components shaping the assembly of ecological communities (de la Sancha et al., 2014; Heino et al., 2015; Henriques-Silva et al., 2013; Leibold et al., 2004).

To assess overall patterns of community assembly in *campos rupestres*, we adopted an approach proposed by Leibold & Mikkelson (2002), allowing the identification of two major structures of community assembly: turnover and nestedness. Turnover represents the replacement of species among communities, with distinct species responding differently to variation in environmental conditions. Low turnover rates are indicative of nested metacommunities (Leibold & Mikkelson, 2002), where the composition of species-poor communities represents subsets of increasingly species-rich communities (Patterson & Atmar, 1986). In general, habitat area, isolation and environmental suitability are typical correlates of nestedness (Wright et al., 1997).

Here we set out to address long-standing debates on the biogeography of *campos rupestres* found across the major biomes of lowland South America: Caatinga, Cerrado, Atlantic Forest, and the Amazon (Fig.1). In so doing, we hope to provide critical knowledge for conservation planning of these threatened environments, including information on their overall patterns of community assembly. As environmental conditions change across space, are communities in harsher conditions assembled from nested subsets of species from more diverse communities? Or are species replaced along environmental gradients, thus leading to overall high levels of endemism in *campo rupestre* plant communities? To answers these overarching questions, we compiled an unprecedented dataset of plant communities in *campos rupestres* across South America, encompassing all plant life-forms (Fig. 1 and 2).

Our aims were two-fold: first, define the major floristic groups of *campos rupestres*, and then explore the importance of environmental (i.e., climatic and edaphic variables) and spatial components in driving floristic differentiation within each group. Considering the observations of previous analyses of tree community composition in *campos rupestres*, we hypothesized that climatic conditions (e.g., Neves et al., 2018) are the main drivers of floristic dissimilarity within *campos rupestres* groups. Second, to test whether variation on climatic and edaphic conditions limit the distribution of plant species within each group of *campos rupestres*. Considering the overall high species richness of plant communities across the distribution of *campos rupestres* (Silveira et al., 2016), we hypothesized that turnover plays a key role in the structure of the *campos rupestres* metacommunities.

Figure 1. *Campos rupestres* found across different substrates in Brazil. (a) Biribiri State Park, in Minas Gerais state: *campo rupestre* on quartzite outcrop in the Southern *Espinhaço* Range; (b) Corumbá, Mato Grosso do Sul state: *campo rupestre* on ironstone outcrop (*canga*) in the Urucum Plateau; (c) Carajás southern mountain range, Pará state: Amazonian *cangas*; (d) Serra do Cipó, Minas Gerais state: *campo rupestre* on a quartzite outcrop matrix in Southern *Espinhaço*; (e) Serra da Moeda, Minas Gerais state: *cangas* from the Iron Quadrangle; (f) Chapada da Diamantina, Bahia state: *campos rupestres* on a quartzite outcrop matrix in the Northern *Espinhaço* Range. Photos: Daniela Oliveira (a and d); Luciana Silva (b); Lucas Perillo (c, e and f).

2. MATERIAL AND METHODS

2.1 Study Area

The extent of study area covered the *campo rupestre* s.l. vegetation in Brazil (21° 42' 17" to 6° 01' 35" S; 57° 38' 43" to 41°27' 00" W) (Fig. 2). The elevation of the sites ranged from 900 m to 2100 m. All sites experience seasonal droughts, with mean annual temperature ranging from 14°C to 26°C, and mean annual precipitation ranging from 701 to 2,432 mm (Alvares et al., 2013).

The *campos rupestres* are known for being a megadiverse ecosystem found on quartzite, sandstone and ironstone outcrop formations. Covering approximately 65,000 km² (Fernandes et al., 2014) they span four primary vegetation "Domains" (Ab'Sáber, 2003; IBGE, 1993): the Atlantic Forest Domain to the east and south (known as Mata Atlântica in Brazil), the Caatinga Domain and the Amazonian Domain to the north and the Cerrado Domain to the west (Giulietti et al., 1997; Hughes et al., 2013; Silveira et al., 2016).

Additionally, *campos rupestres* are recognized as ecosystems with marked climatic seasonality (Silveira et al., 2016). Rupiculous systems in tropical mountains constitute stressful environments for plant communities as they are usually characterized by limiting edaphic resources, low water availability and shallow, nutrient-poor soils. At the same time, many outcrops display complex local topographic heterogeneity, resulting in high microclimatic variation (Campos et al., 2018; de Carvalho et al., 2014; Liu et al., 2018).

Edaphic resources and surface heterogeneity exert a strong influence on the structure of plant communities, modifying local environmental conditions. The isolated, fragmented nature and very old age of these environments have generated plant communities with remarkable ecological adaptations, floristic diversity, and large number of endemic species, in spite of the harsh abiotic conditions (Oliveira et al., 2015; Ribeiro et al., 2014; Silveira et al., 2016).

Quartzites and sandstone are the prevalent formations in *campos rupestres.* Its core area rests along the highlands of the *Espinhaço* Range in the states of Bahia and Minas Gerais. The *Espinhaço* Range is a 1200 km long mountain range, formed predominantly by Proterozoic quartzites. In terms of vegetation, is an ecotonal environment between the Atlantic Forest, Cerrado and Caatinga biomes (Conceição et al., 2016)

Ironstones are mainly found at the Iron Quadrangle of southeast Brazil. The region is in the Atlantic Forest Domain, and is adjacent to the Cerrado Domain. These geosystems, known in Brazil as *cangas*, usually occur in higher relief areas, with tabular tops. As a consequence of the porosity and permeability in *cangas*, they have high water recharge capacity and storage, forming large aquifers that supply springs and cities (Jacobi & Carmo, 2008). Smaller patches of *cangas* areas also occur in the Urucum Plateau region (Mato Grosso do Sul-MS) and Serra do Carajás (Pará-PA), and they are important areas of mineral exploration (Zappi et al., 2017). The Iron Quadrangle and *Serra do Carajás* represent the two largest open-cast iron mining areas in the world, making Brazil second in terms of iron-ore exports (National Minerals Information Center & US Geological Survey, 2017).

2.2 Dataset

We compiled 105 geo-referenced inventories from published and unpublished literature (such as master and PhD thesis), consisting of checklists from *campos rupestres* that comprised all plant life-forms (woody and herbaceous species). Considering that *campos rupestres* are a complex mosaic of microhabitats, only studies held on open vegetation (grasslands) associated to rock outcrops were selected. Each floristic survey was then classified according to the substrate (e.g., canga, quartzite) reported in the publication. Thus, inventories that did not reported physiognomy or substrate were not included in the dataset. Information contained within the publication was used to subdivide the list into sampling sites. The details of the database are available as Supplementary Material (Table S1).

Plant taxonomy was revised and corrected using the “plantminer” function of “taxize” R package (Chamberlain & Szöcs, 2013) according to the Brazilian Flora 2020 project (BFG, 2020). Intraspecific categories (subspecies, varieties, and forms) were treated at the species level, and records without complete identification (e.g., cf., affinis, or not identified to species level) were excluded.

Of the 105 sites compiled in the initial database, seven were excluded after performing exploratory analysis due to inconsistencies in the sampling methods. The 98 sites that remained comprised 5,182 plant species from 1,097 genera and 154 families.

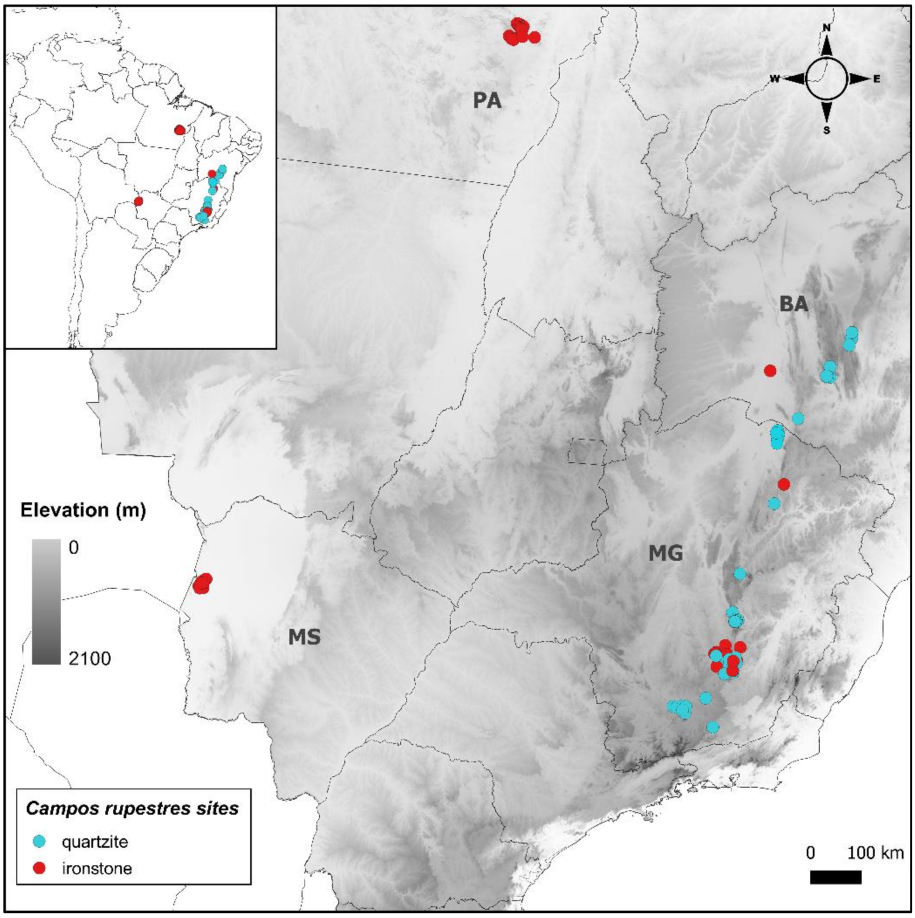

Figure 2. Geographic distribution of the 105 *campos rupestres* plant communities used in this study, classified into quartzite and ironstone (*canga*) according to the substrate informed in the original publication.

2.3 Data Analysis

Cluster analyses: Partitioning by k-means

To explore the floristic identity of the *campos rupestre*, we first conduct a k-means partitioning, which is a method that allows the use of a dissimilarity matrix to group sites that are more similar to each other into K groups, or clusters (Legendre & Legendre, 2012). To perform the analysis, we first excluded 3,309 singletons (species found at a single site), as they commonly increase the noise in most analyses without contributing information (Lepš & Šmilauer, 2003). We used Simpson's dissimilarity index to represent floristic dissimilarity among sites, which is more appropriate to our dataset as it allows comparison even when communities assemblages have different sampling efforts and/or species richness (How & Kitchener, 1997). We ran the analysis several times with different random initial configurations to find the best solution (Borcard et al., 2018). We then performed an ANOSIM test to define the optimal number of clusters considering a threshold of $R > 0.75$. In addition, we visually explore the patterns of floristic differentiation by performing a non-metric multidimensional scaling (NMDS) (McCune & Grace, 2002) based on the Simpson distance among sites. These analyses were performed in R statistical environment (R Core Team, 2017) using the 'recluster' (Dapporto et al., 2013) and 'vegan' (Oksanen et al., 2020) packages.

Environmental data selection

To investigate the role of environmental variables in driving floristic differentiation within each group of *campos rupestres* found in the k-means analyses, we first performed a Principal Component Analysis (PCA) to reduce the dimensionality of the environmental matrices. As climatic variables, we used the 19 bioclimatic variables obtained from WorldClim 2.0 (Fick & Hijmans, 2017) with a 30 arc-sec resolution (~1 km^2 at the Equator). These variables were extracted for each inventory by overlapping the geographic coordinates of our sites onto WorldClim climatic layers. For the edaphic variables, we extracted from SoilGrids v0.5.5 (https://soilgrids.org/; Hengl et al., 2017) all the 11 properties available for download, at four different soil depths (0, 5, 15 and 30 cm), which were then averaged. Then, we used the first component of the PCA as "Climate" or "Soil" predictors. The variables were tested for collinearity based on their variance inflation factor (VIF), with all comparisons showing VIF < 2 (Quinn & Keough, 2002).

Spatial structure

The spatial configuration of sites was described by a distance-based Moran's eigenvector maps (dbMEM), a method based on computing the principal coordinates of a matrix of geographic neighbors (after Borcard et al., 2011). MEM analyses are considered robust and suitable for discriminating between spatial and environmental effects on community composition (Griffith & Peres-Neto, 2006). Each dbMEM-variable represents a spatial pattern at a given scale, from single maxima or minima within the study area to very small-scale variation with many maxima and minima. We included MEM-variables describing significant spatial autocorrelation (only positive eigenvalues, see Dray et al., 2006), to perform an RDA- based partitioning of variation in the community composition matrix together with environmental variables. 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).

Species accumulation curve

Species accumulation curves were generated following Chao et al. (2014), and performed with three methodologies: Hill numbers species richness (q=0), Shannon diversity (q=1) and Simpson diversity (q=2) for individual-based rarefaction and extrapolation curves (Chao et al., 2014). Due to unequal sampling, we used sampled-based rarefaction, and extrapolated our curves by default (endpoint is set to be double the reference sample size (Colwell et al., 2012). The curves are rendered with 95% confidence intervals based on the bootstrap method (1,000 replications), which facilitates the comparison of several communities of extrapolated samples. This analysis was performed using the “iNEXT” package (Hsieh et al., 2016) in software R (R Core Team, 2017).

Community assembly

In order to assess community structure for each of the k-groups, we adopted the metacommunity approach proposed by Leibold and Mikkelson (2002) and further expanded by Presley et al. (2010). First, we organized the sites and species within the presence/absence matrix, with singletons excluded, sorted by the first axis of a redundancy analysis (RDA) (Legendre & Gallagher, 2001). Then we used this matrix to execute a variation partitioning with respect to the significant environmental variables (Climate and Soil), and spatial factors (using dbMEM vectors). 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).

Turnover is assessed by counting the number of times a species replaces another between two sites and comparing this value to the average number of replacements found when randomly sorting the community matrix 1,000 times. More replacements than expected by chance indicate a turnover structure, while fewer imply that the metacommunity follows a nested pattern (Presley et al., 2010).

We used the “Turnover” function of “metacom” package (Dallas, 2014) implemented in the R environment (R Core Team, 2017). We adopted a "curveball" sequential method for binary matrices, from the “vegan” package, that implements the ‘Curveball’ algorithm of Strona *et al.* (2014). The algorithm selects two random rows and finds the set of unique species that occur only in one of these rows. The algorithm randomly distributes the set of unique species to rows, preserving the original row frequencies. Zero to several species are swapped in one step, and usually the matrix is perturbed more strongly than in other sequential methods.

The structure of the variation in the species composition of each group defined in the *k-means* analysis was evaluated through turnover. The results of turnover were expressed as Z-scores. All null models were based on 1,000 permutations.

3. RESULTS

Cluster Analysis

The k-means partitioning analysis recognized six clusters of *campos rupestres* as the optimal number of floristic groups. The 98 sites were classified in: a) Southern Espinhaço (29 sites); b) *Corumbá* (10 sites); c) *Carajás* (16 sites); d) *Serra do Cipó* (15 sites); e) Iron Quadrangle (21 sites); f) Northern Espinhaço (seven sites).

The distribution of the sites in ordination space yielded by NMDS (K = 2; stress = 0.20; Figure 2) revealed two major gradients of compositional variation between *campos rupestres* found on ironstone and quartzite outcrops. Quartzite's core area, the compositional segregation of the *Espinhaço* Range reflects a biogeographical divide between Northern Espinhaço in Bahia and Southern Espinhaço in Minas Gerais. The southern portion of the *Espinhaço* Range was further segregated into a second group, consisting of the largest continuous area of *campos rupestres*: the *Serra do Cipó* in Minas Gerais state.

Ironstone formations, also segregated into three distinct groups: Amazonian *Carajás* in the north, *Corumbá* in central-west Brazil (Urucum Plateau) and the Iron Quadrangle in southeast Brazil (Fig.3). These three distinct groups of *cangas* correspond to different biogeographic regions, covering four different biomes (Amazonia, Pantanal, and an ecotone between Cerrado and Atlantic Forest). The Southern *Espinhaço* sites are placed across intermediate scores of the first NMDS axis, indicating that this group may represent an element of floristic connection amongst all the other five groups.

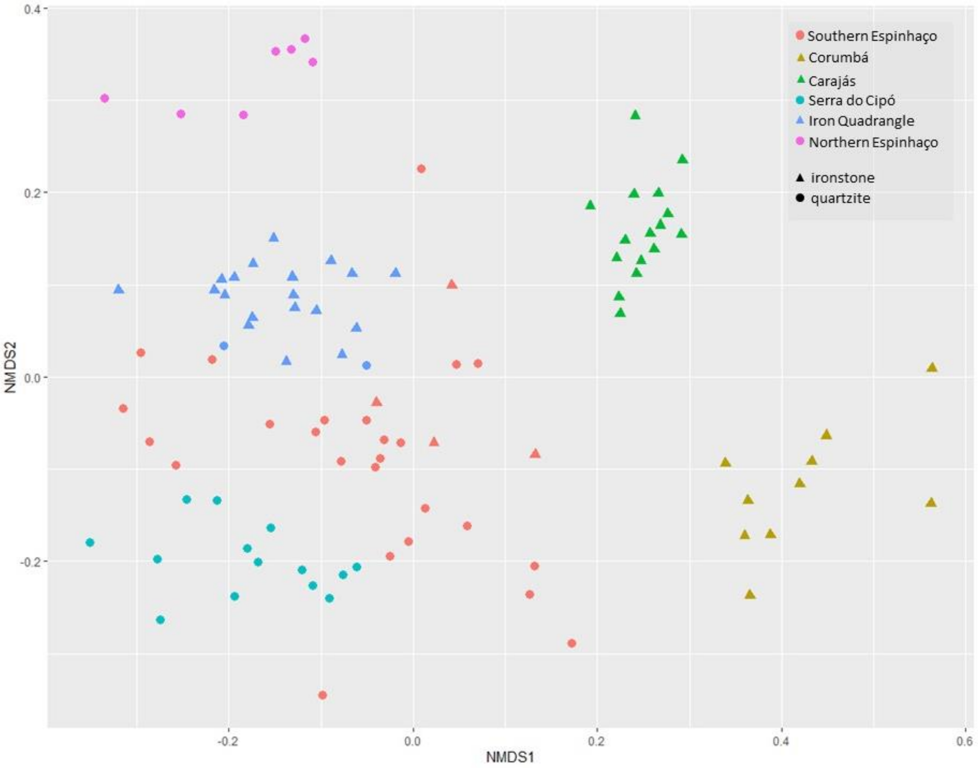

Figure 3. Ordination of 98 *campos rupestres* sites inferred from non-metric multidimensional scaling of their species composition. Colors indicate their classification into six main floristic groups yielded by k-mean analyses. Quartzite outcrops are depicted by filled circles (Southern *Espinhaço*: light red; *Serra do Cipó*: light blue; Northern *Espinhaço*: pink), and ironstone outcrops are depicted by filled triangles (*Corumbá*: light brown; *Carajás*: green; Iron quadrangle: light blue).

Species accumulation curves

The highest values of species richness (observed x estimated) were found for the groups of Southern Espinhaço, with 1,372 species observed and 2,907 as the expected richness. In second comes the Iron Quadrangle, with 1,090 species observed and 2,306 estimated (see Table S2). Both clusters had the highest number of sampling units, respectively 29 and 21 sites, and did not achieve an asymptote in the accumulation curves. *Corumbá* and Northern *Espinhaço* are the groups with the lowest number of sampling units, and seem to have reached an asymptote. Even with a reduced number of sites, both regions were floristically distinct, according to the cluster analysis (Fig. 4).

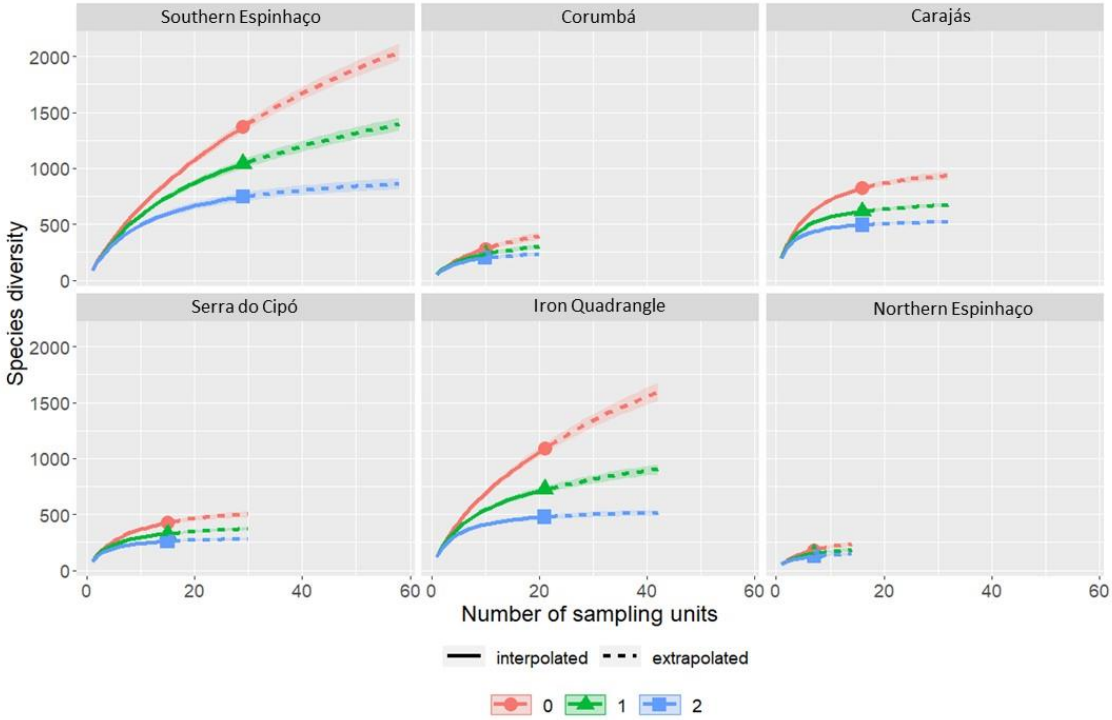

Figure 4. Rarefaction-based species accumulation curves for all six groups. Solid lines are individual-based rarefaction curves. Dashed lines are extrapolation curves. The three curves describe different diversity metrics: Hill number (q=0 in red), Shannon diversity (q=1 in green), and Simpson diversity (q=2 in blue). Confidence intervals 95% (shaded areas).

Compositional variation within groups

The forward selection retained few MEMs for each cluster, all of them are among the first MEMs (1 to 5), which represents a broad-scale positive autocorrelation. Apart from the *Serra do Cipó* group, which shows no clear spatial structure, there seems to be a strong spatial component associated with the assembly of *campos rupestres* (Fig. 5 and 6). This result is further supported by the redundancy analysis (RDA), with more distant sites being placed at extreme values of the first RDA axis (Fig. 5 and 6). Moreover, when geographical distances increase, there is a trend towards variation in species composition.

This pattern is clearly observed within both quartzite and ironstone groups, where compositional variation occurs gradually along mountain range reliefs (Fig. 5 and 6). In addition, environmental factors also play a role in floristic differentiation within each cluster of *campos rupestres*, with climate being relatively more important than the edaphic component (Table S2). The community structure analysis revealed that variation in species composition in all six metacommunities exhibit a turnover pattern, indicated by a significant positive z-score (see Table 1).

Table 1. Turnover values for community structure of the *campos rupestres* k-groups.

	Southern Espinhaço	**Corumbá**	**Carajás**	**Serra Do Cipó**	**Iron Quadrangle**	**Northern Espinhaço**
Re	2601983	15392	788735	288444	1047635	6034
z	14	12	15	19	13	13
p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

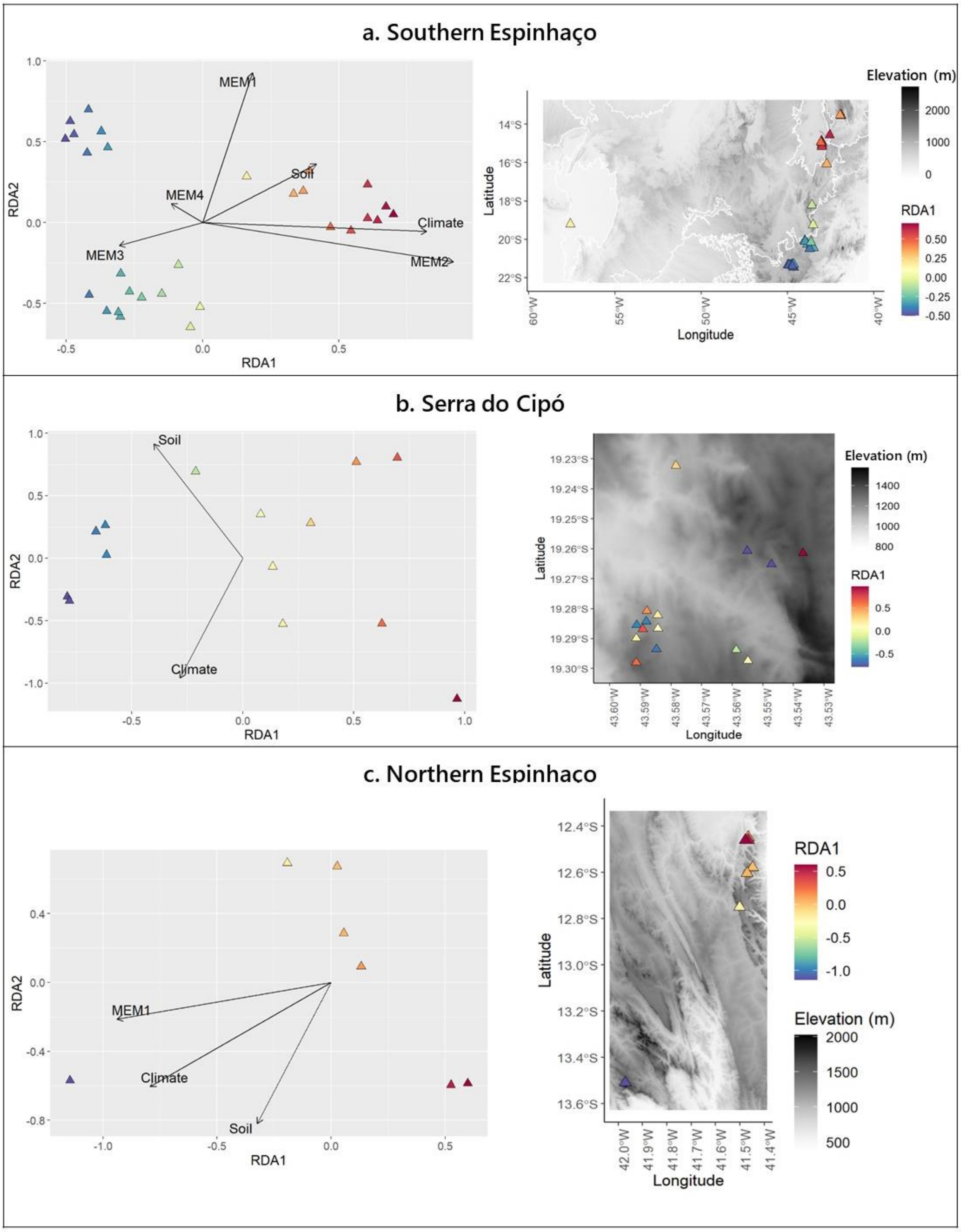

Figure 5. Redundancy analysis (RDA) of the community matrix with climatic (Climate) and edaphic (Soil) variables and spatial factors (using dbMEM spatial vectors) for quartzite floristic groups. Maps on the right side of each panel illustrate the geographical and elevational distribution of campos rupestres (triangles) within each floristic group, (darker areas represent higher elevation). Color gradient across triangles (plant communities) reflect the scores of the first RDA axis (summarizing the major gradient of compositional variation). Warmer colors in the map indicating higher scores, and are identical to colors in the RDA diagram. a) Southern *Espinhaço* cluster; b) *Serra do Cipó* cluster; c) Northern *Espinhaço* cluster.

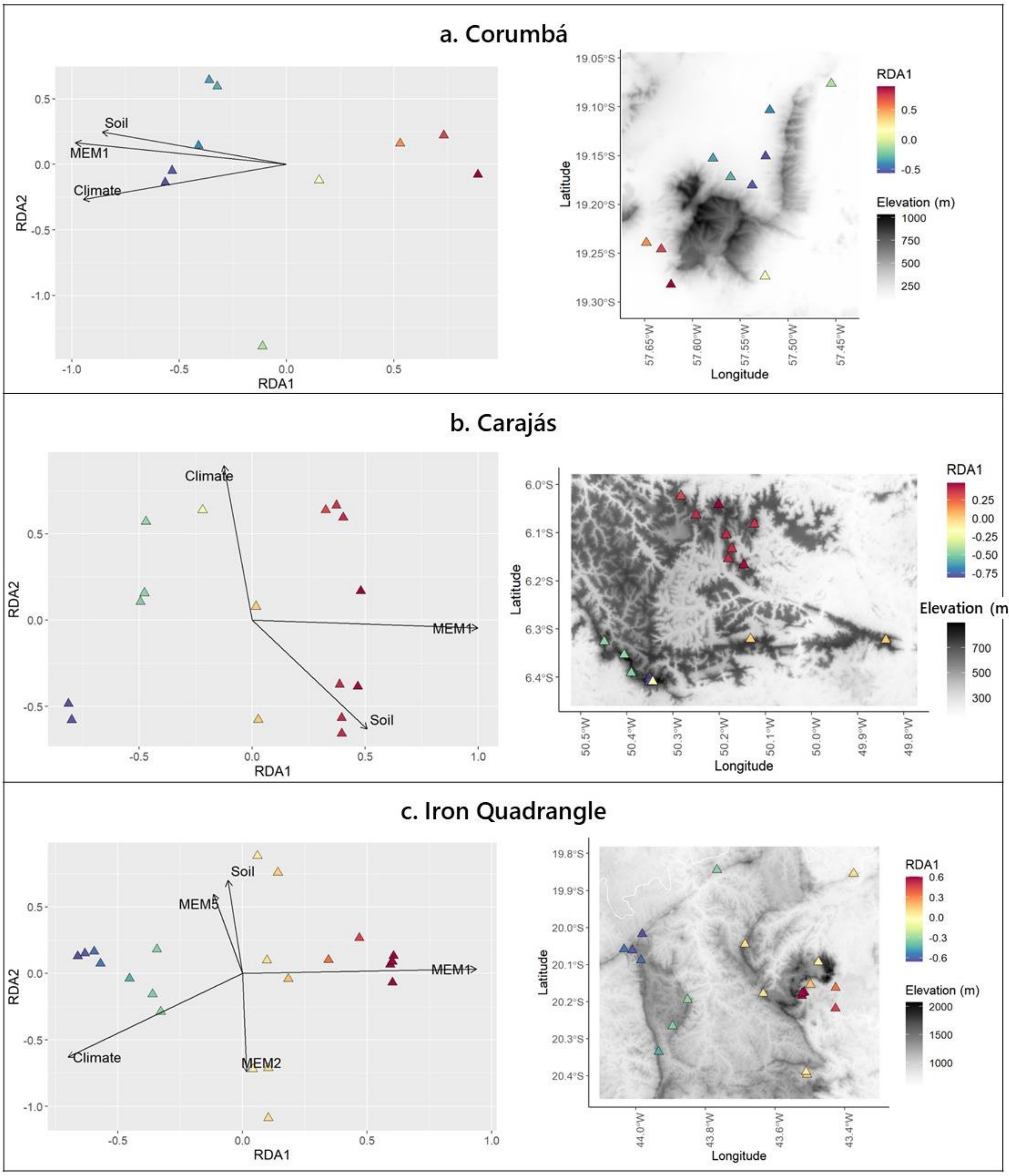

Figure 6. Redundancy analysis (RDA) of the community matrix with climatic (Climate) and edaphic (Soil) variables and spatial factors (using dbMEM spatial vectors) for quartzite floristic groups. Maps on the right side of each panel illustrate the geographical and elevational distribution of campos rupestres (triangles) within each floristic group, (darker areas represent higher elevation). Color gradient across triangles (plant communities) reflect the scores of the first RDA axis (summarizing the major gradient of compositional variation). Warmer colors in the map indicating higher scores, and are identical to colors in the RDA diagram. a) *Corumbá* cluster; b) *Carajás* cluster; c) Iron Quadrangle cluster.

4. DISCUSSION

Our first aim in this paper was to explore the floristic identity of *campos rupestres*. Similar studies, approaching *campos rupestres* and other ecosystems, have focused on changes in tree community composition along environmental gradients (e.g., Bueno et al., 2021; Marcilio-Silva et al., 2017; Neves et al., 2018; Nunes et al., 2015), thus neglecting the largest portion of the biodiversity in tropical plant communities. By expanding the ecological scope of *campos rupestres*, as well as refining analytical approaches, here we have provided information that are both novel and of importance to the conservation biogeography of these unique, albeit threatened ecosystems.

Perspectives from a few studies have created the idea of floristic cohesiveness between plant communities on quartzite and ironstone (*cangas*) outcrops (e.g., Alves et al., 2014; Fernandes, 2016), while our results corroborate others that demonstrate a clear floristic segregation between plant communities on *cangas* versus those associated with quartzite outcrops (Caminha-Paiva et al., 2022; do Carmo & Jacobi, 2016; Fernandes et al., 2020; Jacobi et al., 2007; Messias et al., 2013; Zappi et al., 2017). Although such controversial findings might appear as a simple scientific debate, it could bring a lot of haziness to conservation planning. In Minas Gerais state, for instance, the Provision n◦02/2017 (*SISEMA*, 2017) (hereafter IS02/2017) allowed out-of-kind compensation (in a different vegetation type), in projects involving the suppression of the plant community, like mining pit expansion, as long as there is "ecological equivalence" between the suppressed vegetation and the vegetation type to be set aside for compensation (Silveira et al., 2020).

Regarding that matter, if we are to use scientific evidence to uphold environmental legislation, it is of utmost importance that we address this debate so that conservation planning in biodiverse plant communities are effective. To illustrate the uniqueness of these environments, our database revealed that ironstone sites hold 872 exclusive species, and only share 228 species with quartzite sites. Hence, our findings support a clear segregation between ironstone and quartzite communities and if we intend to protect distinct floristic compositions, we cannot replace ironstone formations with quartzite ones.

Biogeographical novelties

Using a more comprehensive database and state-of-the-science biogeographical analyses, comprising all rupicolous plant life-forms, we found six clusters that constitute *campos rupestres* metacommunities. Three groups of ironstone formation and three from quartzites. We point out the novel recognition of *Serra do Cipó* and *Corumbá* as distinctive groups within Brazilian *campos rupestres*.

Concerning the three groups of *cangas* (Iron Quadrangle, *Corumbá* and *Carajás*), Zappi et al. (2019) found that angiosperm lineages in *Carajás* have clear association with the Amazonia biome, sharing only a few species with the *cangas* in the Iron Quadrangle. Such specificity of *cangas* in *Carajás* indicates that plant communities there might function as island-like systems, where a lateritic crust embedded in a forest matrix provides contrasting environmental conditions at small spatial scales. Combining this island-like configuration with geomorphological diversity, creates an abundance of refuges for species adapted to xeric and mesic conditions (Jacobi et al., 2007; Mota et al., 2018; Silva et al., 2020), which could be linked to the occurrence of outstanding levels of plant endemism in all groups of *cangas* (Bonatelli et al., 2014; Fiorini et al., 2020; Leal et al., 2016; Mota et al., 2020; Perrigo et al., 2020) as well as its regional compositional turnover (as depicted in our results).

A high rate of regional endemism could also be driving the floristic differentiation among the three quartzite groups. Apparently, lineages isolated in the northern region evolved without producing a great number of species when compared with lineages in the southern portion, either because of lower diversification rates or because of higher extinction rates (Rapini et al., 2008). The 300 km disjunction between the *campos rupestres* in Minas Gerais and Bahia represents an important barrier for most endemics, restricting their migration between the two mountain massifs (Harley, 1988). Nonetheless, geography does not seem to explain the floristic segregation of *Serra do Cipó*, which is geographically embedded in the Southern Espinhaço group but shows the highest richness of microendemics (Echternacht et al., 2011).

Furthermore, there is an accentuated difference in geological, climatic and biotic conditions between the northern and southern areas of the *Espinhaço* Range (Bitencourt

& Rapini, 2013; Colli-Silva et al., 2019; Echternacht et al., 2011; Rapini, 2010). The southern sector is more humid, with lower average temperature and higher average elevations, and is more strongly influenced by the Atlantic Forest biome than the northern sector (for a detailed description of the climatic and biotic influences over the *Espinhaço* Range see Alves & Kolbek, 2010). The climate becomes gradually driers towards the norther portion of the *Espinhaço* Range (Echternacht et al., 2011) as the influence of the Caatinga climate increases.

Future perspectives on the biogeography of campos rupestres

Here we stress that future studies should try and address the following paradigmatic finding: although the ironstone clusters are mostly cohesive, some sites clustered with quartzites of the *Espinhaço* Range, and those sites are located on fragmented ironstones (*Serra da Calçada*, *Serra do Rola Moça* in the Iron Quadrangle, *Morraria Santa Cruz* in *Corumbá*, and *Vale do Peixe Bravo* in the central portion of *Espinhaço*). Vegetation on fragmented ironstone is predominantly herbaceous with small shrubs, and the species that develop on this environment grow between crevices on the rocks, and sometimes on a thin layer of soil accumulated directly on top of the rock. Due to these features, species found on this type of ironstone are also found throughout quartzite outcrops of the Espinhaço Range (Carmo & Kamino, 2017; Giulietti et al., 1987; Pirani et al., 2003; Viana & Lombardi, 2007). On the other hand, none of the lateritic crust formation grouped with quartzite, including those geographically close. We thus hypothesize that soil structure, not substrate (i.e., ironstone vs quartzite), are the most important factors controlling species composition in *campos rupestres*, at least outside of the Amazon.

Community assembly

In testing our second hypothesis, we found that both climate and soil are important components driving the major gradient of variation in community composition within each floristic group (summarized by the first axis of the redundancy analyses, see Table S3), though at different spatial scales. While soil was important at smaller spatial scales (within *Carajás, Corumbá*, and *Serra do Cipó*) the importance of edaphic conditions was negligible within floristic groups that span larger areas (Northern *Espinhaço*, Southern

Espinhaço, and the Iron Quadrangle) (Fig. 5 and 6). This was probably due to the coarseness of our soil data, since previous studies that used a finer resolution of edaphic factors have recovered significant association between floristic composition and soil conditions (Caminha-Paiva et al., 2021; Conceição et al., 2016; Nunes et al., 2020).

The climatic and edaphic variation within each cluster of *campos rupestres* seems to be effective in constraining plant species, which are gradually replaced across the geographic space (Fig. 5 and 6). This pattern of species turnover between sites and across environmental gradients indicates that species are spatially segregated according to their niche preferences (Bueno et al., 2021; Rahbek et al., 2007; Valladares et al., 2015), and suggest that communities are responding to a very consistent environmental gradient across scales (Leibold & Mikkelson, 2002; Meynard et al., 2013).

Furthermore, there seems to be striking variation in plant community composition at close geographic distance (Fig. 4), which is not accounted for by the climatic and edaphic variables in our models. When studying *campo rupestres* plant communities across the Espinhaço Range, Carmo and Jacobi (2016) concluded that environmental factors alone were not enough to explain differences in vegetation. Here we argue that fire, herbivory and dispersal limitation, which are important ecological components in *campos rupestres* (Fernandes, 2016; Le Stradic et al., 2015; Neves & Conceição, 2010), should be considered in the experimental design if future studies aim at disentangling the major controls of floristic composition within each of these clusters of *campos rupestres*.

The unique floristic composition of *campos rupestres* clusters and the turnover pattern associated to their community assembly, reinforce the importance of conservation strategies that consider protection areas spanning all climatic and edaphic heterogeneity, making sure to account for the distinct spatial scales of these two environmental factors (as depicted in our results). While protecting the environmental space that harbors species-rich communities would be ideal in metacommunities structured by species loss along environmental gradients (i.e., nestedness), in regions where communities are mainly assembled from species being replaced along environmental gradients (i.e., turnover), many species would be unprotected due to their endemism to optimal, narrow environmental conditions. Finally, ecological restoration must also consider the evidence of turnover in structuring the assembly of *campos rupestres* metacommunities, thus preventing ecosystem homogenization through the misleading use of wrong species in restoration programs and consequent loss of biodiversity and ecosystem services.

5. CONCLUSION

To our knowledge, this is the most comprehensive study addressing large-scale questions on the biogeography of Brazilian montane old-growth ecosystems. Our data and analyses supported the floristic identity of multiple *campos rupestres*, indicating six floristic groups, or metacommunities. Our results further support that climate and edaphic conditions act at distinct spatial scales shaping variation in community composition of *campos rupestres* metacommunities. Lastly, variation in community composition is consistently structured by the turnover, or replacement of species along environmental gradients.

We stress that the conservation planning of these unique ecosystems should consider the floristic circumscription defined in our analyses, placing protected areas at several distinct points along the climatic and edaphic gradients of each *campo rupestre* metacommunity. Moreover, we suggest dropping the term *campo rupestre* sensu lato (i.e quartzite and *canga* lumped together; Silveira et al. 2016) and that compensation measures should take into account not only their distinct geomorphologies, but also the biogeographical groups within each geomorphology.

Lastly, we reinforce the need to create more protected areas (PAs), especially in the ironstone groups (Iron Quadrangle, *Corumbá* and *Carajás*), since there are only a few PAs that provide full legal protection status to these ecosystems. Given their unique species composition, biodiversity loss in these ecosystems cannot be replaced by any other habitat in the world.

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7. SUPPLEMENTARY MATERIAL

Table S1. Locations of floristic inventories and their respective k-means clusters.

Fisionomia	AreaCode	Long10	Lat10	Autor	Ano	Fonte	State	Localidade
canga	CanMG001	-43.513904	-20.175803	Ataide et al	2011	Revista Arvore	MG	Ouro Preto, Serra de Santo Antonio Pereira, canga couracada
canga	CanMG002	-43.513904	-20.175803	Ataide et al	2011	Revista Arvore	MG	Ouro Preto, Serra de Santo Antonio Pereira, canga nodular (Itabirito)
canga	CanMG003	-43.499167	-20.150119	Santos	2010	Tese UFMG_Botanica	MG	Mina Alegria, Mariana
canga	CanMG004	-43.771111	-19.845556	Santos	2010	Tese UFMG_Botanica	MG	Mina Segredao, Sabara
canga	CanMG005	-43.891389	-20.260556	Santos	2010	Tese UFMG_Botanica	MG	Mina Sapecado, Itabirito
canga	CanMS001	-57.580858	-19.193336	Damasceno-Junior et al	2005	Relatorio Consultoria	MS	Corumba, Morraria Santa Cruz
campo_quartzitico	RupMG001	-43.576883	-19.231605	Mattos et al	2019	Plant Ecology	MG	Serra do Cipo, Cedro
campo_quartzitico	RupMG002	-43.554818	-19.293675	Mattos et al	2019	Plant Ecology	MG	Serra do Cipo, Pedra do Elefante
campo_quartzitico	RupMG003	-43.591481	-19.294814	Mattos et al	2019	Plant Ecology	MG	Serra do Cipo, Quadrante 16
campo_quartzitico	RupMG004	-43.536122	-19.266234	Mattos et al	2019	Plant Ecology	MG	Serra do Cipo, Alto Palacio
campo_quartzitico	RupMG005	-43.615833	-20.225556	Nunes et al	2020	Plant Ecology and Evolution	MG	RPPN Fazenda Capanema
campo_quartzitico	RupMG006	-43.483056	-20.433889	Lemes	2009	Dissertacao UFOP_Ecologia	MG	Ouro Preto, Serra do Itacolomi
campo_quartzitico	RupMG007	-43.716111	-20.486389	Lemes	2009	Dissertacao UFOP_Ecologia	MG	Ouro Preto, Serra de Ouro Branco
campo_quartzitico	RupMG008	-43.426111	-20.213333	Messias et al	2012	Acta Botanica Brasilica	MG	Mariana, campo quartzitico
canga	CAL_CAC	-43.983611	-20.093056	Viana and Lombardi	2007	Rodriguesia	MG	Brumadinho, Serra da Calcada, canga couracada
canga	CAL_CNC	-43.983611	-20.093056	Viana and Lombardi	2007	Rodriguesia	MG	Brumadinho, Serra da Calcada, canga nodular
canga	COC_CAC	-43.376389	-19.851667	Mourao and Stehmann	2007	Rodriguesia	MG	Barao de Cocais, Mina do Brucutu
canga	CRJ_S11A	-50.450556	-6.327778	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Sul A

canga	CRJ_S11B	-50.406389	-6.357778	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Sul B
canga	CRJ_S11C	-50.388333	-6.394444	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Sul C
canga	CRJ_S11D	-50.342222	-6.410556	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Sul D
canga	CRJ_SB	-49.841944	-6.327222	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra da Bocaina
canga	CRJ_SN1	-50.280278	-6.026389	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 1
canga	CRJ_SN2	-50.246667	-6.059444	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 2
canga	CRJ_SN3	-50.203333	-6.045556	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 3
canga	CRJ_SN4	-50.185833	-6.106944	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 4
canga	CRJ_SN5	-50.125278	-6.086667	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 5
canga	CRJ_SN6	-50.173611	-6.130833	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 6
canga	CRJ_SN7	-50.178889	-6.158056	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 7
canga	CRJ_SN8	-50.151667	-6.169167	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra Norte 8
canga	CRJ_ST	-50.133889	-6.325833	Zappi et al	2019	PLoS ONE	PA	Carajas, Serra do Tarzan
canga	ITA_CAN	-43.855556	-20.198056	Zappi et al	2017	Frontiers in Plant Sciences	MG	Itabirito, canga
campo_quartzitico	ITA_CRQ	-43.853889	-20.238333	Zappi et al	2017	Frontiers in Plant Sciences	MG	Itabirito, quartzito
canga	RO1_SC	-44.012273	-20.060259	Jacobi et al	2007	Biodiversity and Conservation	MG	Nova Lima, Serra do Rola Moca
canga	RO2_SC	-43.937901	-20.339244	Jacobi et al	2007	Biodiversity and Conservation	MG	Nova Lima, Serra do Rola Moca
canga	SAP_CAC	-43.505016	-20.3974	Scalon et al	2012	MG Biota	MG	Ouro Preto, Morro do Cruzeiro (UFOP), canga couracada
canga	SAP_CAM	-43.5196	-20.179853	Messias et al	2012	MG Biota	MG	Ouro Preto, Serra de Antonio Pereira, canga herbacea
canga	SAP_CNO	-43.512036	-20.39383	Scalon et al	2012	MG Biota	MG	Ouro Preto, Morro do Cruzeiro (UFOP), canga nodular
canga	SAP_CS	-43.5196	-20.179853	Messias et al	2012	MG Biota	MG	Ouro Preto, Serra de Antonio Pereira, canga arbustiva
canga	Canga_01	-50.349722	-6.406111	Nunes	2009	Tese UFV_Botanica	PA	Floresta Nacional de Carajas, canga herbacea
canga	Canga_02	-50.349722	-6.406111	Nunes	2009	Tese UFV_Botanica	PA	Floresta Nacional de Carajas, canga arbustiva
canga	Canga_05	-43.983333	-20.016667	Vincent and Meguro	2008	Brazilian Journal of Botany	MG	Nova Lima, Serra da Mutuca, canga couracada
canga	Canga_06	-44.016667	-20.05	Vincent and Meguro	2008	Brazilian Journal of Botany	MG	Nova Lima, Serra do Rola Moca, canga nodular

canga	Canga_08	-43.429107	-20.159803	Pereira	2010	Dissertacao UFV_Botanica	MG	Mariana, Chapada do Canga
canga	Canga_10	-44.030556	-20.059722	Jacobi et al	2008	Revista Arvore	MG	Serra do Rola Moca
campo_quartzitico	Rupestre_quartzitico_01	-43.587639	-19.286056	Le Stradic et al	2015	Tese UFMG_Ecologia	MG	Serra do Cipo, campo arenoso
campo_quartzitico	Rupestre_quartzitico_02	-43.587639	-19.286056	Le Stradic et al	2015	Tese UFMG_Ecologia	MG	Serra do Cipo, campo nodular
campo_quartzitico	Rupestre_quartzitico_03	-41.471389	-12.459167	Conceicao et al	2007	Acta Botanica Brasilica	BA	Palmares, Plato Cruz
campo_quartzitico	Rupestre_quartzitico_04	-41.473889	-12.456667	Conceicao et al	2007	Acta Botanica Brasilica	BA	Palmares, Plato Dois
campo_quartzitico	Rupestre_quartzitico_05	-44.806944	-21.350278	Andrade	2013	Dissertacao UFLA_Ecologia	MG	Serra da Bocaina, Morro da Janela
campo_quartzitico	Rupestre_quartzitico_06	-44.648611	-21.452778	Andrade	2013	Dissertacao UFLA_Ecologia	MG	Serra da Bocaina, Carrancas
campo_quartzitico	Rupestre_quartzitico_07	-44.980278	-21.330556	Andrade	2013	Dissertacao UFLA_Ecologia	MG	Serra da Bocaina, Boqueirao
campo_quartzitico	Rupestre_quartzitico_08	-44.880278	-21.3425	Andrade	2013	Dissertacao UFLA_Ecologia	MG	Serra da Bocaina, Ingai
campo_quartzitico	Rupestre_quartzitico_19	-43.983333	-20.1	Vincent and Meguro	2008	Brazilian Journal of Botany	MG	Brumadinho, Serra da Calcada
campo_quartzitico	RupMG009	-44.719722	-21.291389	Arruda	2017	Dissertacao UFLA_Botanica	MG	Itutinga, Serra da Chapada
campo_quartzitico	RupMG010	-44.64	-21.308056	Arruda	2017	Dissertacao UFLA_Botanica	MG	Itutinga, Serra do Ouro Grosso
campo_quartzitico	RupMG011	-44.720278	-21.389722	Arruda	2017	Dissertacao UFLA_Botanica	MG	Itutinga, Serras do Pombeiro e Galinheiro
campo_quartzitico	RupMG012	-43.595778	-19.285528	Carvalho	2010	Dissertacao UFMG_Ecologia	MG	Serra do Cipo, Estancia Vellozia, campo de afloramentos
campo_quartzitico	RupMG013	-43.591389	-19.281778	Carvalho	2010	Dissertacao UFMG_Ecologia	MG	Serra do Cipo, Estancia Vellozia, campo turfoso
campo_quartzitico	RupMG014	-43.590056	-19.279861	Carvalho	2010	Dissertacao UFMG_Ecologia	MG	Serra do Cipo, Estancia Vellozia, campo arenoso

campo_quartzitico	RupMG015	-43.587528	-19.286111	Carvalho	2010	Dissertacao UFMG_Ecologia	MG	Serra do Cipo, Estancia Vellozia, campo nodular
campo_quartzitico	RupMG016	-43.590278	-18.201667	Oliveira	2015	Dissertacao UFVJM_Florestal	MG	Diamantina, Parque Estadual do Biribiri
campo_quartzitico	RupBA001	-41.877778	-13.533056	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Pico das Almas, C1
campo_quartzitico	RupBA002	-41.9425	-13.517222	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Pico das Almas, C2
campo_quartzitico	RupBA003	-41.946944	-13.520833	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Pico das Almas, C3
campo_quartzitico	RupBA004	-41.972778	-13.511667	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Pico das Almas, C4
campo_quartzitico	RupBA005	-41.466667	-12.45	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Serra do Sincora, Morro da Mae Inacia
campo_quartzitico	RupBA006	-41.45	-12.583333	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Serra do Sincora, Fumaca
campo_quartzitico	RupBA007	-41.466667	-12.6	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Serra do Sincora, Gerais da Fumaca
campo_quartzitico	RupBA008	-41.5	-12.75	Junca et al	2005	Livro (Biodiversidade e Conservacao da Chapada Diamantina, MMA)	BA	Serra do Sincora, Guine
campo_quartzitico	RupMG017	-43.511667	-19.247167	Pena	2009	Dissertacao USP_Botanica	MG	Serra do Cipo, P1A1
campo_quartzitico	RupMG018	-43.510556	-19.247056	Pena	2009	Dissertacao USP_Botanica	MG	Serra do Cipo, P1A2
campo_quartzitico	RupMG019	-43.552056	-19.26125	Pena	2009	Dissertacao USP_Botanica	MG	Serra do Cipo, P2A1
campo_quartzitico	RupMG020	-43.55075	-19.261417	Pena	2009	Dissertacao USP_Botanica	MG	Serra do Cipo, P2A2
campo_quartzitico	RupMG021	-43.560639	-19.289806	Pena	2009	Dissertacao USP_Botanica	MG	Serra do Cipo, P3A1
campo_quartzitico	RupMG022	-43.587806	-19.289556	Pena	2009	Dissertacao USP_Botanica	MG	Serra do Cipo, P4A1
campo_quartzitico	RupMG023	-43.588333	-19.284583	Pena	2009	Dissertacao_USP_Botanica	MG	Serra do Cipo, P4A2
campo_quartzitico	RupMG024	-43.472778	-20.089167	Oliveira	2010	Dissertacao_UFMG_Biologia_Vegetal	MG	Serra do Caraca, Pico do Carapuca

canga	CanMS011	-57.558611	-19.167222	de Lima et al	2019	Biota Neotropica	MS	Corumba, Estrada Parque
canga	CanMS002	-57.578361	-19.14925	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Band'Alta
canga	CanMS003	-57.645306	-19.236306	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Figueira
canga	CanMS004	-57.528528	-19.274556	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Monjolinho
canga	CanMS005	-57.538639	-19.1795	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Sao Joao
canga	CanMS006	-57.520139	-19.104306	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Sao Sebastiao do Caranda
canga	CanMS007	-57.455611	-19.074667	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Uruba
canga	CanMS008	-57.522778	-19.152222	de Lima et al	2019	Biota Neotropica	MS	Corumba, Fazenda Rabicho
canga	CanMS009	-57.635556	-19.241944	de Lima et al	2019	Biota Neotropica	MS	Corumba, Parque Municipal Piraputangas 9
canga	CanMS010	-57.618333	-19.283889	de Lima et al	2019	Biota Neotropica	MS	Corumba, Parque Municipal Piraputangas 10
canga	CanMG006	-43.630186	-20.180564	Pereira	2016	Tese_UFV_Botanica	MG	Capanema
canga	CanMG007	-43.689969	-20.042442	Pereira	2016	Tese_UFV_Botanica	MG	Serra do Gandarela
campo_quartzitico	RupMG025	-43.631389	-20.145556	Pereira	2016	Tese_UFV_Botanica	MG	RPPN Capivari II
canga	CanMG008	-42.72381	-16.080395	da Mota et al	2017	Livro (O Vale do Rio Peixe Bravo, Pristino)	MG	Vale do Peixe Bravo
campo_arenoso	RupMG026	-43.0375	-14.876944	Oliveira	2018	TCC_UFMG	MG	Parque Estadual Caminho dos Gerais, Ponto 002
campo_arenoso	RupMG027	-43.001833	-14.973978	Oliveira	2018	TCC_UFMG	MG	Parque Estadual Caminho dos Gerais, Trilha do Jatai
campo_arenoso	RupMG028	-43.019056	-15.084336	Oliveira	2018	TCC_UFMG	MG	Parque Estadual Caminho dos Gerais, Rio Taguatinga
campo_arenoso	RupMG029	-43.017003	-15.170619	Oliveira	2018	TCC_UFMG	MG	Parque Estadual Caminho dos Gerais, Trilha Joel e Betinha
campo_arenoso	RupMG030	-43.063067	-14.937519	Oliveira	2018	TCC_UFMG	MG	Parque Estadual Caminho dos Gerais, Trilha para Cachoeira das Piranhas
campo_quartzitico	RupBA009	-42.555278	-14.553611	Campos et al	2016	Brazilian Journal of Botany	BA	Serra Geral de Licinio de Almeida

Table S2. Observed and estimated diversity values for each of the six *campos rupestres* groups according to: Species richness, Shannon and Simpson diversity.

Site	Diversity	Observed	Estimator	s.e.	LCL	UCL
Southern Espinhaço	Species richness	1372	2907.649	148.012	2643.861	3226.149
Southern Espinhaço	Shannon diversity	1040.337	1864.259	52.656	1761.056	1967.462
Southern Espinhaço	Simpson diversity	744.88	1017.922	30.694	957.763	1078.081
Corumbá	Species richness	282	517.102	52.392	434.708	643.953
Corumbá	Shannon diversity	233.816	377.113	16.833	344.121	410.106
Corumbá	Simpson diversity	196.874	280.54	13.242	254.587	306.493
Carajás	Species richness	824	962.335	24.448	922.096	1019.08
Carajás	Shannon diversity	614.728	708.006	8.697	690.96	725.052
Carajás	Simpson diversity	493.49	549.492	7.953	533.904	565.079
Serra do Cipó	Species richness	426	523.145	21.235	489.61	574.36
Serra do Cipó	Shannon diversity	326.167	400.873	8.934	383.363	418.382
Serra do Cipó	Simpson diversity	257.409	302.945	7.984	287.296	318.594
Iron Quadrangle	Species richness	1090	2306.255	137.752	2064.822	2607.484
Iron Quadrangle	Shannon diversity	722.976	1128.933	28.556	1072.966	1184.901
Iron Quadrangle	Simpson diversity	476.227	558.137	14.647	529.431	586.844
Northern Espinhaço	Species richness	180	271	25.833	232.732	337.04
Northern Espinhaço	Shannon diversity	150.548	216.529	10.717	195.524	237.533
Northern Espinhaço	Simpson diversity	127.758	170.466	7.611	155.549	185.384

Table S3. RDA coefficients (axis1) for all *campos rupestres* floristic groups.

	Southern Espinhaço	**Corumbá**	**Carajás**	**Serra Do Cipó**	**Iron Quadrangle**	**Northern Espinhaço**
Climate	0.8224	-0.9472	-0.1245	-0.2815	-0.69878	-0.786
Soil	0.4183	-0.8578	0.509	-0.4012	-0.05744	-0.3088
MEM 1	0.1833	-0.984	0.999	-	0.93822	-0.9357
MEM 2	0.9204	-	-	-	0.01717	-
MEM 3	-0.3063	-	-	-	-	-
MEM 4	-0.1152	-	-	-	-	-
MEM 5	-	-	-	-	-0.116	-