FLORISTIC MOSAICS OF THE THREATENED BRAZILIAN CAMPO RUPESTRE

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The increase in rates of habitat loss requires an understanding of how biodiversity is distributed. Campo rupestre is an old, climatically buffered, and infertile landscape located in Brazil. Considered a biodiversity hotspot, the campo rupestre is mainly threatened by mining activity that requires a large operating area. Campo rupestre is known for its restricted distribution area and high abiotic heterogeneity, which modulates species coexistence and richness. To recognise the association between habitat type and plant communities, we propose to describe the floristic composition of herbaceous and shrub components in four habitats of the campo rupestre comprising quartzite and ferruginous substrate. We classified habitat types by the main surface soil features. In each habitat, we sampled ten 100-m^2 plots to access information on the shrub and ten 1-m^2 plots for the herbaceous component. Altogether we sampled 153 species, belonging to 38 families. The cluster analysis ordered by Sorensen metric indicates a clear distinction of species composition in the shrub component in the four habitats. However, the floristic composition of the herbaceous component was similar between the four habitats but showed a distinction when contrasting with the substrate type. Our results highlight the local taxonomic distinction between habitat types and substrates, indicating that the ecological distinction among substrate types of the campo rupestre cannot be overlooked in conservation and restoration actions.

Key words: canga, herbaceous, plant community, phytosociology, quartzite, rupestrian grassland, shrub

Introduction

The world is witnessing an unprecedented increase in rates of fragmentation and habitat loss, which comes along with abrupt increases in species extinction, loss of genetic diversity, and ecosystem services. Conserving ecosystems and their biotic and abiotic characteristics is a fundamental strategy to ensure biodiversity preservation. Traditionally, conservation efforts have focused the attention on forest environments that surely represents important refuge of species biodiversity (Veldman et al., 2015). However, open vegetation habitats, such as old-growth grasslands, are also centres of endemism and play a critical role in services related to human wellbeing (Veldman et al., 2015; Fernandes, 2016; Hopper et al., 2016). Therefore, it is time to extend our attention to the preservation of these ecosystems.

Brazil is home to the campo rupestre (rupestrian grassland), a speciose old-growth grassland located largely on the southeast mountaintops of the country (Giulietti et al., 1997; Fernandes, 2016; Miola et al., 2021). The campo rupestre forms a complex landscape composed of a variety of habitats such as quartzite and ferruginous outcrops interconnected by stony, gravel, sandy, acidy, nutrient-poor, and low water retention soils (Conceição & Pirani, 2005; de Carvalho et al., 2014; Fernandes, 2016; Schaefer et al., 2016a,b; Silveira et al., 2016). This edaphic diversity is one of the main local modulators of the coexistence of plant species, often endemic and rare (Giulietti et al., 1997; Jacobi et al., 2007; Messias et al., 2013; Fernandes, 2016; Gomes et al., 2021). Despite its restricted area (ca. 0.83% of Brazil's surface), the campo rupestre harbours ca. 15% of the Brazilian flora and 3% of the world species (Silveira et al., 2016; Fernandes et al., 2018). Therefore, to address effective conservation strategies in this ecosystem is essential to understand how local drivers of species coexistence (Zappi et al., 2019).

Recently, the campo rupestre has been recognised as an «old, climatically buffered, and infertile landscape» (OCBIL; Hopper et al., 2016; Silveira et al., 2016), along with worldwide ecosystems such as African fynbos and Australian kwongkan (Silveira et al., 2021). These OCBIL ecosystems harbour plant species with unique ecological strategies to face the harsh conditions of these ecosystems, including specific nutrient acquisition strategies, slow growth species from old evolutionary lineages, limited dispensability, and low resilience, which make a great challenge to conserve and restore ecosystems (Fernandes et al., 2016). On top of that, many OCBILs occur frequently in metal-rich environments creating a huge economic pressure to explore these ecosystems (Hopper et al., 2016). In Brazil, the Iron Quadrangle (IQ) comprises one of the most remarkable areas of the campo rupestre on both quartzite and ferruginous substrate. Due to biological and social importance the IQ is a UNESCO Biosphere Reserve (UNESCO, 2016) but has lost up to 50% of the original area due to mining activity (Jacobi & Carmo, 2011; Salles et al., 2019). In this sense, it is extremely important to develop studies that evaluate the biodiversity dimensions of the campo rupestre to generate knowledge about this ecosystem and then foster databases for conservation and ecological restoration projects.

Understanding the vegetation composition in various campo rupestre habitats allows designing more efficient actions for ecological restoration and conservation. For instance, by considering species habitats preference it is possible to better assist the choice of species to be implemented at the beginning and/or during a restoration (Jacobi et al., 2008; Fernandes et al., 2016; Gomes et al., 2018; Gastauer et al., 2020). Also, understanding the similarities and singularities between the vegetation of various habitat types provides a better basis for determining areas for conservation even when a gap between science and politics takes place (Silveira et al., 2020).

Here, we aim to characterise the composition and structure of the herbaceous and shrub components of various campo rupestre habitats in the IQ. If abiotic conditions select the local species composition, we expect the floristic species composition will differ according to the habitat evaluated (Jacobi & Carmo, 2011; Messias et al., 2013). In this respect, conservation practice for the campo rupestre should focus on the preservation of multiple conservation units, to ensure the persistence of a high floristic diversity of the ecosystem.

Material and Methods

Study area

We conducted the study in the region of the Natural Monument Serra da Calçada, located in the Iron Quadrangle between the municipalities of Nova Lima and Brumadinho, Minas Gerais, Brazil (Fig. 1). The local climate is considered subtropical highland climate (Cwb) according to the Köppen-Geiger classification, with two well-defined seasons, dry from April to October, and rainy from November to March. The Serra da Calçada region includes environments of riparian forest, woodland forest, and open grassland over quartzite and ferruginous substrates. In this study, we have evaluated four types of open habitats on quartzite and ferruginous substrate: quartzite outcrop (QO), quartzite grassland (QG) canga couraçada (CC), canga nodular (CN), respectively. We have classified habitat types according to their main surface soil features, as follows: i) QO, as sites in sloped terrain with exposed quartzite rocks; ii) QG, as flatter sites without exposed rocks and sandy soils; iii) CC, as sites with continuous bare iron rocks; iv) CN, as sites with fragmented iron rocks. The altitude of the sampling sites approximately ranged from 1289 m a.s.l to 1488 m a.s.l.

Sampling

The sampling was carried out from March to May 2018. In each of the four habitats, we established 10 plots (10 m × 10 m), 10 m apart and distributed them along a 200 m transect. To analyse the composition of the shrub vegetation, we identified and recorded all individuals with a stem diameter at ground level (DGL) greater than or equal to 10 mm. For the herbaceous vegetation, we sampled a 1 m^2 plot in the lower right corner of each 100 m^2 plot and measured the DGL of each individual. We identified the plant samples using botanical literature, consultation with specialists, and by comparison with specimens stored in the BHCB herbarium. We checked the names and authors of species in the World Checklist of Vascular Plants (WCVP) database (https://wcvp.science.kew.org/). To calculate the Importance Value Index (IVI) we used the following formula (Cavassan et al., 1984):

$$\text{IVI} = \frac{\text{relative frequency} + \text{relative density} + \text{relative dominance}}{3}$$

Where,

$$\text{Relative frequency} = \frac{\text{number of plots where a species occurs / total number of plots}}{\text{frequency of all species} \times 100}$$

$$\text{Relative density} = \frac{\text{number of species individuals / total sampled area}}{\text{density of all individuals} \times 100}$$

$$\text{Relative dominance} = \frac{\text{total basal area of a species / total sampled area}}{\text{total species dominance} \times 100}$$

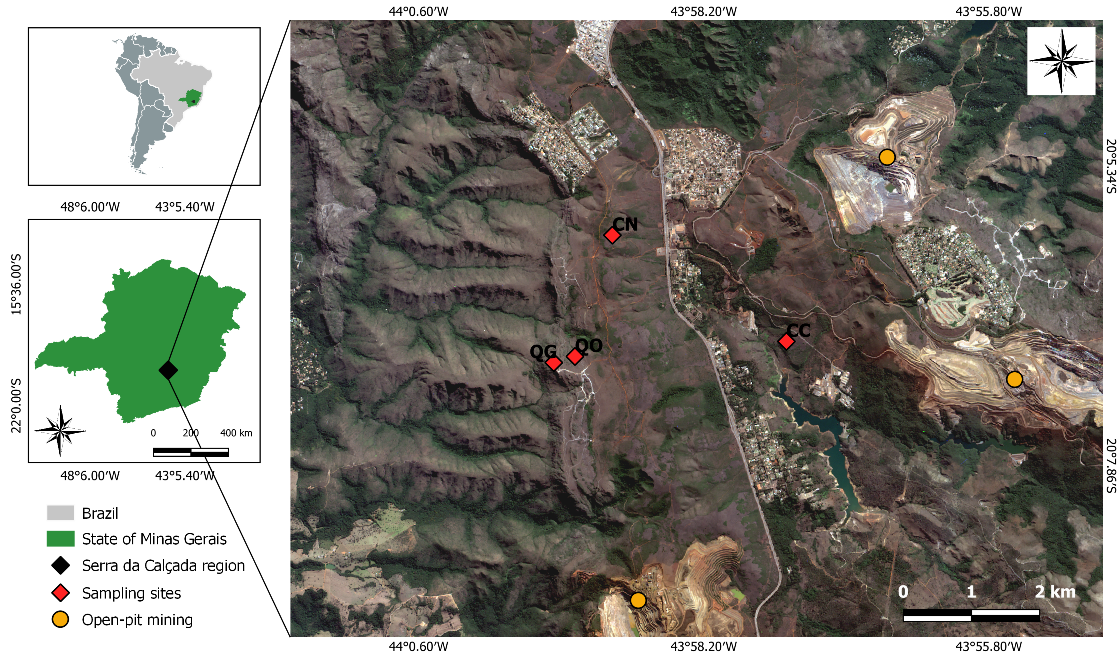

Fig. 1. Studied sites and location of four habitats evaluated in Serra da Calçada, Minas Gerais, Brazil. Designations: QO – quartzite outcrop; QG – quartzite grassland; CC – canga couraçada; CN – canga nodular. Open-pit mining in surrounding is shown.

Statistical analysis

To verify the similarity of the floristic composition between habitat types, we converted the floristic surveys into matrices with species incidence (presence/absence) per sample plot. Subsequently, we used a cluster analysis with the unweighted pair group method with arithmetic mean (UPGMA) as a linkage metric. To order the sampled communities, we used Sorensen's metric which uses presence/absence values (Gotelli & Ellison, 2004; Magurran, 2004; Chao et al., 2006). We generated dendrograms from Sorensen's distance with the «vegdist» function from the «vegan» package (Oksanen et al., 2015), and then used the «hclust» and «as.dendrogram» function from the «stats» package. We applied a principal co-ordinate analysis (PCoA) to calculate the two principal axes of variation contained in the floristic composition matrix. To visualise the positioning of habitats within the plane contained in the first two axes of the PCoA, we made a factor map using the package «ade4» (Dray & Dufour, 2007). We performed all analyses in the R environment (R Development Core Team, 2018).

Results

We sampled along the two vertical vegetation components 153 species belonging to 38 families, with 116 shrubs and 37 herbaceous species. We recorded 43 species in CC (35 shrub and eight herbaceous species); and 78 species in CN (61 shrub and 17 herbaceous species), totalling 91 species in ferruginous habitats (Fig. 2a). We found 91 species in the QO (68 shrub and 23 herbaceous species); 52 species in QG (31 shrub and 21 herbaceous species), totalling 99 species in habitats of quartzite substrate (Fig. 2b). The families with the highest species richness were Asteraceae (30 species), Poaceae (19 species), Melastomataceae, and Myrtaceae (both with 11 species), and Malpighiaceae (eight species).

In the QO habitat, the dominant shrub species (i.e. with IVI above 10%) were *Vellozia caruncularis* Mart. ex Seub. and *V. compacta* Mart. ex Schult. & Schult.f. (Table 1S), while the dominant herbaceous species were *Lagenocarpus rigidus* (Kunth) Nees, *Rhynchospora ciliolata* Boeckeler, and *Echinolaena inflexa* (Poir.) Chase (Table 2S). In the QG habitat, the dominant shrub species were *Vellozia caruncularis*, *Microlicia martiana* O.Berg ex Triana, and *Vellozia compacta* (Table 1S), while the dominant herbaceous species were *Rhynchospora ciliolata*, *Axonopus marginatus* (Trin.) Chase ex Hitchc., and *Apochloa euprepes* (Renvoize) Zuloaga & Morrone (Table 2S). In the CC habitat, the dominant shrub species were *Lychnophora pinaster* Mart., *Baccharis serrulata* DC., and *Lippia grata* Schauer (Table 1S), while the dominant herbaceous species were *Vellozia graminea* Pohl, *Trachypogon spicatus* (L.f.) Kuntze, and *Andropogon bicornis* L. (Table 2S). In the CN habitat, the dominant shrub species was *V. variabilis* (Table 1S), while the dominant herbaceous species were *Trachypogon spicatus*, *Axonopus siccus* (Nees) Kuhlm., and *Rhynchospora ciliolata* (Table 2S). We observed the presence of an invasive exotic grass *Melinis minutiflora* P. Beauv.

in QO and QG habitats (Table 2S), and two native species with invasive behaviour, the shrub *Ageratum fastigiatum* (Gardner) R.M.King & H.Rob. in habitats QO, CC and CN (Table 1S), and the grass *Andropogon bicornis* in the CC habitat (Table 1S).

Our results show that distinct but locally adjacent campo rupestre habitats exhibit different floristic compositions. However, the scale of floristic differentiation was distinct according to the vegetation component. We found five shrub species occurring in all the four habitats evaluated, while 62 species were observed exclusively in one of the habitats (Table 1S). Indeed, the floristic similarity of the shrub component was distinct among the habitats considered, only one plot from the QG habitat (QG27) showed to be more similar to the QO plots than to the other QG plots (Fig. 3a). In the herbaceous component, six species occurred in all four habitats, while 17 species occurred exclusively in one of the habitats (Table 2S). The floristic composition of the herbaceous component, however, showed a high overlap of species among the four habitats analysed (Fig. 3b). This floristic similarity between habitats ranged from a relatively low degree of similarity, e.g., CC with the other habitats, to a high degree of similarity; e.g. the QG composition completely nested with the QO.

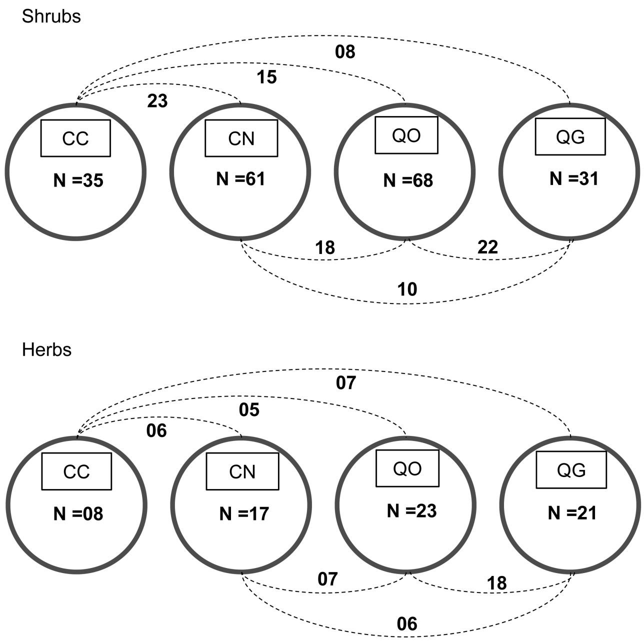

Fig. 2. Diagram of the number of species sampled by habitat type on the shrub and herbaceous components of the four habitats evaluated in Serra da Calçada, Minas Gerais, Brazil. The total number of species sampled in each site (N) and the number of species shared by different habitat types (number on dashed line) are shown. Designations: CC – canga couraçada; CN – canga nodular; QO – quartzite outcrop; QG – quartzite grassland.

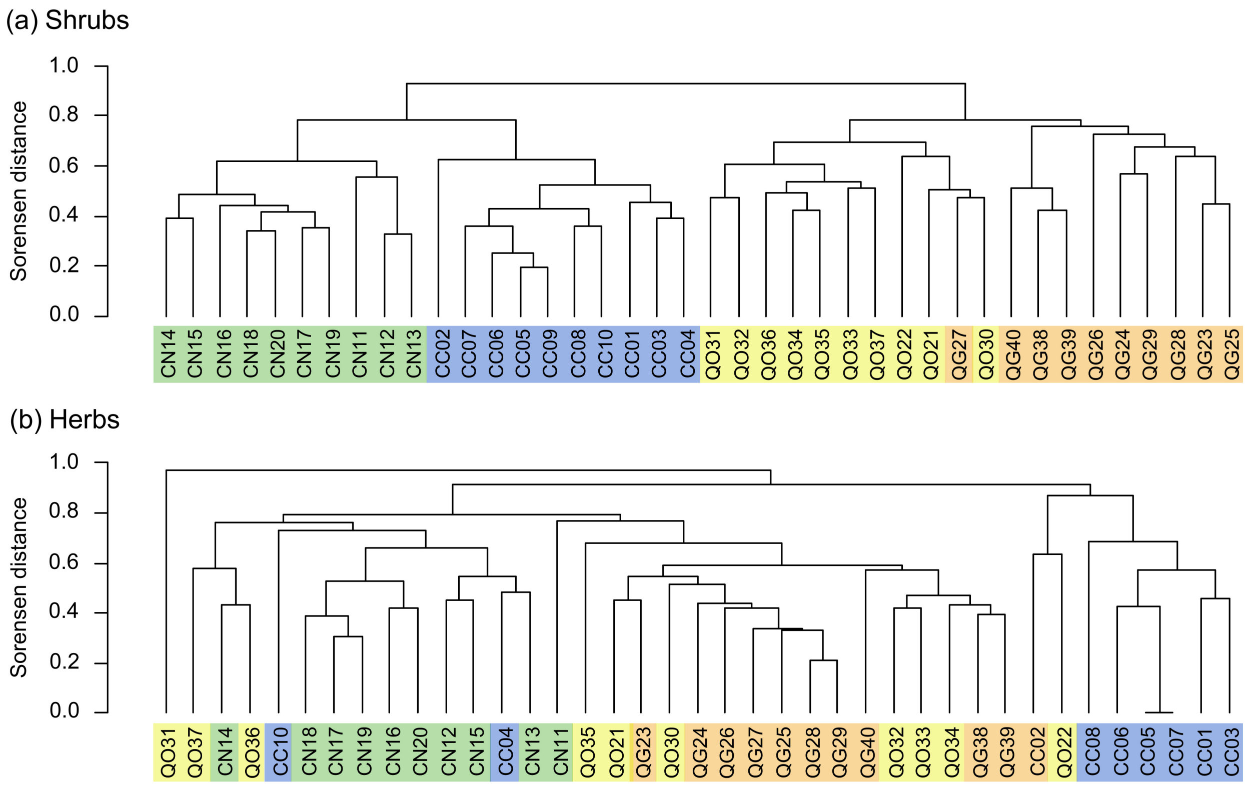

Fig. 3. Cluster analysis based on Sorensen distance of the shrub (a) and herbaceous (b) components of the four habitats evaluated in Serra da Calçada, Minas Gerais, Brazil. Designations: QO – quartzite outcrop (yellow); QG – quartzite grassland (orange); CC – canga couraçada (blue); CN – canga nodular (green). The numbering following the habitat code refers to the sample plot. Cluster analysis was based on the UPGMA linkage metric and used the presence and absence values of the species in the sample plots.

The first two axes of the PCoA analysis of the shrub component explained 48.1% of the variation in floristic composition. The first axis partitioned the floristic groups according to habitat type (Fig. 4a). By this axis, along with the negative to the positive end, the habitats were ordered in the following order CC, CN, QO, and QG. There was a small overlap between the floristic composition of the habitats of the same substrate (CC with CN, and QO with QG). The second axis ordination explained the variation in three clusters, in which the most positive group was the CC habitat, and the most negative was the CN habitat. Additionally, between the clusters of canga habitats, QO and QG habitats were highly overlapping.

The PCoA analysis of the herbaceous component explained 44.1% of the variation in floristic composition in the first two axes. The clusters formed were highly overlapping on both axes (Fig. 4b). However, the first axis showed a trend to separate groups according to the type of substrate. Habitats on quartzite substrate were almost exclusively positioned on the negative portion of the first axis. On the other hand, the canga habitats were mostly located on the positive part of the first axis of the PCoA (Fig. 4b).

Discussion

We have observed a clear differentiation of floristic composition according to habitat type. Our results indicate that even at a scale of a few metres, the floristic composition of the campo rupestre can be modulated by specific local conditions. In this way, we corroborate the already established statement that the diversity of old and resource-poor grasslands is locally modulated by habitat heterogeneity (do Carmo & Jacobi, 2016; Hopper et al., 2016; Fernandes et al., 2020a; Silveira et al., 2021).

The processes of formation and maintenance of high species diversity in the campo rupestre are complex and occur at various spatial scales (Fernandes, 2016). However, at both continental and local scales, environmental heterogeneity is pointed out as one of the main modulators of the maintenance of high species diversity. In this sense, the disjunct geographic distribution of the campo rupestre, associated with large latitudinal, altitudinal, and topographic variations, allows a large number of species to coexist. At the same time, biomes adjacent to the campo rupestre greatly influence the species composition and high species turnover (Giulietti et al., 1997; Silveira et al., 2016; Neves et al., 2018; Rapini et al., 2021). Similarly, at the local scale, microclimatic, topographic, and edaphic variations support the formation of a heterogeneous floristic mosaic (do Carmo & Jacobi, 2016; Fernandes, 2016; Silveira et al., 2016). Hence, instead of observing a single floristic group of species distributed across the landscape, we find a different composition of species often specialised in one habitat type.

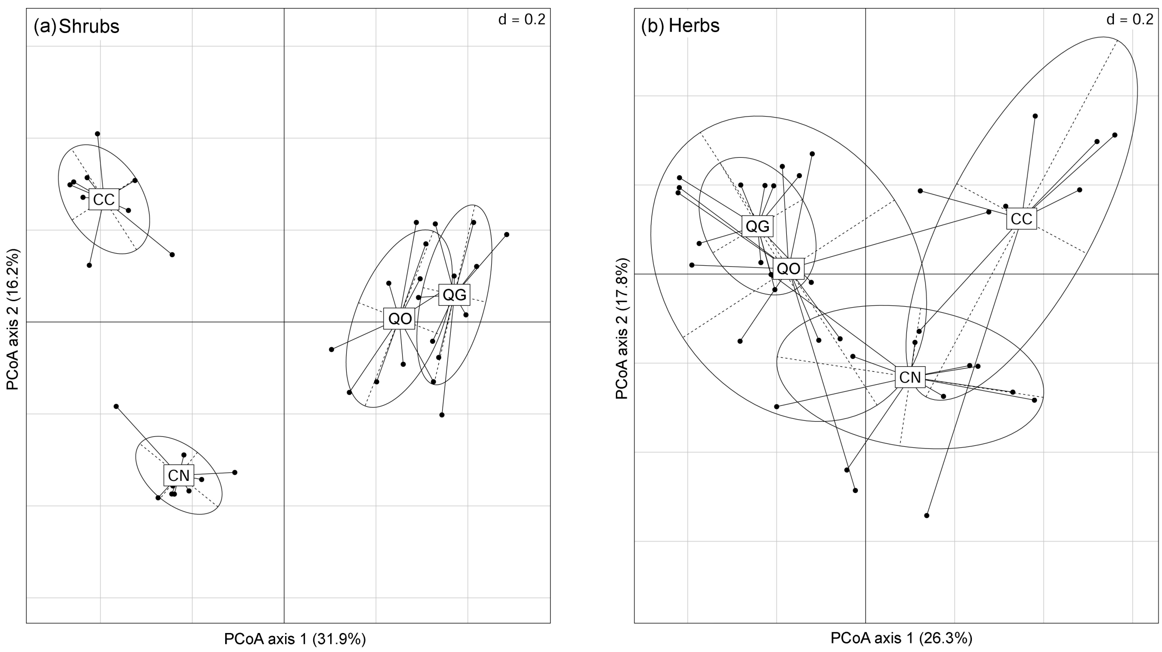

Fig 4. Principal co-ordinate analysis (PCoA) was applied to Sorensen distance using the presence and absence values of shrub (a) and herbaceous (b) species on the sample plots. The four habitats are represented at the centroid of the sample plots. The percentage of variation explained by each axis is shown in parentheses. Vertical and horizontal grid lines are separated by 0.2 units (d) at the scale of each axis. Designations: QO – quartzite outcrop; QG – quartzite grassland; CC – canga couraçada; CN – canga nodular.

We have also found a similar number of shrub species richness between the two substrate types. However, the CC and QG habitats showed considerably lower richness than CN and QO. Canga couraçada habitats are recurrently described as restrictive environments for vegetation establishment. This is because, besides presenting acidic and iron-rich soils that hinder the nutrients mobilization (do Carmo & Jacobi, 2016), CC habitats have a large proportion of exposed rock, which contributes to high soil temperatures (Jacobi & Carmo, 2011; Schaefer et al., 2016b) and less physical space available for plant establishment (Jacobi et al., 2007; do Carmo & Jacobi, 2016). Being combined, these abiotic constraints generate a strong environmental pressure that restricts species' traits (Caminha-Paiva et al., 2021; Tameirão et al., 2021), which may lead to a restricted group of species able to thrive on these sites (Jacobi et al., 2007). On the other hand, the CN and QO habitats apparently harbour a greater heterogeneity of the relief, which contributes to an increase in the number of microhabitats and, therefore, allows the spatial coexistence of a greater number of species (do Carmo et al., 2016). In the herbaceous component, the number of species in each type of substrate was substantially different, in which the ferruginous habitats presented a lower number of species than the habitats of quartzite substrate. This pattern must again fall back on the high temperatures and lack of physical space observed on the surface of canga soils, which must be especially damaging to species with shallow root systems such as the graminoids.

The OCBIL flora is well known to be naturally fragmented and edaphic specialised (Hopper et al., 2016; Gosper et al., 2021). Although the degree of specialisation can vary from a few metres to a landscape scale (see Corlett & Tomlinson, 2020), it is a requirement to take edaphic heterogeneity into account in conservation strategies. Our results reinforce the existing taxonomical distinction between campo rupestre in quartzite and ferruginous (canga) substrates, and the necessity to include multiple habitat types, as well as the various types of substrates to guarantee the conservation of this ecosystem. Also, we indicate that small campo rupestre conservation units are probably not effective to protect the biodiversity of this ecosystem (Zappi et al., 2019). Likewise, active campo rupestre restoration plans should account for reference ecosystems, relying on species occurrences according to habitat type, or at least considering substrate type, to ensure the effectiveness of the initiatives (Fernandes et al., 2016; Fernandes et al., 2020b). Old and nutrient-poor ecosystems have low resilience to anthropogenic disturbances, thus the appropriate selection of species is fundamental to the success of these actions (Fernandes et al., 2016).

Conclusions

In summary, our results highlight the influence of habitat and substrate types in shaping the floristic composition of shrub and herbaceous communities in the campo rupestre. The substrate quality (e.g. physical-chemical features and relief heterogeneity) seems to modulate patterns of species richness and composition, which indicates that each habitat type needs specific conservation plans to protect the biodiversity of the whole campo rupestre ecosystem. Also, the heterogeneity of each habitat type in terms of abiotic and floristic components evidences that conservation strategies in OCBIL ecosystems must consider the importance of local drivers of species diversity, which can allow the persistence of endemic species and rich communities.

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Supporting Information

Taxonomic lists of shrub and herbaceous plants with their importance value indices found in the campo rupestre habitats (Electronic Supplement. Floristic mosaics of the threatened Brazilian campo rupestre) may be found in the **Supporting Information**.

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ФЛОРИСТИЧЕСКАЯ МОЗАИКА СООБЩЕСТВ КАМПО-РУПЕСТРЕ БРАЗИЛИИ, НАХОДЯЩИХСЯ ПОД УГРОЗОЙ ИСЧЕЗНОВЕНИЯ

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Увеличение темпов сокращения местообитаний требует понимания пространственного распределения биоразнообразия. Кампо-рупестре представляет собой старовозрастной, с благоприятным климатом, ландшафт на бедных питательными веществами почвах, расположенный в Бразилии. Кампо-рупестре, считающийся «горячей точкой» биоразнообразия, в основном находится под угрозой исчезновения из-за горнодобывающей деятельности, которая требует большой территории для проведения работ. Кампо-рупестре известен своим ограниченным ареалом распространения и высокой абиотической неоднородностью, которая регулирует сосуществование и разнообразие видов. Чтобы выявить связь между типом местообитания и растительными сообществами, мы предлагаем описать флористический состав компонентов травянистых растений и кустарников в четырех местообитаниях кампо-рупестре, включающих кварцит и железистые субстраты. Мы классифицировали типы местообитаний по основным поверхностным характеристикам почвы. В каждом пункте исследования мы отобрали десять участков площадью 100 м^2 для получения информации о кустарниках и десять участков площадью 1 м^2 для травянистого компонента. Всего было отобрано 153 вида из 38 семейств. Кластерный анализ на основании метрики Соренсена показал четкие различия в видовом составе кустарников среди четырех местообитаний. Тем не менее, флористический состав компонента травянистых растений был сходным для всех четырех местообитаний, но показал различия при включении в анализ типа субстрата. Наши результаты подчеркивают локальные различия в таксономическом составе растений между типами местообитаний и субстратами. Это указывает на то, что экологические различия между типами субстратов кампо-рупестре нельзя упускать из виду в действиях по его сохранению и восстановлению.

Ключевые слова: канга, кварцит, кустарник, растительное сообщество, скальные луга, травянистые растения, фитоценология