Floristic composition and edaphic relationships in ferruginous *campo rupestre* reference ecosystems

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Abstract: Land use change and occupation have led to modifications in the environment causing loss of biodiversity and ecosystem services throughout the planet. Some environments with high economic relevance, such as the ferruginous *campo rupestre* (rupestrian grassland known as *Canga* in Brazil), are even more susceptible to severe impacts due to their extreme habitat conditions and low resilience. The determination of reference ecosystems based on the intrinsic characteristics of the ecosystem is essential for conservation as well as to the implementation of ecological restoration. We proposed the reference ecosystem of the three main types of habitats of the ferruginous *campo rupestre* based on their floristic composition. We described the floristic composition of each habitat and evaluated the physicochemical properties of the soils and the relationship between plants and soils. All three habitats showed high diversity of plant species and many endemic species, such as *Chamaecrista choriophylla*, *Cuphea pseudovaccinium*, *Lychnophora pinaster*, and *Vellozia subalata*. The distribution of vegetation was strongly related with the edaphic characteristics, with a set of species more adapted to high concentration of base saturation, fine sand, organic carbon, and iron, while another set of species succeeded in more acidic soils with higher S and silt concentration. We provide support for the contention that the ferruginous *campo rupestre* is a mosaic of different habitats shaped by intrinsic local conditions. Failure to recognize the floristic composition of each particular habitat can lead

to inappropriate restoration, increased habitat homogenization and increased loss of biodiversity and ecosystem services. This study also advances the knowledge base for building the reference ecosystem for the different types of ferruginous *campo rupestre* habitats, as well as a key database for highlighting those species contribute most to community assembly in this diverse and threatened tropical mountain ecosystem.

Keywords: *Canga*; Ecological restoration; Extreme ecosystem; Non-forest ecosystems; Rupestrian grassland; Taxon environment relationships

1 Introduction

Freshwater availability and food production are under serious threat from climate extremes, such as changes in precipitation patterns and temperature increases. These climate changes have been further exacerbated by anthropogenic pressures caused by land use change and misleading management strategies. Altogether, these resulted in the conversion of more than 75% of the Earth's land surface (Millard et al. 2021). Thus, one of the greatest challenges of this century is to mitigate the impacts of climate and land-use change on natural environments (Barlow et al. 2016), as these are the main drivers of biodiversity loss and ecosystem services (Gann et al. 2019). Loss and fragmentation of old growth ecosystems have increased worldwide, especially in tropical and subtropical regions where biodiversity and ecosystem services are highly valued (Barlow et al. 2016; Hansen et al. 2013).

In these regions, conservation and restoration efforts have focused primarily on forest ecosystems, which are indeed important biodiversity refuges, while many non-forest ecosystems, such as savannas and grasslands, harbor a high proportion of biodiversity and endemism and provide essential ecosystem services to millions of people (Fernandes 2016b; Fernandes et al. 2018, 2020b). Despite their high conservation importance, most open environments are under intense and accelerating disturbances (Fernandes 2016bc; Fernandes et al. 2014, 2020b). While programs to preserve the functionality and biodiversity contained in these ecosystems are urgently needed, the investment on it has been anecdotal at best (see Pougy et al. 2015).

One open environment with high biodiversity is the *campo rupestre* (also known as rupestrian grassland), a non-forest formation mainly distributed in the Espinhaço mountain range (the second largest mountain range in South America after the Andes) (Fernandes 2016b), associated with ancient geological formations of quartzite and itabirite rocks (Barbosa and Fernandes 2016; Schaefer et al. 2016; Miola et al. 2021). The historical isolation of *campo rupestre* has favored high rates of endemism, with more than 40% of the Brazilian endemic plant species found in this region (Echternacht et al. 2011; Barbosa et al. 2015; Fernandes 2016b; Silveira et al. 2016; Neves et al. 2018; Colli-Silva et al. 2019; Velazco et al. 2023). In addition to the high endemism, new species, and many new interspecific ecological interactions have been unveiled in this ecosystem (Fernandes et al. 2020b; Ramos et al. 2022; Barbosa et al. 2023). But in spite its singular ecology and relevance, threats to the *campo rupestre* are enormous and augmenting (Fernandes et al. 2020b). These are primarily composed by the introduction of exotic species, extensive cattle ranching, unregulated occupation, and intense impacts of mining and road expansion (e.g. Fernandes et al. 2014, 2018, 2020b; Fernandes 2016c; Silveira et al. 2016). The high anthropogenic pressure on this ecosystem makes the *campo rupestre* one of Brazil's most critical biodiversity hotspots (Fernandes et al. 2014, 2018).

The high levels of endemism and diversity in the *campo rupestre* are the result of strong environmental filters, primarily caused by the acidic and nutrient-poor soils and by the highly seasonal and low water availability (Jacobi et al. 2007; Negreiros et al. 2014; Tameirão et al. 2021; Rago et al. 2023). *Campo rupestre* is characterized by herbaceous and shrub vegetation distributed in a mosaic of diverse habitat types that occur side by side due to soil depth, topography, and microclimate variations in the mountainous environment (e.g. Le Stradic et al. 2015; Fernandes 2016b; Schaefer et al. 2016; Silveira et al. 2016; Rago et al. 2023). Nutrient availability in soils is low, and heavy metal concentration is high, so that some key soil factors (e.g. granulometry, Ca, Mg, K and Al contents: Marschner 1995), vary abruptly within a few meters, favoring the high floristic variation and high levels of endemism and rare species (e.g. Jacobi et al. 2007; de Carvalho et al. 2014; Negreiros et al. 2014; Le Stradic et al. 2015; Rapini et al. 2021).

Campo rupestre occurs on three lithological rock types: quartzite, sandstone, and itabirite (Schaefer et al.

2016). The *campo rupestre* developed on itabirite is called ferruginous *campo rupestre*, ironstone *campo rupestre*, or *canga* (in Portuguese). It is a formation composed of ferruginous fragments and hard hematite cemented by limonite (hydrated iron oxide) (Pomerene 1964), originated more than 2 billion years ago (Pinheiro 2018), and represents the main source of iron ore in Brazil. The iron-rich and acid soils and the massive proportion of exposed rock in the ferruginous *campo rupestre* play an important role in the plant establishment. This is because of the limited nutrient mobilization (do Carmo and Jacobi 2016), and high temperatures of the soil (Ferrari et al. 2016). Consequently, the plant assemblage in this ecosystem displays morphological, physiological, and life history traits that better allow them to establish and thrive in these harsh environments (Jacobi et al. 2007). Some of the traits displayed by plants in the ferruginous *campo rupestre* ecosystem include metallophytes and metal-tolerant species, which are usually related to a conservative use of resources (Caminha-Paiva et al. 2021; Tameirão et al. 2021; Rago et al. 2023). These traits allow plants to decrease the energy expenditure, to grow at slow rates, conserving the nutrients in their living parts (e.g. Fernandes and Price 1991; Schradin et al. 2023). This set of traits restricts plant species able to survive in this ecosystem (Jacobi et al. 2007) and makes the ferruginous *campo rupestre* highly vulnerable to changes in environmental conditions and soil quality (e.g. Bahia et al. 2020; Tameirão et al. 2021).

The ferruginous *campo rupestre* is mainly located in one of the most important mineral reserves in the world, the Iron Quadrangle in Minas Gerais, where 70% of the iron ore produced in Brazil is found (Viana and Lombardi 2007; Spier et al. 2003). These mining activities greatly alter the landscape and cause high environmental and social impacts. A large part of this ecosystem has already been lost due to mining activities, as well as by real estate expansion and road construction (Viana & Lombardi 2007; Fernandes et al. 2014, 2018; Neves et al. 2016), perhaps representing one of the most threatened ecosystems in Brazil (Jacobi et al. 2007, 2011; Fernandes et al. 2018). On top of that, climate projections indicate temperature increases of up to 2°C in South America, directly affecting droughts' duration and frequency (Xu et al. 2019). Mountain ecosystems are the first to suffer from global climate change (e.g. Beniston 2003; Nagy et al. 2023), and some projection models indicate that *campo rupestre* could lose up to 82% of its area in 50 years as climate change intensifies (Barbosa and Fernandes 2016; Fernandes et al. 2018; Hoffmann et al. 2020).

Anthropogenic factors act synergistically with climate change, making conservation and restoration strategies for these fragile ecosystems extremely urgent (Fernandes 2016c, 2020b; Hoffmann et al. 2020; Velazco et al. 2023). *Campo rupestre* generally has low ecological resilience, making restoration projects even more difficult (Le Stradic et al. 2014, 2018; Fernandes et al. 2016; Arruda et al. 2023). Although the exclusive use of native species is a big challenge, in such a fragile ecosystem it is necessary to restore the biological integrity and ecosystem services (Le Stradic et al. 2015; Fernandes et al. 2016, 2020a). The principle of ecological restoration is the identification of a reference ecosystem to serve as a guide for restoration projects, where the restored environment should resemble the previously established reference ecosystem (Fernandes et al. 2016; Gann et al. 2019; Rosenfield et al. 2022; reviewed by Toma et al. 2023). We aim to identify a reference ecosystem to guide restoration projects in the ferruginous *campo rupestre*. As the *campo rupestre* represents a mosaic of habitats shaped by soil heterogeneity (see Fernandes 2016ab; Schaefer et al. 2016), understanding the relationships between edaphic properties and vegetation composition is fundamental for restoration projects in this ecosystem (Fernandes et al. 2016). Otherwise, such an endeavor is hampered by the anecdotal knowledge on basic information on the different habitats that compose this ecosystem. In this way, we evaluated the floristic composition of three different habitat types of the ferruginous *campo rupestre* (ferruginous grassland, ephemeral pond, and *candeal*) and related it to fine-scale edaphic heterogeneity. In addition, we investigated the pattern of shared species diversity between habitats and their similarity based on floristic and edaphic factors, providing the basis for building an ideal context-dependent reference ecosystem to guide restoration projects in this highly endangered tropical mountain ecosystem.

2　Material and Methods

2.1 Study area

The study was conducted in the southern region of the Espinhaço Mountain Range, Minas Gerais, Brazil (Fig. 1), comprising the municipalities of Catas Alta

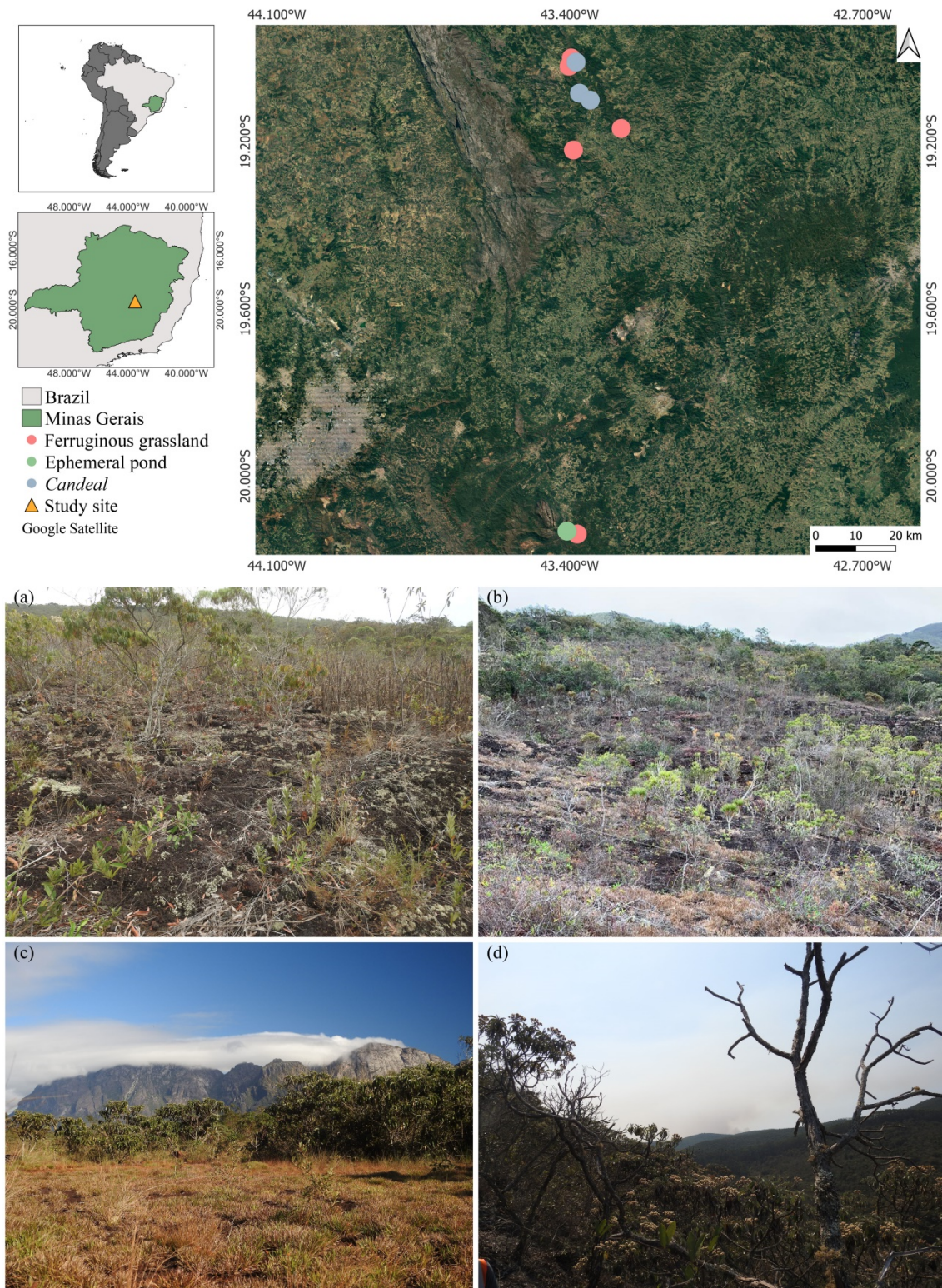**Fig. 1** Map highlighting the location of nine sampling sites (circles) in ferruginous grassland (red), ephemeral pond (green), and *candeal* (blue) located in the Iron Quadrangle, Minas Gerais, southeastern Brazil. Illustrative examples of the three sampled ferruginous *campo rupestre* habitat types: ferruginous grasslands (a, b), ephemeral pond (c), and *candeal* (d). Photos by Dario C. PAIVA.

(20°08'07.6" S, 43°23'19.6" W), Morro do Pilar (19°13'07.2" S, 43°23'36.5" W), and Conceição do Mato Dentro (19°00'13.9" S, 43°23'23.1" W). The sites are inside a private protected area with considerable size that comprises different habitats and physiognomies of the target ecosystem. Additionally, the sites have not yet been studied and were also chosen according to their accessibility. The climate of the region is classified as Cwb for Catas Altas (with dry winter and temperate summer), and Cwa for both Morro do Pilar and Conceição do Mato Dentro (with dry winter and hot summer) according to Köppen climate classification, with a regional average annual temperature ranging from 15.8°C and 21.5°C, and an annual rainfall of 1562.3 mm, mainly concentrated between October and March (Alvares et al. 2013).

The selection of our reference sites was based on the concept of "optimal references" (see Toma et al. 2023), where the selected areas were in a good state of conservation, in a strongly threatened environment. This is the only way to achieve, in the shortest possible time, connectivity between areas still of environmental quality, with real gains in biodiversity, maintenance of functionality and ecosystem services.

The ferruginous *campo rupestre* is defined here as a comprehensive ecosystem that group distinct vegetation types occurring in Fe-rich rocks and soils derived from the various degrees of decomposition of ferruginous substrate (Schaefer et al. 2016). In this study, we evaluated the composition and structure of the plant community in three distinct habitat types of ferruginous *campo rupestre*: ferruginous grassland, ephemeral pond, and *candeal* (Fig. 1). These habitats display a distinct soil configuration regarding soil waterlogging and how the rocky substrate is exposed, which makes it easy to classify them, in terms of habitat type, through direct observations. The ferruginous grassland can be defined as an open vegetation composed mainly by herbs and shrubs, along with rarer treelets (Jacobi et al. 2007, 2008), encompassing continuous plates of banded ironstone (also called *canga couraçada*) and iron-rich stones and gravels (also called *canga nodular*) (Caminha-Paiva et al. 2022). The ephemeral pond comprises a grassland structurally similar to the ferruginous grasslands, but in contrast with other xeric types of grassland, these habitats are seasonally flooded, mainly during the rainy summer (Jacobi et al. 2007). The *candeal* habitat have a hyperdominance of *Eremanthus* spp. (colloquially known as "candeia"). The inclusion of this

habitat in the present study is justified because of a local prevalence of this habitat, and the need to understand the structure of such homogenized vegetation.

2.2 Sampling

We sampled nine different sites from each three habitat types of ferruginous *campo rupestre*: five sites of ferruginous grassland, one site of ephemeral pond, and three sites of *candeal* (Fig. 1). In each site, we randomly established ten plots of 10 m × 10 m, spaced at least 10 m apart, totaling 1,000 m² per site (*n*= 90 plots). Therefore, considering the three different habitat types, we sampled 9,000 m² of ferruginous *campo rupestre* for the shrub stratum. For the herbaceous stratum, we sampled a 1 m² quadrat at one vertex of each plot totaling 90 m² for all studied habitat types (*n*= 90 plots). We calculated the following phytosociological parameters: absolute and relative values of density (total number of individuals), dominance (cover area based on stem area at soil height and crown cover projection, respectively, in shrub and herb strata), frequency (occurrence number of plots), and importance value (IV) (see Mueller-Dombois and Ellenberg 1974). To calculate the importance value (IV) the average of the relative density, relative dominance, and relative frequency percentages were used.

We treated the collected vegetative material for the shrub and herbaceous strata according to conventional herbarium techniques. We deposited them in the Herbarium BHCB of the Department of Botany of the Institute of Biological Sciences, Federal University of Minas Gerais and the Herbarium BHZB of the Botanical Garden of the Zoo-Botanical Foundation of Belo Horizonte-MG, Brazil. Synonymy verification, standardization of nomenclature, and species authors were obtained through the 'flora' package (Carvalho 2022) in the R environment (R Core Team 2022).

In each 100 m² plot, we collected five soil samples from 0 to 20 cm depth at the vertices and in the center of the plot to form a composite sample. Soil collection at 0-20 cm depth is based on procedures adopted in phytosociology and plant ecology studies in tropical ecosystems (e.g. Le Stradic et al. 2015). At this depth range, the plant individuals recycle a higher concentration of nutrients (Jobbagy and Jackson 2001). The chemical and texture of soil parameters

were assumed to be proxies of nutrient status and soil water availability, respectively, in the studied system (Schaefer et al. 2016); the analyses were performed in the Soils Department (Universidade Federal de Viçosa, Brazil). Soil granulometric analyses (coarse sand, fine sand, silt, and clay fractions) were done according to Donagemma et al. (1997). The pH in water was measured using 1:2.5 (v/v) soil: solution ratios. The total carbon content was determined by the Walkley-Black method. The exchangeable cations Ca^{2+}, Mg^{2+}, and Al^{3+} were extracted using a 1 mol·L^{-1} KCl solution. The Ca^{2+} and Mg^{2+} contents were determined in the extract by titration with EDTA 0.01 mol_c·L^{-1}, and the Al^{3+} contents by titration with NaOH 0.025 mol_c·L^{-1}, according to Silva et al. (1999). The elements P, K, Zn, Fe, Mn, and Cu were extracted by the Mehlich 1 solution, the sulphur (S), by a solution of monocalcium phosphate in acetic acid, and the contents of these elements in the extracts were determined by spectrophotometry. Potential acidity (H+Al) was extracted by a 0.5 mol·L^{-1} calcium acetate solution at pH 7.0 and determined by alkalimetric titration of the extract. The base saturation and aluminum saturation were calculated, respectively, according to the expressions:

Base saturation =
$$[(K+Ca^{2+}+Mg^{2+})/(K+Ca^{2+}+Mg^{2+}+H+Al)] \times 100\%$$
Aluminium saturation =
$$[Al^{3+}/(K+Ca^{2+}+Mg^{2+}+Al^{3+})] \times 100\%$$

2.3 Statistical analysis

All statistical analyses were done in R environment (R Core Team 2022) except where indicated. We evaluated the pattern of species sharing among the three studied habitats through Venn diagrams constructed for the shrub and herbaceous strata using the package 'VennDiagram' (Chen and Boutros 2011). To quantify the partition of species diversity among habitat types, we calculated the proportion of alfa and beta diversity according to de Bello et al. (2010) using the 'ade4' package (Dray and Dufour 2007) and 'Rao.r' function (de Bello et al. 2010). To verify the similarity of floristic composition among the 12 studied locations, we used a cluster analysis with UPGMA (unweighted pair group method with arithmetic mean) as a linkage measure. We used the Bray-Curtis metric to order the sampled sites, which uses abundance data (in this study, represented by the relative dominance of each species at each location)

(Gotelli and Ellison 2004). We generated the Bray-Curtis 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 to generate the dendogram. The shrub and herbaceous strata were treated separately due to intrinsic differences in sampling methodology (e.g. sampling plot size and cover area estimation).

We performed a co-inertia analysis to determine the relationship between soil parameters and the shrub, and herb species community. This robust and flexible analysis measures the agreement (co-structure) between two multivariate data sets (Dray et al. 2003). We performed the co-inertia analysis (COIA) for each habitat's shrub and herb strata separately. For each habitat type, the edaphic matrix was defined as the values of 19 soil factors in the 30 plots, while the floristic matrix consisted of the incidence (presence and absence) of plant species in 30 plots. To meet the assumptions of the parametric analyses, we performed square root transformation for aluminum content (Al), and logarithmic transformation for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), manganese (Mn), zinc (Zn), and base saturation. The COIA outputs a value called RV coefficient, which measures the strength of the association between the two matrices (i.e. floristic and edaphic). The RV value is bounded to 0 (i.e. no association) and 1 (i.e. maximum association). The significance of the RV (*p*-value) is defined by Monte Carlo permutation, performed with 10,000 randomizations. To perform the COIA a PCA (mean = 0; standard deviation = 1) was used for the soil matrix, and a centered PCA (mean = 0) was used for each floristic matrix according to Dray et al. (2003). A Pearson correlation was used to establish the association between each soil parameter and the plot coordinates on axis 1 of the COIA. The association between species and COIA axis 1 was defined by the species coordinates on this axis. The COIA was performed using the 'ade4' package (Dray and Dufour 2007).

3 Results

A total of 125 species belonging to 33 families were sampled in the three ferruginous *campo rupestre* habitat types, with 106 shrub species belonging to 29 families and 18 herbaceous species belonging to 5 families. In the ferruginous grassland habitat, 76 species were recorded (67 shrubs belonging to 22

families and 9 herbs belonging to 5 families). In the ephemeral pond habitat, 16 species were recorded (10 shrubs belonging to 7 families and 6 herbaceous species belonging to 3 families). In the *candeal* habitat, 69 species were recorded (61 shrubs belonging to 18 families and 8 herbaceous species belonging to one family, Poaceae). In the shrub stratum, the families with the highest species richness in all habitats were Myrtaceae with 15 species, followed by Asteraceae (14 species), Fabaceae (13 species), Melastomataceae (9 species), and Malpighiaceae (8 species). For the herbaceous stratum, the family with the highest species richness was Poaceae (11 species), followed by Cyperaceae (3 species), and Velloziaceae (2 species).

Regarding the shrub stratum, the species with the highest importance value (IV) in the ferruginous grassland habitat were *Vellozia scabrosa* (IV: 25.5%), *Eremanthus incanus* (IV: 8.7%), and *Heteropterys byrsonimifolia* (IV: 5.4%) (Appendix 1). In the ephemeral pond habitat, the species with the highest IV were *Stachytarpheta glabra* (IV: 28.6%), *Pleroma heteromallum* (IV: 16.6%), and *Eremanthus erythropappus* (IV: 12.4%) (Appendix 2). The species with the highest IV in the *candeal* habitat were *Eremanthus incanus* (IV: 54.8%), *Miconia albicans* (IV: 4.9%), and *Baccharis reticularia* (IV: 2.8%) (Appendix 3).

Regarding the herbaceous stratum, the species with the highest IV in the ferruginous grassland habitat were *Apochloa poliophylla* (IV: 31.8%), *Vellozia minima* (IV: 12.5%), and *Apochloa euprepes* (IV: 12.5%) (Appendix 4). In this habitat, all herbaceous species are native, and most are endemic to *campo rupestre*. In the ephemeral pond habitat, the most important species were *Vellozia graminea* (IV: 47.7%), *Bulbostylis fimbriata* (IV: 24.1%) endemic to the

Cerrado biome, and *Axonopus siccus* (IV: 13.6%), a native species but recurrent in disturbed areas (Appendix 5). The species with the highest IV in the *candeal* habitat were *Trichanthecium distichophyllum* (IV: 35.6%), followed by the invasive exotic *Melinis minutiflora* (IV: 18.7%), and *Andropogon* sp. (12.9%) (Appendix 6).

As expected, we found many species with occurrence restricted to a single habitat type. We recorded 78 species (73.6%) of the shrub stratum and 14 species (77.8%) of the herbaceous stratum occurring exclusively in a single habitat. The ferruginous grassland habitat showed 39 unique shrub species (58.2% of the shrub species in this habitat; Fig. 2a), and 5 unique herbaceous species (56% of the herbaceous species in this habitat, all endemic to *campo rupestre*; Fig. 2b). The ephemeral pond habitat showed no exclusive shrub species (Fig. 2a), and only two herbaceous species exclusive to this habitat (Fig. 2b). The *candeal* habitat had 39 unique shrub species (63.9% of the total shrub species in this habitat; Fig. 2a) and 7 unique herbaceous species (87.5% of the herbaceous species in this habitat; Fig. 2b). The high number of exclusive species in the different habitat types can be confirmed by the high species substitution among the evaluated habitats, demonstrated by the beta diversity of 49.3% for both shrub and herbaceous strata (Fig. 2c).

The assessed habitats show low species sharing; 4 shrub species: *Baccharis reticularia*, *Byrsonima variabilis*, *Eremanthus erythropappus*, and *Pleroma heteromallum* (3.8% of total shrub species; Fig. 2a). Only one herbaceous species; *Trichanthecium distichophyllum* occurred in all three studied habitats (Fig. 2b). Regarding floristic similarity, sampling sites were roughly grouped based on habitat type. In the
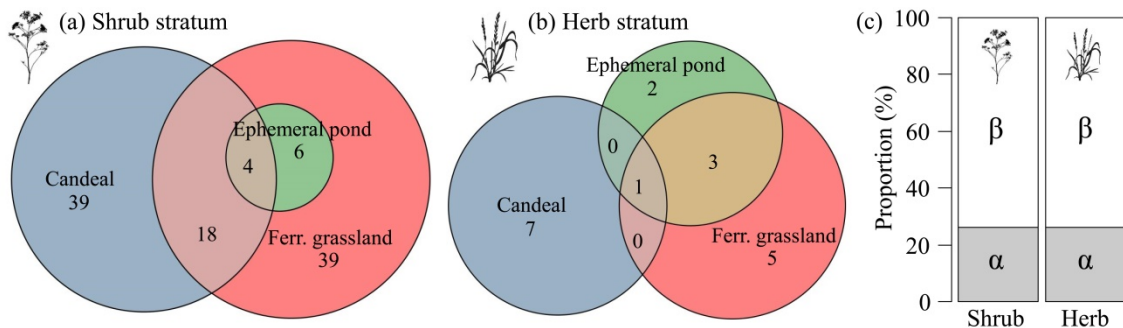

Fig. 2 Euler diagram showing the number of shrub (a) and herbaceous (b) species shared among the three evaluated ferruginous *campo rupestre* habitat types, ferruginous grassland (red circle), ephemeral pond (green circle), and *candeal* (blue circle). (c) Partition of species diversity into α (local) and β (between the nine sites of the three habitat types) components for each studied stratum.

shrub stratum, the three sites of *candeal* habitat were grouped together, forming a cluster with four ferruginous grassland sites. The most external group was formed by the ephemeral pond and a ferruginous grassland site (Fig. 3a). On the other hand, based on the herbaceous stratum, the influence of habitat type was less apparent, since the sites formed clusters without clear separation based on the habitat (Fig. 3b).

In the shrub stratum, the co-inertia analysis (COIA) indicated a clear edaphic-floristic gradient in the shrub stratum in the ferruginous grassland (Fig. 4) and *candeal* (Fig. 5a) habitats. In the ephemeral pond habitat, the connection between edaphic and floristic matrices was non-significant (RV = 0.58; $p > 0.05$). In the ferruginous grassland, the association between edaphic and floristic composition was highly significant (RV = 0.47; $p < 0.001$), and the COIA axis 1 and axis 2 explained, respectively, 35.2% and 28.6% of the covariation between edaphic and floristic matrices. The positive side of axis 1 represented plots with a higher proportion of fine sand, base saturation, and Fe (Fig. 4a). The species with the highest association with the positive side of this axis were *Lippia origanoides*, *Calliandra fasciculata*, *Cuphea lutescens*, and *Eriope macrostachya* (Fig. 4a). On the other hand, the negative side of the COIA 1 axis represented plots with higher concentration of silt, coarse sand, S, Al, and Zn. The species most associated with the negative side of this axis were, *Evolvulus scoparioides*, *Cordiera elliptica*, *Croton argyrophyllus*, *Stachytarpheta*

glabra, and *Peixotoa tomentosa* (Fig. 4a). There is another edaphic-floristic gradient evident in the COIA axis 2, where the positive side of this axis represents plots with a higher proportion of H+Al, K, organic C, Al, Mg, Fe, Ca, and P. The species with the highest association with the positive side of COIA axis 2 were *Heteropterys byrsonimifolia*, *Cordiera elliptica*, *Lippia origanoides*, *Periandra mediterranea*, *Peixotoa tomentosa*, and *Eremanthus incanus* (Fig. 4b). The negative side of the COIA 2 axis represented plots with higher concentration of S, coarse sand, and higher pH. The species most associated with the negative side of this axis were *Byrsonima variabilis*, *Lychnophora pinaster*, *Baccharis reticularia*, *Vellozia compacta*, and *Croton argyrophyllus* (Fig. 4b).

In the shrub stratum of the *candeal* habitat, the association between edaphic and floristic matrices was highly significant (RV = 0.60, $p < 0.001$) for COIA axis 1, which explained 65.9% of the covariation between edaphic and floristic matrices. The positive side of axis 1 represented plots with a higher proportion of fine sand, Fe, P, Zn, and Ca (Fig. 5a). The species with the highest association with the positive side of this axis were *Dasyphyllum sprengelianum*, *Centrosema coriaceum*, *Pleroma heteromallum*, *Diplusodon hirsutus*, and *Cuphea pseudovaccinum* (Fig. 5a). On the other hand, the negative side of the COIA 1 axis represented plots with higher concentration of clay, organic C, K, silt, and higher pH. The species most associated with the negative side of this axis were
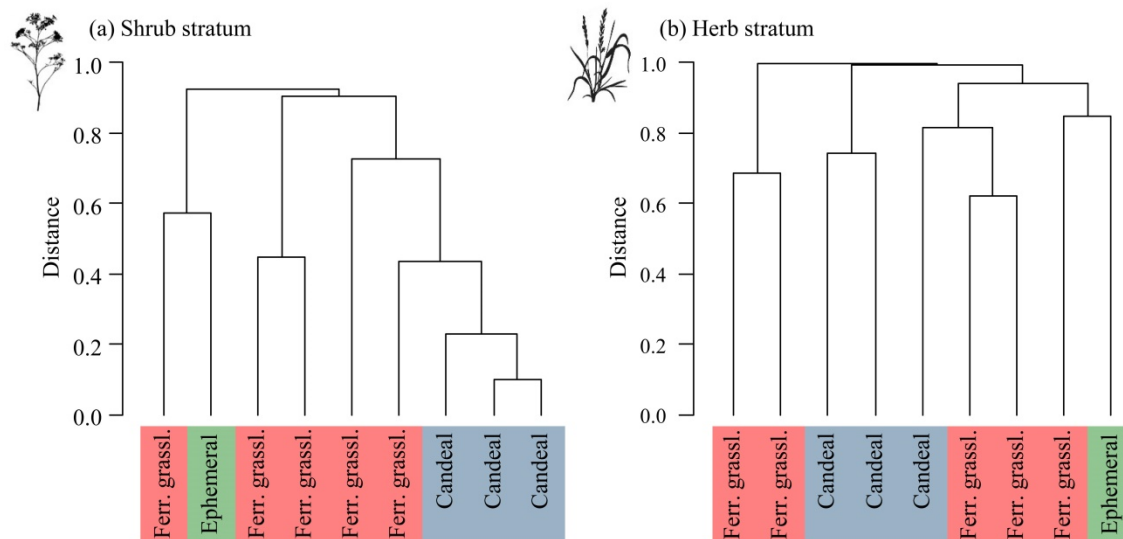

Fig. 3 Cluster analysis based on the floristic composition of the shrub (a) and herbaceous (b) strata of the nine studied sites of ferruginous *campo rupestre*. Dendrogram was constructed based on the Bray-Curtis distance using the species' abundance values (relative dominance) at the sampling sites. Ferr. grassl.: ferruginous grassland habitat (red); Ephemeral: ephemeral pond habitat (green); Candeal: *candeal* habitat (blue).

(a) Ferruginous grassland – shrub (axis 1)

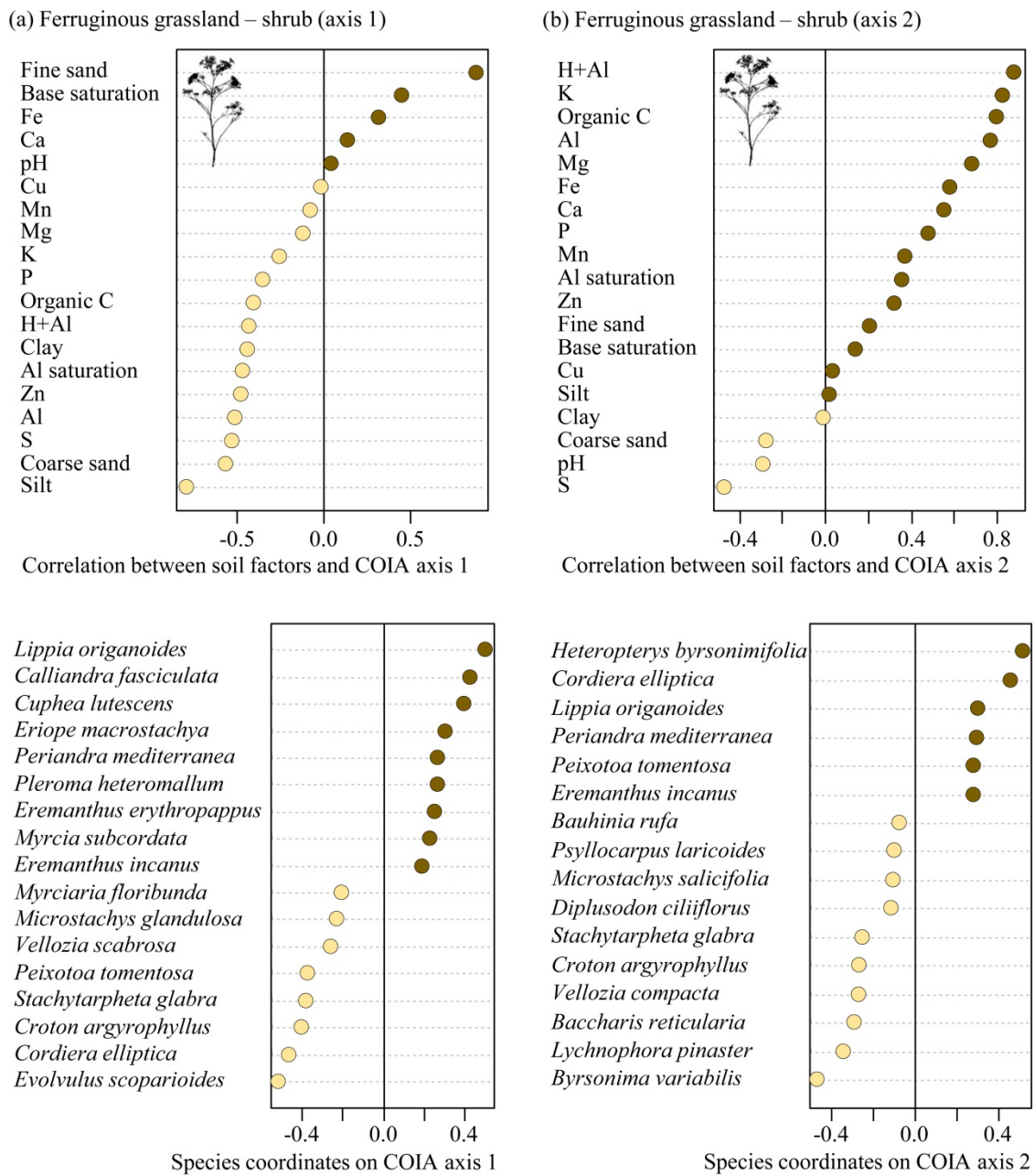(b) Ferruginous grassland – shrub (axis 2)

Fig. 4 Co-structure between edaphic factors and shrub species community in axis 1 (a) and axis 2 (b) sampled in the ferruginous grassland habitat of ferruginous *campo rupestre* located in the Iron Quadrangle, MG, southeastern Brazil. The upper dot charts show the Pearson correlation between edaphic factors and the coordinates of the plots in axis 1 and 2 of the co-inertia analysis (COIA). The bottom dot charts show the coordinates of the species with the highest association with the positive and negative sides of COIA axis 1 and 2. The light yellow and brown circles represent negative and positive correlation values (upper) or coordinates (bottom) on COIA axis 1 and 2.

Miconia albicans, *Eremanthus erythropappus*, *Xylopia aromatica*, *Baccharis reticularia*, *Mabea fistulifera*, and *Baccharis retusa* (Fig. 5a).

The association between edaphic and floristic composition was highly significant for the herbaceous stratum (RV = 0.36, *p* < 0.001) with the three habitat types together, and the COIA axis 1 explained 54.9% of

the covariation between edaphic and floristic matrices. The positive side of axis 1 represented plots with a higher proportion of K, H+Al, Al, Mg, organic C, and fine sand (Fig. 5b). The species with the highest association with the positive side of this axis were the exotic *Melinis minutiflora*, along with the endemic native *Apochloa poliophylla*, and *Andropogon* sp. (Fig.
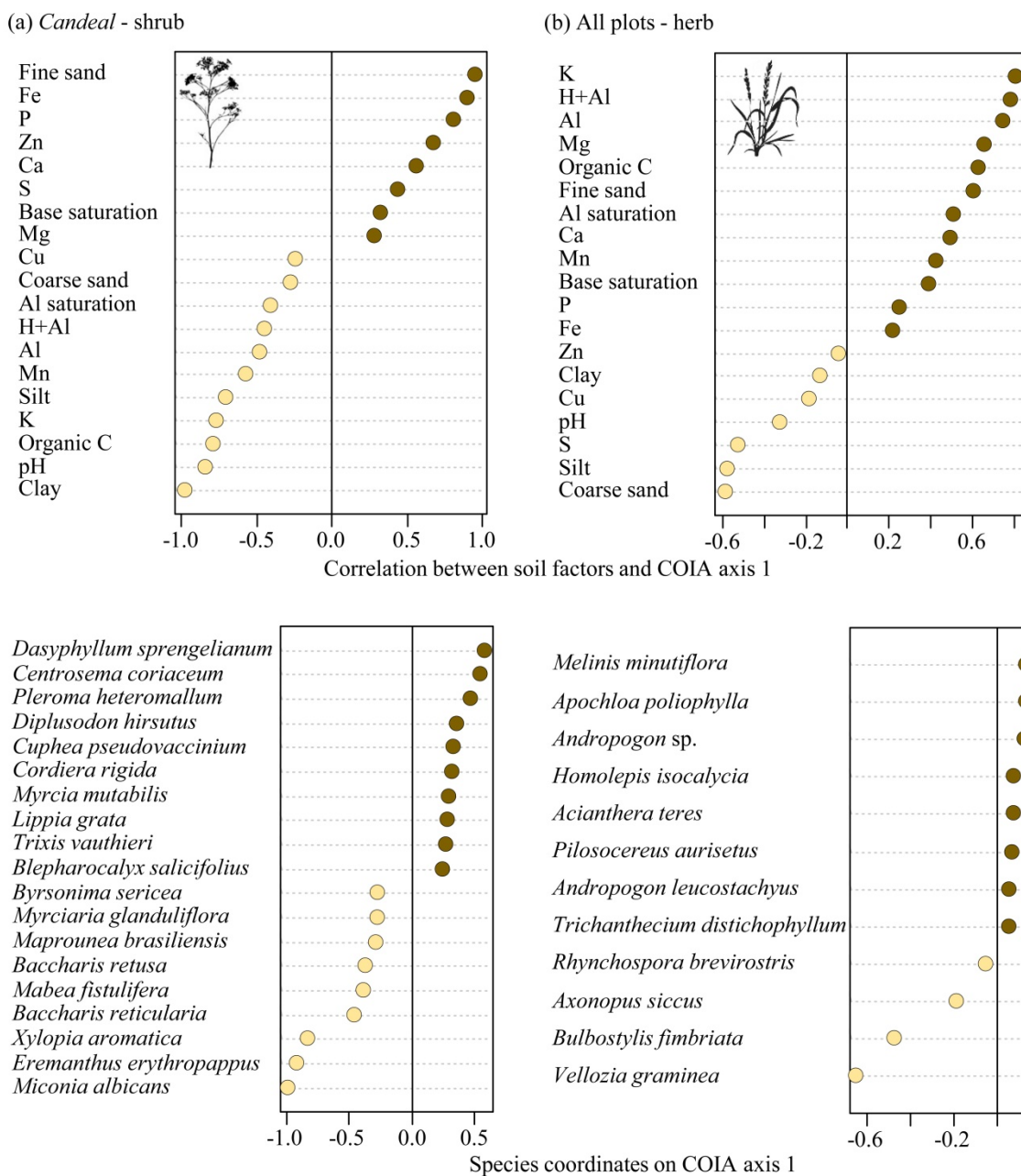
Fig. 5 Co-structure between edaphic factors and community of shrub species from the *candeal* habitat (a) and herbaceous species from all habitats together (b) sampled in the ferruginous *campo rupestre* located in the Iron Quadrangle, MG, southeastern Brazil. The upper dotcharts show the Pearson correlation between edaphic factors and the coordinates of the plots in axis 1 and 2 of the co-inertia analysis (COIA). The bottom dotcharts show the coordinates of the species with the highest association with the positive and negative sides of COIA axis 1 and 2. The light yellow and brown circles represent negative and positive correlation values (upper) or coordinates (bottom) on COIA axis 1.

5b). On the other hand, the negative side of the COIA 1 axis represented plots with higher concentration of coarse sand, silt, S, and higher pH. The species most associated with the negative side of this axis were, *Vellozia graminea*, *Bulbostylis fimbriata*, and *Axonopus siccus* (Fig. 5b).

4 Discussion

Environmental recovery and restoration are ambitious goals of the UN Decade of Ecosystem Restoration (Bustamente et al. 2019; Medeiros et al. 2022). In neglected open ecosystems, such as the

campo rupestre, these goals become even more complex (Fernandes et al. 2016; Gibson-Roy et al. 2023). While the *campo rupestre* is the ecosystem of the Cerrado that harbors the greatest richness of plant species (see reviews in Fernandes 2016a), it is also the one most challenged by human disturbances (e.g. Jacobi et al. 2007, 2011; Fernandes et al. 2014, 2016, 2018). Therefore, the establishment of sound plans for its recovery and restoration is of utmost and strategic relevance for Brazilian biodiversity, and protection of ecosystem services such as climate resilience, food and water security, among others (Fernandes et al. 2018, 2020b; Velazco et al. 2023). In this study, we provide the basis for defining the reference ecosystem for three habitats of the ferruginous *campo rupestre*, in support of restoration projects in the Espinhaço mountain range. We recorded variations in floristic composition among the ferruginous grassland, ephemeral pond, and *candeal* habitats assessed in the ferruginous *campo rupestre*. Soil characteristics are decisive for the formation of specific habitats that shape the distribution of species that occur in unique conditions in this mountain ecosystem (e.g. Barbosa et al. 2015; Le Stradic et al. 2015; Schaefer et al. 2016; Silveira et al. 2016; Tameirão et al. 2021; Rago et al. 2023). This heterogeneous mosaic of habitats favors the high diversity and endemism of species in this environment (e.g. Messias et al. 2013; do Carmo and Jacobi 2016; Fernandes 2016b, 2020a; Caminha-Paiva et al. 2022).

The high species diversity in ferruginous *campo rupestre* reported in our field surveys, many of them endemic, further increases the urgency of policies to protect this ecosystem and of adequate ecological restoration projects. The vegetation is composed of herbaceous and shrub strata that grow on distinct soil conditions, as suggested by the edaphic-floristic gradients shown in this study. The families with the highest species richness were, Myrtaceae, Asteraceae, Fabaceae, Melastomataceae, Poaceae, and Cyperaceae. These families are among the 10 richest plant families of *campo rupestre* (e.g. Silveira et al. 2016) and well represented in floristic surveys along the Serra do Espinhaço (Mota et al. 2018), and in the Iron Quadrangle (Jacobi and do Carmo 2011). The genus *Eremanthus* (Asteraceae) presented high importance value in all the evaluated habits, as also shown by Messias et al. (2012). *Stachytarpheta glabra* (Verbenaceae) had the highest IV in the ephemeral pond habitat. *Stachytarpheta* is one of the most diverse genera of *campo rupestre*, with many native

and endemic species, perhaps because of its restricted distribution (Cardoso and Salimena 2020). In addition, the flowers of these species are important resource for many animal species throughout the year (Guimarães et al. 2023). The Velloziaceae, specially *Vellozia graminea* and *Vellozia minima*, showed high importance value in the ferruginous *campo rupestre*. This monocot family has been commonly reported in all vegetation studies in the *campo rupestre*, in which it is often reported as a predominant family (e.g. Jacobi et al. 2008; Messias et al. 2012; Silveira et al. 2016). Species in this family have an efficient adaptative strategy of suspending photosynthetic activity in periods of water deficit (Porembski et al. 2021), which ensure survival to the extreme conditions found in these environments.

For the herbaceous stratum evaluated in all habitats, species of the Poaceae and Velloziaceae families stand out with a high IV. Poaceae, Velloziaceae and Cyperaceae families are commonly found in these harsh habitats of the *campo rupestre* (Conceição and Pirani 2007; Le Stradic et al. 2015), as they have developed a repertoire of physiological adaptations to live in environments with shallow soils and high radiation (e.g. Messias et al. 2013; Oliveira et al. 2016; Teodoro et al. 2019).

The high number of exclusive species observed in each habitat should be viewed with great caution, as it indicates that the habitats have intrinsic characteristics that favour this group of species. In addition, these habitats should be treated as distinct entities in conservation, management and restoration programmes to avoid habitat loss and biotic homogenisation (Toma et al. 2023). Species shared between habitats are rarer, suggesting that the subtle features specific to each habitat are sufficient to filter the community into specific types, confirming what was observed by Caminha-Paiva et al. (2022).

It is important to point out that we did not find any exotic shrub species in this study, indicating they are indeed good reference systems. The only exception is *Waltheria indica* that, contrary to what is stated by Flora e Funga do Brasil (2023) is an exotic and invasive species (Maia and Fernandes 2005) that occurred in the ferruginous grassland habitat. For the herbaceous stratum, we observed that most species from ferruginous grassland and ephemeral pond are native and restricted to the *campo rupestre*. On the other hand, the *candeal* habitat presented a worrying de-characterization of the native herbaceous species, as

the second most important herbaceous species in this habitat was the invasive and exotic *Melinis minutiflora*. Also, all herbaceous species found in *candeal* habitat belonged to Poaceae family, reinforcing the low phylogenetic diversity in this habitat. This observation indicates that this habitat was associated with cattle ranching is the past, a common activity in the region, and therefore the use of herbaceous list for the *candeal* habitat must be used with caution in future restoration and management programs.

Small-scale edaphic variation contributed significantly to explaining the composition of shrub and herbaceous communities. As reported in many studies in these regions, edaphic variation in the *campo rupestre* shapes the composition and structure of plant communities (e.g. Negreiros et al. 2014; Mota et al. 2016; Schaefer et al. 2016; Rago et al. 2023). Soil characteristics favor diversity and endemism in the *campo rupestre*; therefore, restoration projects must be implemented to create favorable edaphic environments capable of maintaining high floristic and habitat diversity. Transplantation of native plant seedlings to degraded areas is positive because it favors the establishment and recruitment of native species and conserves soil, making it a viable alternative for the restoration process of degraded areas of *campo rupestre* (Fernandes et al. 2016; Gomes et al. 2018). Techniques for producing seedlings of native species have been effective in *campo rupestre* restoration (e.g. Le Stradic et al. 2014; Gomes et al. 2018; Bahia et al. 2020). We emphasize that restoration projects in these areas must be able to maintain the soil properties of each habitat. Thus, this work brings the relevance of edaphic and floristic bases for the definition of reference environments for the ferruginous *campo rupestre*, in order to facilitate the implementation of effective restoration projects.

Species from *campo rupestre* have evolved adaptations to be tolerant to the stresses of these environments (Negreiros et al. 2014; Fernandes 2016a,b; Caminha-Paiva et al. 2021; Tameirão et al. 2021; Rago et al. 2023). The use of soil improvement techniques in *campo rupestre* restoration projects can be problematic, as it favors the invasion by exotic species (Hilário et al. 2011; Fernandes et al. 2015) and stimulates habitat homogenization. In addition, in an experiment with nutrient supplementation of *Vellozia nanuzae*, a species endemic to the *campo rupestre*, researchers found that in natural, nutrient-poor soils, plants would grow and develop better compared to nutritionally improved soil conditions (Cunha-Blum et al. 2020).

The results brought in this study confirm that small-scale edaphic variation is an important filter that shapes the composition of shrub and herbaceous strata in the ferruginous *campo rupestre*. We also point out that the floristic composition of the *campo rupestre* is a mosaic shaped by intrinsic local conditions, and detailed studies to evaluate the association between species and soils are essential before the implementation of ecological restoration projects. In other words, restoration proposals must respect the distinct characteristics of each habitat, focusing on the nature of the different habitats, which can vary even within the same mountain. Failure to take these specificities into account may lead to ecosystem homogenization, result in biodiversity and ecosystem service losses, and even favor the establishment of invasive species (see Fernandes et al. 2016). Current environmental policies must take in consideration the advances of the science produced in this ecosystem and urgently chance general procedures and guidance or they will provide legal ground for misleading restoration practices and biodiversity loss in the most threatened Brazilian ecosystem.

There is a high plant species turnover in the ferruginous *campo rupestre* due to the archipelagic distribution of the habitats in this ecosystem, perhaps representing true sky islands (do Carmo & Jacobi 2016, Silveira et al. 2016; Mota et al. 2018; Fernandes et al. 2020b). Although this study advances our understanding of the reference ecosystem of the ferruginous *campo rupestre*, we advocate that more studies of this nature encompassing all habitats must be produced along the distribution of this ecosystem to support sound ecological restoration programs. We hope we have provided the knowledge base for the construction of the reference ecosystem for the different habitat types of ferruginous *campo rupestre*, and highlighted which species contribute most to community assembly in this diverse and threatened tropical mountain ecosystem.

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Author Contribution

LR, DN, VMG, GWF: Conceptualization; JCB, DCP, VMG, GWF: Field data collection; DN, JCB: Data curation; DN: Formal analysis, Visualization; LR: Writing- Original draft preparation; DN, DCP, JCB, VMG, GWF: Methodology; LR, DN, DCP, GWF, JCB, VMG: Writing- Reviewing and Editing.

Ethics Declaration

Availability of Data/Materials: The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Conflict of Interest: The authors declare no conflict of interest with the content of this work.

Supplementary Material

Supplementary material (Appendixes 1-6) is available in the online version of this article. https://doi.org/10.1007/s11629-023-8333-x

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