



Original Paper

Zooming in on quartzitic outcrops: micro-habitat influences on flora and vegetation

Clara da Cruz Vidart Badia^{1,2}, Maria Cristina Teixeira Braga Messias^{2,3} & Livia Echternacht^{2,4,5}

Abstract

Rock outcrop vegetation is recognized worldwide by its singular and biodiverse flora. *Campo Rupestre* forms hyperdiverse mosaics in rocky environments across a wide latitudinal and altitudinal gradient, with high species turnover at macro- and micro-scales. The surrounding biomes, climate, and geological formations are the main drivers of species turnover on a macro-scale while micro-habitat seems to be the main one determining the peculiarities of the *Campo Rupestre* on a micro-scale. In a quartzitic *Campo Rupestre* area we evaluate how the outcrop micro-habitats influence floristic composition and functional traits. The study area is located in the municipality of Ouro Preto, Minas Gerais state, southeastern Brazil. Two main outcrop habitats were considered: top surfaces, with bare rock, shallow depressions and ephemeral ponds; and lateral surfaces, with clefts and crevices. We recorded the vascular species, their respective life-forms (according to Raunkiaer's system) as well as their coverage in 18 plots. We identified 71 species in 31 families. The floristic spectra and species composition were similar between top and lateral surfaces. There was no significant difference among the vegetational spectra. However, hemicryptophytes were slightly dominant on top, while on the sides chamaephytes were the dominant life-form. Understanding plant adaptations to these environments provides insights into the mechanisms underlying geomorphological heterogeneity in plant communities.

Key words: biological spectra, Brazilian flora, Campo Rupestre, life-form, Quadrilátero Ferrífero.

Resumo

A vegetação de afloramentos rochosos é reconhecida mundialmente pela biodiversidade e singularidade de sua flora. O Campo Rupestre forma mosaicos hiperdiversos em ambientes rochosos distribuídos ao longo de um amplo gradiente latitudinal e altitudinal, com altas taxas de substituição de espécies em macro e microescalas. Em macroescala, os biomas adjacentes, clima e formações geológicas influenciam as taxas de substituição de espécies, enquanto os micro-habitats parecem influenciar as peculiaridades do Campo Rupestre em microescala. Este estudo foi realizado no município de Ouro Preto, Minas Gerais, Brasil. Visamos avaliar como os micro-habitats de afloramentos rochosos quartzíticos determinam a composição florística e os atributos funcionais considerando dois habitats principais: superfície superior, com rocha exposta, depressões rasas e poças efêmeras; e superfície lateral, com fendas e fissuras. Espécies vasculares e suas respectivas formas de vida e cobertura foram registradas em 18 parcelas. Identificamos 71 espécies pertencentes a 31 famílias. O espectro florístico e a composição de espécies foram similares entre os habitats. Não houve diferença significativa entre os espectros vegetacionais. Entretanto, hemicriptófitas foram ligeiramente dominantes na superfície superior e caméfitas, na lateral. Compreender as adaptações das plantas a esses ambientes fornece informações sobre os mecanismos subjacentes à heterogeneidade geomorfológica nas comunidades vegetais.

Palavras-chave: espectro biológico, flora brasileira, Campo Rupestre, formas de vida, Quadrilátero Ferrífero.

¹ Universidade Federal de Viçosa, Depto. Biologia Vegetal, Viçosa, MG, Brazil. ORCID: <<https://orcid.org/0000-0002-1168-0721>>.

² Universidade Federal de Ouro Preto, Inst. Ciências Exatas e Biológicas, Depto. Biodiversidade, Evolução e Meio Ambiente, Ouro Preto, MG, Brazil.

³ ORCID: <<https://orcid.org/0000-0003-0300-9038>>.

⁴ ORCID: <<https://orcid.org/0000-0003-1534-7181>>.

⁵ Author for correspondence: livia.echter@ufop.edu.br

Introduction

Rocky outcrops present a vegetation pattern distinct from their surroundings, often selecting for xeric-adapted species that are able to survive harsh climatic conditions (Porembski & Barthlott 2000; Michael & Lindenmayer 2012). The distinct geomorphological features formed by rock outcrops create micro-habitats that further enhance biodiversity (Burnett *et al.* 1998). Campo Rupestre presents an extremely biodiverse vegetation and is defined by the presence of rocky outcrops; they are recognized as a mosaic of micro-habitats, with many endemics and stenotopic species (Conceição & Pirani 2005; Conceição *et al.* 2007; Echternacht *et al.* 2011; Silveira *et al.* 2016; Castro *et al.* 2018). Studies on the heterogeneity of Campo Rupestre have been performed at several levels, from kilometric (Neves *et al.* 2018) to centimetric scales (Carmo *et al.* 2016).

From a broad perspective, the very existence of the Campo Rupestre is conditioned by structurally resistant lithotypes, mainly quartzite and itabirite, which form a higher relief above the surrounding (Rizzini 1979; Benites *et al.* 2007; Schaefer *et al.* 2016a). The most continuous geological formation of this type is found in the Espinhaço Mountain Range (Giulietti *et al.* 1997), in eastern Brazil, which extends over a thousand kilometers northerly-southerly throughout Bahia and Minas Gerais states, with rocks protruding at the top, usually from 900 m to 2,100 m.a.s.l., ranging in latitude from 10°00'S to 20°30'S. Its inherent disjunct distribution and large latitudinal, altitudinal, and climatic influences determine high species turnover (beta diversity) and endemism (Echternacht *et al.* 2011; Silveira *et al.* 2016; Castro *et al.* 2018). In the southern portion of Espinhaço Range, there is the Quadrilátero Ferrífero, a mountain complex of quadrangular relief and ferrous or quartzitic rocks at mountaintops, located between the municipalities of Ouro Branco, Belo Horizonte, Catas Altas and Moeda. In spite of different geological origins for the Espinhaço Range and the Quadrilátero Ferrífero, they may be considered as a biogeographic unit (Echternacht *et al.* 2011; Colli-Silva *et al.* 2019).

At the macro-scale, the Campo Rupestre is highly influenced by the biomes in which they are inserted: from the north by the Caatinga, from the west by the Cerrado, and from the southeast by the Atlantic Forest (IBGE 2012). At an intermediate scale, rock types and geofoms are important

determinants of the flora and vegetation patterns (Giulietti *et al.* 1997; Vincent & Meguro 2008; Messias *et al.* 2013; Schaefer *et al.* 2016a, 2016b). Rock composition, hardness, metamorphism, and relief are determinants, forming two main types of Campo Rupestre: the quartzitic, with mainly siliciclastic rocks, and the ferruginous (Cangas) (Uhlein & Noce 2012).

On a small scale, micro-habitats and phytophysionomies play an important role in determining local diversity. They may be regarded as vegetational patches associated with and interspersed among the outcrops, as for example the open herbaceous grassland among marshes and riparian forests (Rapini *et al.* 2008). Focusing on the diversity of Campo Rupestre, cracks and crevices play an important role in supporting plant species in the outcrops, as they accumulate soil and retain water, providing less arid conditions and reducing over-heating and drought (Alves & Kolbek 1993; Conceição & Pirani 2005; Porembski 2007). In addition, the influence of fine-scale surface heterogeneity on rock vegetation was analyzed by Carmo *et al.* (2016), who showed that the microtopography of fissures, cracks and rock fragments affect the distribution of functional groups.

Human exploitation of mineral resources is the main impact on Campo Rupestre, especially the open pit mining in the Quadrilátero Ferrífero, leading to irreversible biodiversity losses (Roeser & Roeser 2010; Silva 2016; Carmo *et al.* 2017; Fitzsimons & Michael 2017), especially on ferruginous outcrops but also on quartzite ones. Detailed studies regarding plant communities in post-mining areas have focused mainly on recovery and succession of natural communities (*e.g.*, Schulz & Wiegler 2000; Heras *et al.* 2008; Gould 2011). Understanding the distribution of species in preserved areas may contribute to restoration strategies and increase the current knowledge for restoring mined areas in Brazil and worldwide (Bétard 2013; Lemke *et al.* 2013; Sharma & Chaudhry 2018).

In spite of the great endemism of Campo Rupestre, it is hardly defined by floristics and taxonomy alone (Alves & Kolbek 2009; Neves *et al.* 2017). Studies on plant functional traits and life forms may contribute to uncover patterns of plant species composition in different phytophysionomies (Raunkiaer 1934; Coelho *et al.* 2018; Silva Mota *et al.* 2018).

Several studies have shown how habitat or micro-habitat in rock outcrops determine different flora and vegetation patterns (Porembski *et al.* 1997; Conceição & Pirani 2005; Gröger & Huber 2007; Jacobi *et al.* 2007; Porembski 2007; Paula *et al.* 2017). According to these authors, patterns are related with soil depth, humidity and shading. These variables are higher in crevices, common in the lateral quartzite rock blocks, compared with the soil pools on the top of the rock blocks. We analyzed two micro-habitats (top and lateral surfaces of quartzite rock) to evaluate the influences, in a meter scale, of habitat heterogeneity on the plant community in terms of floristic, vegetational and functional aspects in Campo Rupestre. We hypothesized that these micro-habitats would determine different flora, vegetation and functional traits, since they are under different soil and sunlight conditions. We expect higher flora and life-form diversity in lateral habitat, since it is more heterogeneous. We described the species composition, floristic and vegetational spectra as a reflex of these environmentally distinct habitats. Further discussion concerning species and rock outcrops conservation are provided.

Material and Methods

Study Area

The study was carried out at the Serra das Camarinhas locality, municipality of Ouro Preto, southeastern of the Quadrilátero Ferrífero, Minas

Gerais state, Brazil (Fig. 1), at 20°22'S and 43°30'W, 1,357 m to 1,433 m above sea level. The study site is within the Área de Proteção Ambiental (APA) Cachoeira das Andorinhas, a conservation unit of sustainable use, and neighbor to the Parque Natural Municipal da Cachoeira das Andorinhas, a fully protected conservation unit. The Quadrilátero Ferrífero is strongly affected by quarrying, which is one of its main anthropic impacts (Roeser & Roeser 2010; Silva 2016; Carmo *et al.* 2017; Fitzsimons & Michael 2017). In the study site, urban expansion is the main current threat (Myr 2017).

Rocks associated with Campo Rupestre may present distinct geological origins. Most of the Campo Rupestre is located on the Espinhaço Mountain Range and belongs to the Espinhaço Supergroup (Alkmim 2012; Uhlein & Noce 2012). The Quadrilátero Ferrífero has multiple geological formations and the quartzitic outcrops of this survey belong to the Caraça Group, Minas Supergroup (Baltazar *et al.* 2005).

The climate of the region is classified as Cwb according to Köppen, *i.e.* mesothermic, with a warm and rainy season from September to April and a cold and dry season from May to August (Alvares *et al.* 2013). The vegetation on the rocky outcrops is distributed as patches, perceived as vegetation islands within a montane Atlantic Forest matrix (Porembski *et al.* 1998; Caiafa & Silva 2005; Paula *et al.* 2017) (Fig. 2a).

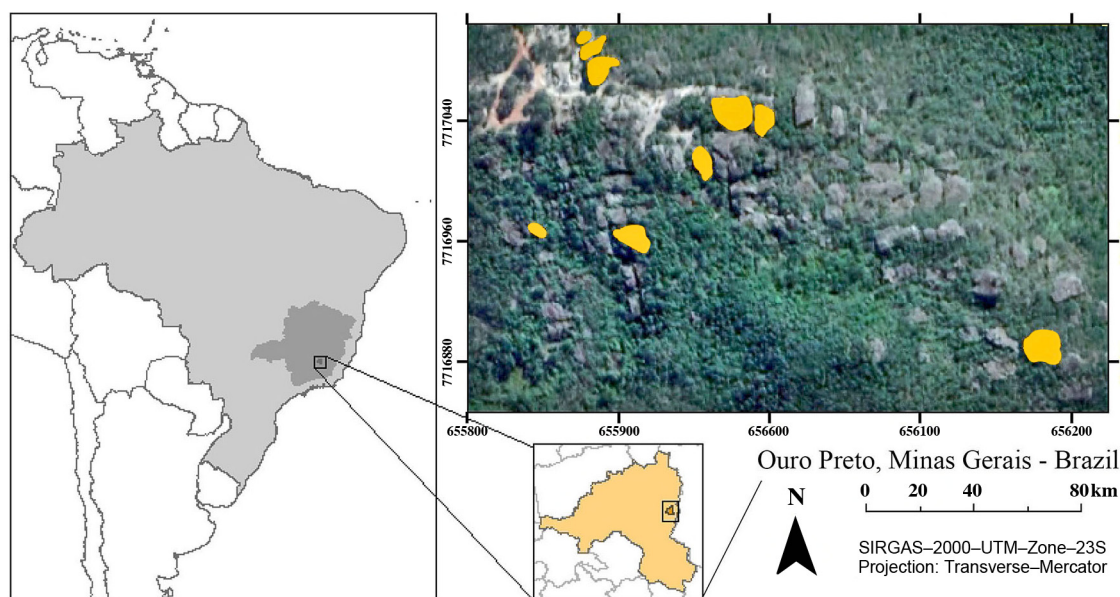


Figure 1 – Map with location and image from aerial view of the study area. The sampled outcrops are delimited by the yellow polygons, surrounded by Atlantic Forest.

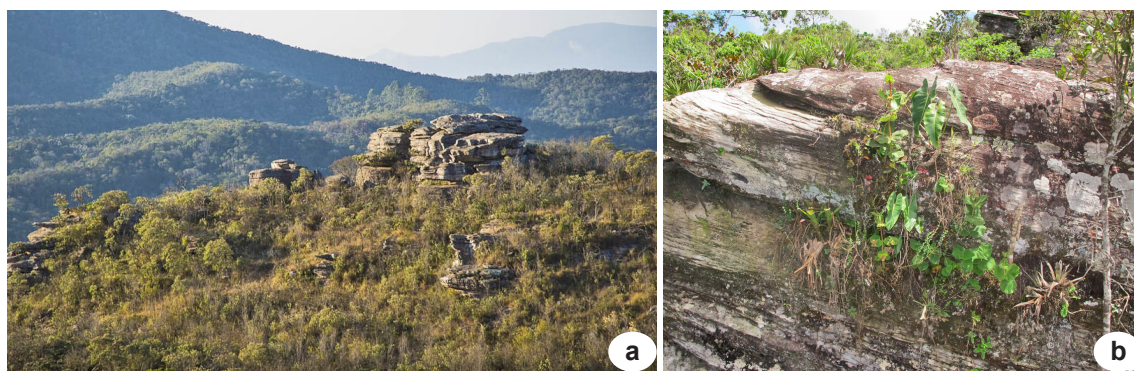


Figure 2 – a. An overview of the study area, with rocky outcrops surrounded by Atlantic forest matrix. b. Quartzitic outcrop with top and lateral habitats and related vegetation. Photos: a. Rodrigo Alves; b. Clara C.V. Badia.

Sampling

To perform this survey, nine quartzitic outcrops were selected. Two main habitats were considered (Fig. 2b): (1) outcrop top surface, which is defined by flat or slightly tilted surfaces (corresponding to a slope less than 45 degrees) and comprises mainly bare rocks, with small depressions filled with shallow sandy substrate and ephemeral ponds, very exposed to sunlight and wind; and (2) outcrop lateral surface, defined by steepness higher than 45 degrees, composed mainly of clefts and crevices, with deeper soil accumulation, high humidity and shading. The first habitat is sunnier, exposed, more xeric. The second is more shaded and mesic, sheltered by projections of the outcrop and by the surrounding vegetation. These two environments represent the heterogeneity and complexity of micro-habitats of outcrops in the area.

The survey was carried out from August/2017 to June/2018 by monthly field trips in 18 sampling plots of the selected outcrops. Nine plots were sampled for each habitat, corresponding to 1,000 m² for the outcrop top surface and 450 m² for the outcrop lateral surface, totaling 1,450 m². All the individuals of vascular species with at least four definitive leaves were sampled in order to evaluate the floristic composition and the dominance of each registered species. All vascular species were collected, identified, grouped by family according to the Angiosperm Phylogeny Group IV System (APG IV 2016) and to the Pteridophyte Phylogeny Group I System (PPG I 2016). Vouchers were deposited in the Herbarium “Professor José Badini” (OUPR) of the Federal University of Ouro Preto. Each species was also classified into life-forms as

stated by Raunkiaer’s System (Raunkiaer 1934). Species were identified by direct comparison with physical herbarium specimens (OUPR), consultation with specialists, and specialized literature (Araujo *et al.* 2005; Dutilh 2005; Kinoshita & Simões 2005; Amaral 2007; Rolim 2007; Coser & Paula 2008; Rolim 2011; Montserrat & Mello-Silva 2013; Almeida *et al.* 2014; Coelho & Giulietti 2010; Amaral-Lopes & Cavalcanti 2015; Guarçoni 2015; Gonzaga *et al.* 2017).

Analysis

The following phytosociological parameters were measured for each species: absolute frequency, relative frequency, absolute dominance, relative dominance and importance value (IV). Dominance was assessed by coverage. The cover area of each species in each habitat was estimated visually by the vertical projection of the aerial parts of each species as a percentage of the total area of the plot (Mueller-Dombois & Ellenberg 1974). Many other authors (Conceição & Giulietti 2002; Conceição & Pirani 2005; Conceição *et al.* 2007; Messias *et al.* 2011; Gastauer *et al.* 2012) have used coverage as a measure of dominance in herbaceous communities, since the many tussock of caespitose species make it difficult to assess density. In addition, cover data estimation is more independent of the plot size and can be assessed by the same way in all the life-form types, from small herbs to trees (Mueller-Dombois & Ellenberg 1974).

The classification of species in life-forms was performed following Raunkiaer’s major classes: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes (Raunkiaer 1934). In this way, epiphytes and lianas were grouped into

phanerophytes. In our samples, the cryptophyte class was represented only by geophytes.

Data regarding the life-form of each species were used to construct floristic and vegetational spectra. The floristic spectra represent the species richness in each life-form while the vegetational spectra represent the dominance or abundance of each life-form (Mueller-Dombois & Ellenberg 1974). Each species was assigned to a single life-form, being always considered the one in which renewing buds were less protected. To construct the floristic spectrum, each life-form was weighted by the number of species that occur in each habitat, whereas in the vegetational spectrum, each life-form was weighted by its coverage. In order to test if life-form proportions were significantly different, the biological spectra of each habitat were compared pairwise by using the G-test with Williams correction (Zar 1999).

The species similarity of the habitats was also compared by using the Jaccard index and organized into a Venn diagram (Magurran 2004).

Results

Floristics

In this survey, 71 vascular species (62 angiosperms and nine monilophytes) belonging to 31 families were identified (Tab. 1). The monocotyledonous families with the highest species richness were Orchidaceae (12 species), Bromeliaceae (five) and Poaceae (four). The richest families of eudicotyledons were Apocynaceae, Asteraceae (five each), Melastomataceae and Gesneriaceae (three each). Amongst the ferns, the richest families were Hymenophyllaceae and Polypodiaceae (three each).

The richest genera among angiosperms were *Ditassa* R.Br. and *Mandevilla* Lindl. (Apocynaceae), *Anthurium* Schott (Apocynaceae) and *Vellozia* Vand. (Velloziaceae), presenting two species each. Regarding the monilophytes, the richest genus was *Hymenophyllum* Sm. (Hymenophyllaceae), with three species.

The top-surface habitat presented 15 exclusive species while the lateral, 21. The 35 shared species indicate high similarity (49.3%) between these habitats (Fig. 3).

Phytosociological parameters

In the top outcrop surfaces, the species with the highest Importance Values (IV) were *Nematanthus strigillosus* (Mart.) H.E.Moore,

Sinningia magnifica (Otto & A.Dietr.) Wiehler, *Vellozia albiflora* Pohl, *Christensonella subulata* (Lindl.) Szlach., *Bulbophyllum weddellii* (Lindl.) Rchb.f., *Billbergia elegans* Mart. ex Schult. & Schult.f., *Pleroma heteromallum* D.Don, *Vriesea* cf. *marceloi* Versieux & T.Machado and *Philodendron minarum* Engl. (Tab. 2). The species with the highest IV on the lateral outcrop surfaces were *Barbacenia damaziana* Beauverd, *Vellozia albiflora*, *Christensonella subulata*, *Anthurium minarum*, *Ichnanthus* sp., *Paliavana sericiflora* Benth., *Matayba marginata* Radlk., *Panicum* sp., *Nematanthus strigillosus*, *Pleroma heteromallum* and *Deluciris rupestris* (Ravenna) Lovo & A.Gil (Tab. 2; Fig. 4).

Biological spectra

Considering the floristic spectrum, hemicyptophyte was the predominant life-form for both (top and lateral surfaces) habitats, followed by phanerophyte, chamaephyte, geophyte and therophyte (Figs. 5-6). No significant difference was found between the floristic spectrum of the two studied habitats ($G = 1.5234$; d.f. = 4; $p = 0.8225$).

Taking into account the vegetational spectrum (Figs. 5, 7), the phytophysionomies of the two habitats were not significantly different ($G = 3.7897$; g.l. = 4; $p = 0.2851$). Hemicyptophytes presented higher coverage in both habitats. Phanerophytes presented higher coverage in the lateral (29%), when compared with the top habitat (18%), and hemicyptophytes were more predominant in the top habitat.

Conservation

Threatened species were found in the studied area, occurring in both micro-habitats (CNCFlora 2020): *Dyckia rariflora* Schult. & Schult.f. (Bromeliaceae, Endangered), *Hippeastrum morelianum* Lem. (Amaryllidaceae, Vulnerable), *Nematanthus strigillosus* (Gesneriaceae, Near Threatened), *Senecio pohlii* Sch.Bip. ex Baker (Asteraceae, Near Threatened), *Sinningia magnifica* (Gesneriaceae, Least Concern), and *Vellozia albiflora* (Velloziaceae, Near Threatened).

Discussion

Plant species diversity in Campo Rupestre has been accessed at several scales (e.g., Giulietti *et al.* 1997; Silveira *et al.* 2016), throughout floristics, biogeography and ecology (e.g., Jacobi *et al.* 2007; Messias *et al.* 2011; Mota *et al.* 2018),

Table 1 – Vascular species from rocky outcrops of Serra das Camarinhas, Cachoeira das Andorinhas Park, Ouro Preto, Minas Gerais state, Brazil. PHAN = phanerophyte; CHAM = chamaephyte; HEM = hemicryptophyte; GEO = geophyte; THER = therophyte. Voucher numbers are those of C.C.V. Badia (OUPR).

Family / Species	Voucher	Life-forms
Amaryllidaceae		
<i>Hippeastrum morelianum</i> Lem.	17	GEO
Anacardiaceae		
<i>Tapirira guianensis</i> Aubl.	31	PHAN
Apocynaceae		
<i>Dipladenia</i> cf. <i>gentianoides</i> Müll.Arg.	92	CHAM
<i>Ditassa mucronata</i> Mart.	129	PHAN
<i>Ditassa</i> sp.	142	PHAN
<i>Mandevilla pohliana</i> (Stadelm.) A.H.Gentry	92	PHAN
<i>Mandevilla tenuifolia</i> (J.C.Mikan) Woodson	53	THER
Araceae		
<i>Anthurium minarum</i> Sakur. & Mayo	77	HEM
<i>Anthurium scandens</i> (Aubl.) Engl.	72	HEM
<i>Philodendron minarum</i> Engl.	78	PHAN
Asteraceae		
<i>Baccharis serrulata</i> (Lam.) Pers.	54	PHAN
<i>Calea clematidea</i> Baker		PHAN
<i>Eremanthus glomerulatus</i> Less.	15	PHAN
<i>Moquinia racemosa</i> (Spreng.) DC.	56	PHAN
<i>Senecio pohlii</i> Sch.Bip. ex Baker	73	PHAN
Bromeliaceae		
<i>Billbergia elegans</i> Mart. ex Schult. & Schult.f.	7	HEM
<i>Hoplocryptanthus schwackeanus</i> (Mez) Leme et al.	118	HEM
<i>Dyckia rariflora</i> Schult. & Schult.f.	27	HEM
<i>Pitcairnia</i> sp.	65	HEM
<i>Vriesea</i> cf. <i>marceloi</i> Versieux & T.Machado	85	HEM
Cactaceae		
<i>Hattoria salicornioides</i> (Haw.) Britton & Rose	30	CHAM
Celastraceae		
<i>Monteverdia imbricata</i> (Mart. ex Reissek) Biral	145	PHAN
Clusiaceae		
<i>Clusia mexiae</i> P.F.Stevens	112	PHAN
Commelinaceae		

Family / Species	Voucher	Life-forms
<i>Dichorisandra hexandra</i> (Aubl.) Standl.	127	PHAN
Dioscoreaceae		
<i>Dioscorea debilis</i> Uline ex R.Knuth	95	PHAN
Ericaceae		
<i>Agarista virgata</i> Judd	48	PHAN
Eriocaulaceae		
<i>Paepalanthus exiguus</i> (Bong.) Körn.	Borsanelli, F.A. 11	HEM
Erythroxylaceae		
<i>Erythroxylum gonocladus</i> (Mart.) O.E.Schulz	106	PHAN
Gesneriaceae		
<i>Nematanthus strigillosus</i> (Mart.) H.E.Moore	51	CHAM
<i>Paliavana sericiflora</i> Benth.	29	PHAN
<i>Sinningia magnifica</i> (Otto & A.Dietr.) Wiehler	89	GEO
Iridaceae		
<i>Deluciris rupestris</i> (Ravenna) Lovo & A.Gil	50	GEO
Melastomataceae		
<i>Leandra aurea</i> Cogn.	49	PHAN
<i>Miconia corallina</i> Spring	59	PHAN
<i>Pleroma heteromallum</i> D. Don (D. Don)	113	PHAN
Myrtaceae		
<i>Myrcia splendens</i> (Sw.) DC.	107	PHAN
Orchidaceae		
<i>Acianthera teres</i> (Lindl.) Borba	123	HEM
<i>Bifrenaria tyrianthina</i> (Lodd. ex Loudon) Rchb.f.	57	HEM
<i>Bulbophyllum weddellii</i> (Lindl.) Rchb.f.	10	HEM
<i>Christensonella subulata</i> (Lindl.) Szlach., Mytnik, Gómiak & Śmiszek	125	HEM
<i>Elleanthus</i> sp.	66	HEM
<i>Epidendrum secundum</i> Jacq.	99	HEM
<i>Gomesa warmingii</i> (Rchb.f.) M.W.Chase & N.H.Williams	86	HEM
<i>Habenaria petalodes</i> Lindl.	12	HEM
<i>Heterotaxis</i> sp.	87	PHAN
<i>Prosthechea vespa</i> (Vell.) W.E.Higgins	122	HEM
<i>Zygopetalum maculatum</i> (Kunth) Garay	141	HEM
sp. 1	90	HEM
Piperaceae		

Family / Species	Voucher	Life-forms
<i>Peperomia tetraphylla</i> (G.Forst.) Hook. & Arn.	62	CHAM
Poaceae		
<i>Panicum</i> sp.	131	HEM
<i>Ichnanthus</i> sp.	120	HEM
<i>Chusquea</i> sp.	128	HEM
sp. 1	94	HEM
Portulacaceae		
<i>Portulaca mucronata</i> Link	45	THER
Rubiaceae		
<i>Coccocypselum erythrocephalum</i> Cham. & Schldl.	64	CHAM
<i>Hillia parasitica</i> Jacq.	117	PHAN
Sapindaceae		
<i>Matayba marginata</i> Radlk.	104	PHAN
Velloziaceae		
<i>Barbacenia damaziana</i> Beauverd	39	CHAM
<i>Vellozia albiflora</i> Pohl	42	CHAM
<i>Vellozia compacta</i> Mart. ex Schult. & Schult.f.	119	PHAN
Verbenaceae		
<i>Lantana</i> sp.	19	PHAN
<i>Stachytarpheta glabra</i> Cham.	98	PHAN
Monilophyte species		
Blechnaceae		
<i>Blechnum polypodioides</i> Raddi	81	HEM
Dryopteridaceae		
<i>Elaphoglossum tectum</i> (Willd.) T. Moore	76	HEM
Hymenophyllaceae		
<i>Hymenophyllum elegans</i> Spreng.	74	HEM
<i>Hymenophyllum fragile</i> (Hedw.) C.V.Morton	83	HEM
<i>Hymenophyllum hirsutum</i> (L.) Sw.	69	HEM
Polypodiaceae		
<i>Melpomene pilosissima</i> (M.Martens & Galeotti) A.R.Sm. & R.C.Moran	70	HEM
<i>Pecuma chnoophora</i> (Kunze) Salino & F.C.Assis	137	HEM
<i>Serpocaulon latipes</i> (Langsd. & Fisch.) E.R.Sm.	80	HEM
Pteridaceae		
<i>Lytoneuron lomariaceum</i> (Klotzch) Yesilyurt	97	HEM

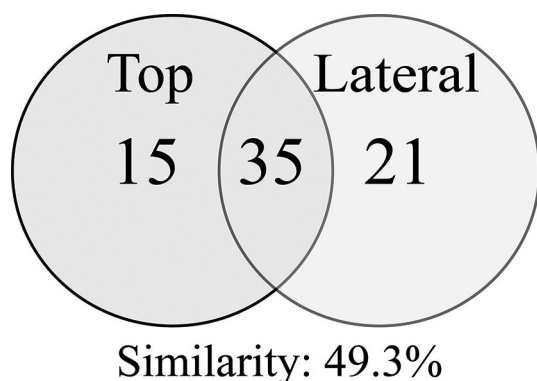


Figure 3 – Venn diagram representing the number of exclusive and shared species in the top and lateral rock surface habitats.

demonstrating the role of micro-habitat and soil structure, among others (e.g., Conceição & Pirani 2005; Carmo *et al.* 2016). Microenvironmental heterogeneity may contribute to species coexistence and to the extraordinary richness of the Campo Rupestre.

Floristic patterns

The main families of the study area exhibit great representativeness in other Campo Rupestre of the Quadrilátero Ferrífero (Messias *et al.* 2011, 2012; Oliveira *et al.* 2018) and on the septentrional *Espinhaço* (Conceição & Giuletta 2002; Conceição *et al.* 2007), and are also frequent in granitic (Caiafa & Silva 2005; Porembski 2007; Couto *et al.* 2017; Paula *et al.* 2017) and carbonatic rocks (e.g., Melo *et al.* 2013). The richness and predominance of monocots found here corroborates the pattern described for Neotropical rocky outcrops (Ibisch *et al.* 1995; Porembski *et al.* 1998; Conceição *et al.* 2007).

Epilithic Orchidaceae, Bromeliaceae and Araceae species were frequent in the top surface habitat. These families present strategies for maintaining water balance, like water-storing pseudobulbs in Orchidaceae (Santana *et al.* 2016), tank-leaves (Males & Griffiths 2017) or foliar water uptake (Berry *et al.* 2019) that enable them to occupy xeric environments such as bare rock (Porembski 2007).

In the heterogeneous environments of the Campo Rupestre, habitats suitable for growth and survival of species are sparsely distributed. Within this landscape, there is low probability for seeds to be dispersed to patches better than the parental one (Elmqvist & Cox 1996). Thus, clonal growth,

common in hemicryptophytic species, may be an advantageous adaptation. In addition, vegetative organs involved in clonal reproduction and storage, like rhizomes, may enhance resistance to fire and drought as well as favor regrowth at favorable seasons (Grace 1993).

Desiccation-tolerant species were also present, as *Vellozia albiflora* Pohl (Alcantara *et al.* 2015), which occurs at top and lateral surfaces, often forming monocotyledonous mats with non-desiccation-tolerant Poaceae species in both habitats. A desiccation-tolerant genus of monilophyte was also present in both habitats [*Lytoneuron lomariaceum* (Klotzsch) Yesilyurt]. Dried leaves resulting from desiccation, together with the growth of vegetative organs of monocotyledons, mostly hemicryptophytes, promote litter accumulation and soil water storage, thus creating a favorable environment for the development of other plant species (Burbanck & Phillips 1983; Tyler 1997).

Monocots, being non-woody plants, predominate in open environments such as Campo Rupestre (Burkart 1975). Nevertheless, eudicotyledons present features that allow them to occupy shallow depressions and crevices on exposed and shaded habitats of the outcrop. Amongst the eudicots with higher Importance Values (IV), we observed species with bulbs (e.g., *Sinningia magnifica*); water-storing leaves (e.g., *Nematanthus strigillosus*); and the metallophyte *Pleroma heteromallum*.

Among the eudicots, *Clusia* L. plays an important role as a nurse plant when growing in stressful, sandy habitats at the periphery of the Atlantic rainforest complex and in ironstone outcrops, together with bromeliads (Scarano 2002; Jacobi *et al.* 2007). This ecological role possibly occurs for *Clusia mexiae* P.F. Stevens in our survey area, as seedlings of other plants species were observed under its canopy.

The top habitat is less species rich than the lateral, with most species presenting adaptations to xeric environment. However, in shaded spots of the top habitat, species as *Hillia parasitica* Jacq. and *Coccocypselum erythrocephalum* Cham. & Schltdl. were found, which are typical from montane cloud Atlantic Forest understory (Costa & Mamede 2002; Oliveira 2010). These shaded micro-habitats also shelter *Peperomia tetraphylla* (G.Forst.) Hook. & Arn., a species noted in the literature as an epiphyte (Mucunguzi 2007; Alves *et al.* 2008; Ceballos *et al.* 2016).

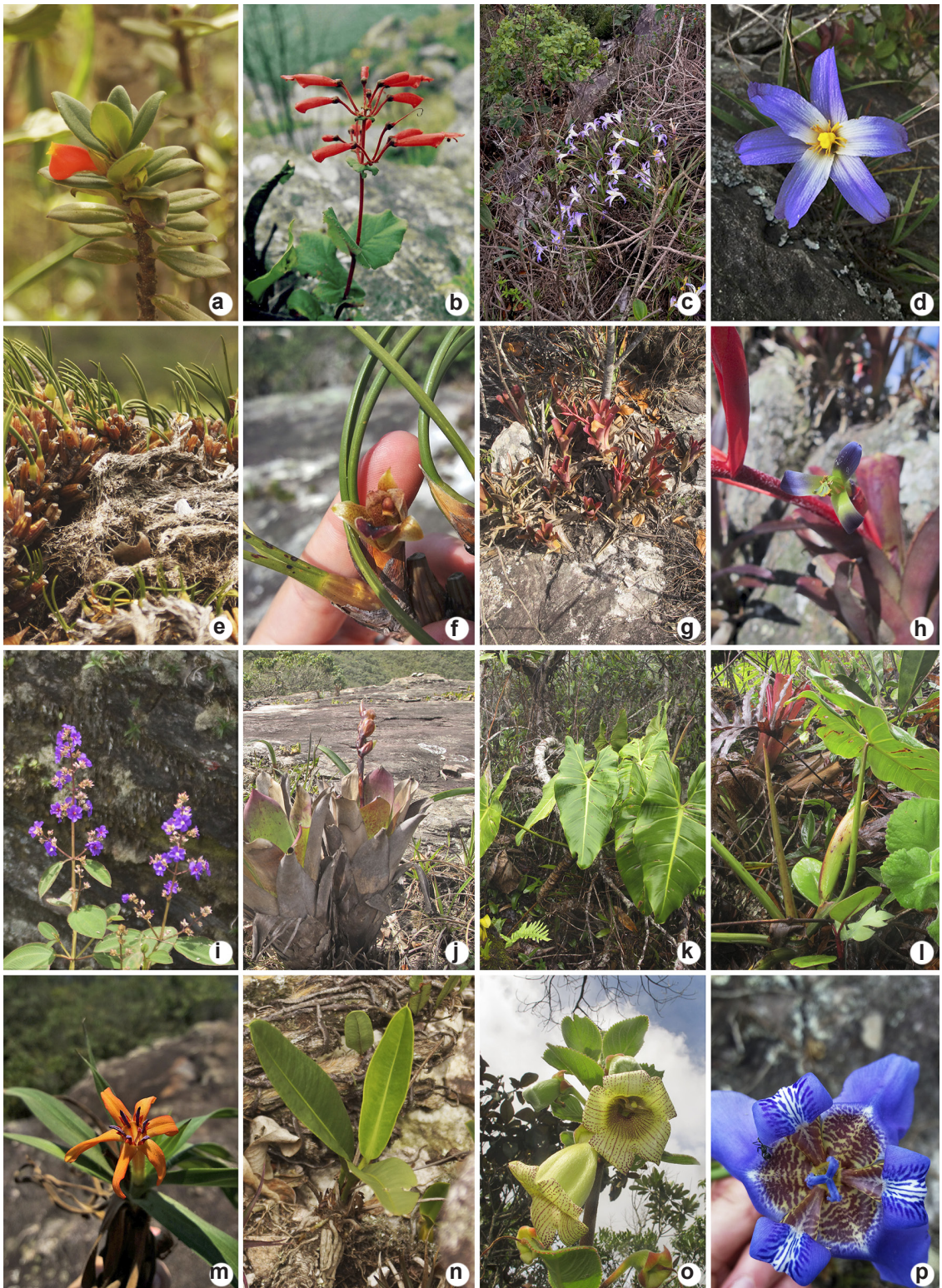


Figure 4 – a-p. Vascular species with the highest IV of top and lateral habitats – a. *Nematanthus strigillosus*; b. *Sinningia magnifica*; c-d. *Vellozia albiflora*; e-f. *Christensonella subulata*; g-h. *Billbergia elegans*; i. *Pleroma heteromallum*; j. *Vriesea* cf. *marceloi*; k-l. *Philodendron minarum*; m. *Barbacenia damaziana*; n. *Anthurium minarum*; o. *Paliavana sericiflora*; p. *Deluciris rupestris*.

Table 2 – Vascular species occurring on top and lateral outcrop surfaces with the highest Importance Values (IV), totaling up to 50% of IV scores. RF = Relative frequency; RDo = Relative dominance.

Top habitat			
Species	RF (%)	RDo (%)	IV (%)
<i>Nematanthus strigillosus</i> (Mart.) H.E.Moore	5.04	15.58	10.31
<i>Sinningia magnifica</i> (Otto & A.Dietr.) Wiehler	5.04	11.46	8.25
<i>Vellozia albiflora</i> Pohl	4.20	8.38	6.29
<i>Christensonella subulata</i> (Lindl.) Szlach., Mytnik, Górnjak & Śmiszek	6.72	5.66	6.19
<i>Bulbophyllum weddellii</i> (Lindl.) Rchb.f.	3.36	7.13	5.25
<i>Billbergia elegans</i> Mart. ex Schult. & Schult.f.	3.36	6.37	4.87
<i>Pleroma heteromallum</i> (D.Don) D.Don	5.04	2.56	3.80
<i>Vriesea</i> cf. <i>marceloi</i> Versieux & T.Machado	5.04	2.53	3.79
<i>Philodendron minarum</i> Engl.	1.68	4.82	3.25
Lateral habitat			
Species	RF (%)	RDo (%)	IV (%)
<i>Barbacenia damaziana</i> Beauverd	3.85	10.73	7.29
<i>Vellozia albiflora</i> Pohl	3.08	10.14	6.61
<i>Christensonella subulata</i> (Lindl.) Szlach., Mytnik, Górnjak & Śmiszek	3.85	8.20	6.02
<i>Anthurium minarum</i> Sakur. & Mayo	6.15	3.02	4.59
<i>Ichnanthus</i> sp.	2.31	6.44	4.38
<i>Paliavana sericiflora</i> Benth.	3.08	5.17	4.12
<i>Matayba marginata</i> Radlk.	0.77	6.82	3.79
<i>Panicum</i> sp.	0.77	6.82	3.79
<i>Nematanthus strigillosus</i> (Mart.) H.E.Moore	3.85	3.10	3.48
<i>Pleroma heteromallum</i> (D.Don) D.Don	3.85	2.71	3.28
<i>Deluciris rupestris</i> (Ravenna) Lovo & A.Gil	1.54	4.86	3.20

In addition, the genus *Peperomia* was described by Gröger & Huber (2007) as presenting shade-tolerant lithophyte species. Therefore, the typical, more xeric conditions of the top habitat, may be attenuated if the surrounding forest shadows the outcrops.

The totality of species shared between both habitats occurs in other Campo Rupestre localities (Giulietti *et al.* 1987; Oliveira 2010; Gastauer *et al.* 2012). The higher habitat heterogeneity of lateral surfaces favored not only rupicolous or saxicolous species, but also terricolous species of distinct life-forms [*e.g.*, *Calea clematidea* Baker, *Dioscorea*

debilis Uline ex. R.Knuth, *Leandra aurea* Cogn. and *Monteverdia imbricata* (Mart. ex. Reissek) Biral]. The occurrence of soil accumulations in some places like the vertical fissures in the rocks of the lateral habitat allows the rooting of taller species like phanerophytes (Giulietti *et al.* 1997; Jacobi *et al.* 2007).

Phytosociological parameters

The predominant life-forms, hemicyptophyte, phanerophyte and chamaephyte, observed in our study are well represented in other studies regarding biological spectra of outcrops

in different lithotypes of Campo Rupestre, inselbergs and other montane grasslands. The lower proportion of therophytes and geophytes has also been found in the biological spectra of

other rocky outcrop sites (Vitta 1995; Meirelles *et al.* 1999; Conceição & Giulietti 2002; Caiafa & Silva 2005; Jacobi *et al.* 2007; Ribeiro *et al.* 2007; Messias *et al.* 2011; Paula *et al.* 2017).

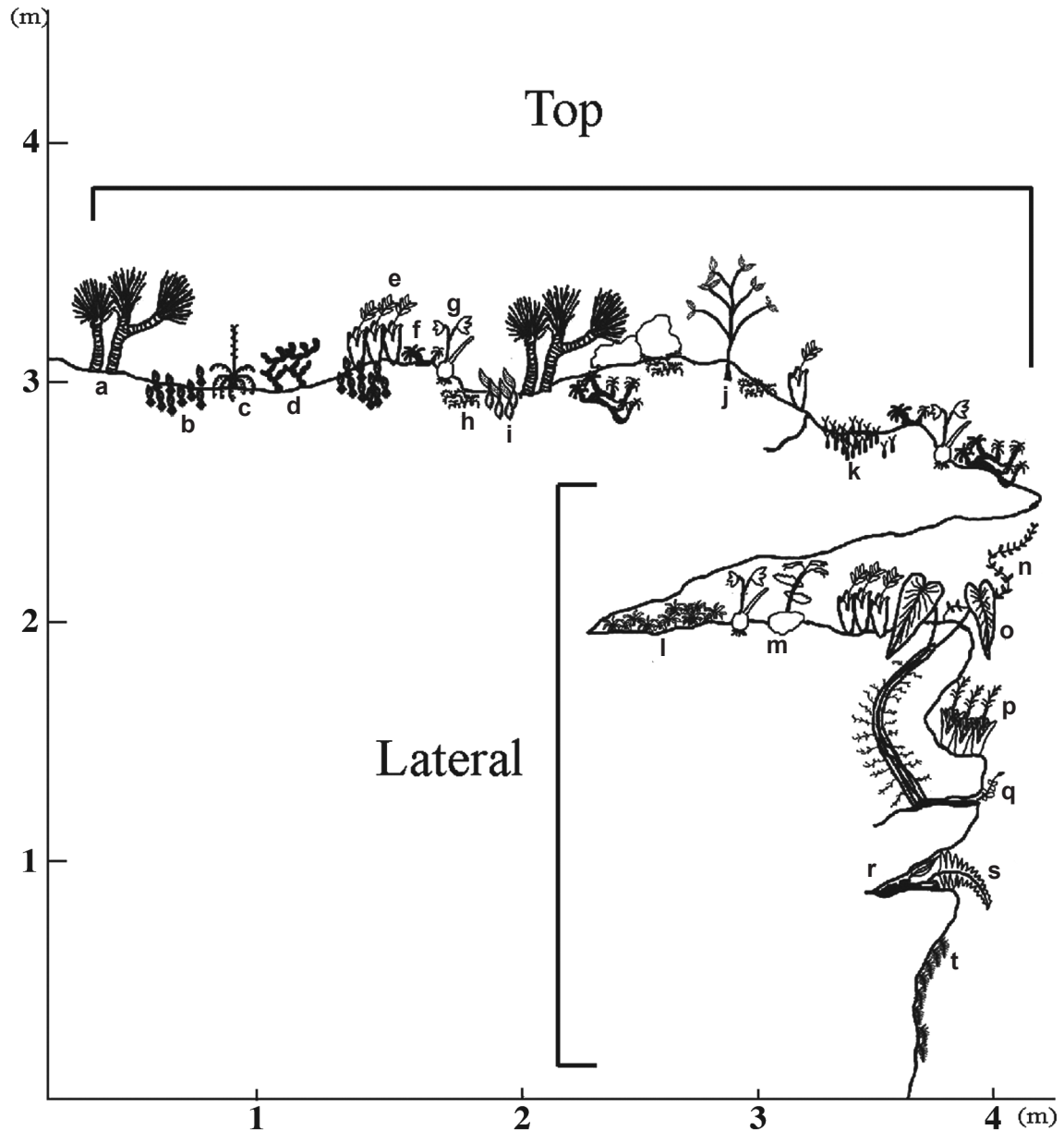


Figure 5 – Profile diagram indicating species occurrence in the two main habitats of a sampled outcrop (the top surface comprises micro-habitats such as bare rock, cracks, shallow depressions and stacked boulders; and the lateral surface, with cavity, crevice and crack micro-habitats). The following species are represented: a. *Vellozia compacta*; b. *Habenaria petalodes*; c. *Dyckia rariflora*; d. *Hattoria salicornioides*; e. *Vriesea cf. marceloi*; f. *Vellozia albiflora*; g. *Hippeastrum morelianum*; h. *Hoplocryptanthus schwackeanus*; i. *Bifrenaria tyrianthina*; j. *Pleroma heteromallum*; k. *Christensonella subulata*; l. *Barbacenia damaziana*; m. *Sinningia magnifica*; n. *Ditassa mucronata*; o. *Philodendron minarum*; p. *Billbergia elegans*; q. *Peperomia tetraphylla*; r. *Anthurium minarum*; s. *Serpocaulon latipes*; t. *Hymenophyllum elegans*.

The low nutrient budgets on rocky outcrop substrates do not favor the fast growth and establishment of therophytes (Ribeiro *et al.* 2007). The low frequency of cryptophytes in rocky outcrops is due to their characteristic underground systems, which need soil to develop (Raunkiaer 1934).

The biological spectra and the species with higher IV values for top and lateral habitats showed that hemicryptophytes were common at both habitats, similar to several other studies of rocky outcrops (Vitta 1995; Conceição & Giulietti 2002; Caiafa & Silva 2005; Ribeiro *et al.* 2007). The environmental constraints of rocky outcrops, especially the xeric conditions, favor the prevalence of hemicryptophytes, which are dominant in both outcrop habitats.

Woody species like chamaephytes and phanerophytes stood out in the lateral habitat when compared with the top habitat. They are represented mainly by shrub and subshrub species like *Paliavana sericiflora*, *Matayba marginata* and *Pleroma heteromallum*. The presence of organic and fibrous soil in lateral depressions and the shady micro-habitats may explain the higher phanerophyte coverage of this habitat. However, many of the phanerophytes counted were lianas and epiphytes (according to Raunkiaer 1934), which increased the proportion of this life-form for this habitat.

Other studies in rocky outcrops also found chamaephyte as a dominant class (Conceição & Giulietti 2002; Conceição *et al.* 2007). Aside from the environmental conditions that shape the distribution of plant life-forms, distinct methods have been used to perform these studies. The lack

of a clear pattern to measure life-form biological spectra makes comparison unequitable, although there are some general tendencies in studies of life-forms among rocky outcrops.

Another outstanding result of this study was that the lateral surface stood out from the top surface in some parameters regarding species richness. Even though the lateral surface presented half of the total area of the top surface, it showed higher total species richness (56), a higher richness of phanerophytes and an equitable richness of hemicryptophytes. These results reinforce the importance of micro-habitat heterogeneity in the maintenance of saxicolous flora richness and diversity.

Despite the striking differences of micro-habitat composition of the two habitats studied, they presented analogous floristic spectra. Thus, the species richness within each life-form is similar. The redundancy of species that play the same role in processes that are fundamental to the maintenance of biodiversity ensures that if one of them is locally reduced, it may be replaced by similar forms, giving continuity to the ecological function of the whole community.

The floristic spectrum represents the taxonomic aspects of the flora. However, in ecological investigations, assessing the vegetation response with a description of the physiognomy complements the floristic data. The floristic spectra differed from vegetational spectra in both habitats ($p < 0.05$). The vegetational spectra revealed that chamaephytes play an important role in Campo Rupestre vegetation, even though their species richness was not so expressive. This result offers evidence that life-form coverage reflects the functional trait preference to the environment.

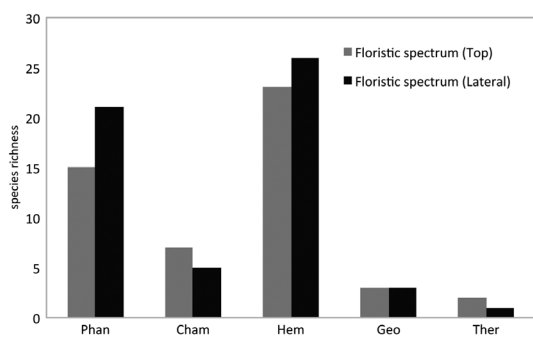


Figure 6 – Floristic life-form spectrum of top and lateral habitats of quartzitic rocky outcrops. Phan = phanerophyte; Cham = chamaephyte; Hem = hemicryptophyte; Geo = geophyte; Ther = therophyte.

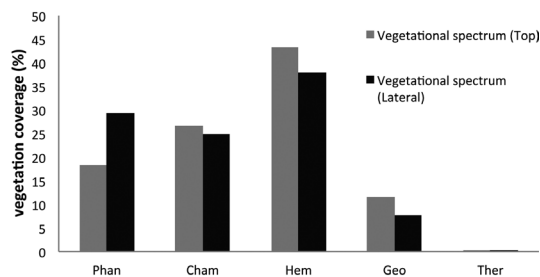


Figure 7 – Vegetational life-form spectrum of top and lateral habitats of quartzitic rocky outcrops. Phan = phanerophyte; Cham = chamaephyte; Hem = hemicryptophyte; Geo = geophyte; Ther = therophyte.

Quartzitic Campo Rupestre in a studied site in Chapada Diamantina (northern Espinhaço Range) presented a higher proportion of phanerophytes (Conceição & Pirani 2005), as well as near our study site in Ouro Preto (Messias *et al.* 2011). According to Mota *et al.* (2018), the proportion of hemicyptophytes increases and that of woody species decreases with increasing altitude. Indeed, in both studies (Conceição & Pirani 2005; Messias *et al.* 2011), hemicyptophytes were more frequent in higher altitudes. The predominance of hemicyptophytes in our study may be partly explained by a higher altitude of our study site. These peculiarities of Campo Rupestre spectra give evidence of how complex the functionality of this ecosystem is and the importance of its conservation as a whole.

Endemism

The majority (81%) of endemic species of the Quadrilátero Ferrífero occurs in Campo Rupestre, 45% of them in quartzitic outcrops (Borsali 2012). In the Quadrilátero Ferrífero there is a great number of plant species which are known by their type population only and are thus considered micro-endemic. Heterogeneous sampling efforts among distinct areas may hamper the evaluation of the conservation status of these species, since populations may be undersampled (Madeira *et al.* 2008; Borsali 2012; Le Stradic *et al.* 2015; speciesLink 2019).

The type population of *Barbacenia damaziana* (Velloziaceae) is from the Itacolomi State Park, very close to our study area (Ouro Preto, Minas Gerais state), and the species occurrence is limited to Ouro Preto (Borsali 2012). Despite its narrow occurrence, the conservation status of this species was not yet formally evaluated (CNCFlora 2020). This evaluation should be prioritized as the southern Espinhaço Mountain Range presents endemism rates of 70% for Velloziaceae (Mello-Silva 2009) and micro-endemic species are more susceptible to extinction.

Bromeliaceae has many endemic species in the Quadrilátero Ferrífero, among which the xeromorphic *Hoplocrypanthus schwackeanus* was recorded at the study site. *Vriesea marceloi* is known from the Serra do Caraça only, about 25 km from the site studied here (Versieux & Machado 2012), and possibly occurs in the study site; unfortunately, it was not possible to confirm the identification for the lack of the diagnostic organs on the collected specimen.

Mining and natural revegetation

Mining negatively impacts the habitat and biodiversity of rock vegetation, since outcrops are broken into smaller boulders, turning the ecosystem into a homogeneous, soilless environment (Kolbek & Alves 2008; Bétard 2013). The loss of micro-habitats decreases the richness of native species and increases colonization by invasive species (Holmes & Richardson 1999). Due to their life-history and functional traits, invasive and r-strategist species tend to begin the colonization of post-mining areas going through natural revegetation (Romoff 1986; Řehounková & Prach 2010). Revegetation with native species requires dedicated management (Romoff 1986; Silc 2010).

In our survey area we recorded several species described in the literature as important to the restoration of degraded areas such as *Anthurium minarum*, *Leandra aurea*, *Pleroma heteromallum*, *Acianthera teres* (Lindl.) Luer, *Epidendrum secundum* Jacq., *Gomesa warmingii* (Rchb.f.) M.W.Chase & N.H.Williams, *Vellozia albiflora* and *Vellozia compacta* (Jacobi *et al.* 2008; Lima *et al.* 2016). These species present features such as clonal growth and metal-tolerance and should be considered for *ex situ* cultivation in order to revegetate nearby areas undergoing quartzite exploitation.

Nine quartzitic outcrops were studied here at single rock-blocks, a level of focus that revealed the complexity of Campo Rupestre at meter-scale. In each block two habitats were recognized: the top surface with bare rock, small pools and cracks, shallow depressions and stacked boulders; and the lateral surface with cavities, crevices and cracks, more soil accumulation, and more shelter. Our results point out that more than 50% of the species are unique to each of these habitats, despite the floristic and vegetation spectra being statistically similar. The dominance of hemicyptophytes, such as epilithic or saxicolous species, shows them to be well adapted to the environmental constraints of the outcrops. Chamaephytes and phanerophytes were slightly more dominant in the lateral habitat, with a higher proportion in clefts and crevices, which allow for the development of deeper root systems. Our results contribute to the understanding of the influences of habitat heterogeneity on the plant community, in terms of floristic, vegetational and life-form aspects. Restoration strategies should take into account

plant preferences regarding the micro-habitats created by the relief of rock-blocks.

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