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THE COMPLEX PLANT COMMUNITIES OF THE CAMPO RUPESTRE HABITATS UNTALGLED BY TRAIT-BASED APPROACH

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Dissertação apresentada ao Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais como requisito parcial para a obtenção do título de Mestre em Ecologia, Conservação e Manejo da Vida Silvestre.

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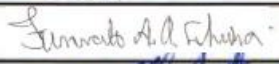
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Dario Caminha Paiva

No dia 27 de fevereiro de 2020, às 13:30 horas, na sala 236, bloco I 3 do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, teve lugar a defesa de dissertação de mestrado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) mestrando(a) Dario Caminha Paiva, intitulada: "**The complex plant communities of the campo rupestre habitats untangled by trait-based approach**". Abrindo a sessão, o(a) coorientador(a) e Presidente da Comissão, Doutor(a) Daniel Negreiros A. Pereira, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Fernando Augusto de Oliveira e Silveira (UFMG), Marcel Giovanni Costa França (UFMG) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

☒ Aprovação da dissertação, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;

☐ Reavaliação da dissertação com avaliação pelos membros da banca do documento revisado, sem nova defesa, no prazo máximo de 30 dias, sob possibilidade de reprovação;

☐ Reformulação da dissertação com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG a ao Regimento do PPG-ECMVS;

☐ Reprovação

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 27 de fevereiro de 2020.

Comissão Examinadora	Assinatura
Doutor(a) Daniel Negreiros A. Pereira	
Doutor(a) Fernando Augusto de O. e Silveira	
Doutor(a) Marcel Giovanni Costa França	

Resumo

Paisagens antigas, climaticamente estáveis e inférteis (OCBILs) são habitats com uma notável diversidade de espécies. Porém a estruturação de suas comunidades ecológicas ainda é pouco conhecida. O principal objetivo deste estudo foi compreender como os filtros edáficos conduzem a estrutura funcional da comunidade de plantas em um habitat antigo e pobre em nutrientes. Realizamos uma amostragem funcional em quatro tipos de habitats de campo rupestre com diferentes condições edáficas. Nós investigamos as relações entre características funcionais em substrato quartizítico e ferruginoso para obter os valores de característica ideais para cada condição. Além disso, construímos redes uni-partidas para explorar relações traço-traço com o objetivo de avaliar a coordenação funcional entre órgãos. Por último, executamos o K de Blomberg para testar o sinal filogenético da característica. Quanto maior a acidez do solo e menor o potencial de retenção de água no solo, maior a proporção de folhas menores, massa seca do tecido e densidade, resultando em espécies de plantas e comunidades mais conservadoras de recursos. As funções dos atributos foram fortemente correlacionadas entre os órgãos, tanto localmente quanto no nível individual, indicando uma tendência de integração morfológica. Os atributos de arquitetura foram centrais na coordenação, sugerindo seu papel principal na integração do transporte de seiva, suporte mecânico e exibição de folhas. A maioria das características apresentou baixo sinal filogenético e as características estatisticamente significativas foram normalmente associadas ao suporte mecânico / transporte de seiva. Concluímos que os ajustes de características em resposta aos parâmetros do solo são um mecanismo importante para a coexistência de um grande número de espécies na paisagem de campo rupestre.

Palavras-chave: Média ponderada da comunidade. Ecologia funcional. Ecossistemas severos. Sinal filogenético. Campos rupestres. Centroide de nicho de espécie. Rede de atributos.

Abstract

Old, climatic buffered and infertile landscapes (OCBILs) are remarkably species-diverse habitats, and the structuring of their ecological communities is scarcely known. The main objective of this study was to understand how edaphic filters drive the functional structure of plant community-in an ancient and nutrient-impoverished habitat. We carried out a functional screening across four types of *campo rupestre* habitats with different edaphic conditions. We investigated trait-soil relationships for ironstone and quartzitic substrate to obtain the optimal trait values of each condition. Also, we built unipartite networks to explore trait-trait relationships aiming to assess functional coordination among organs. Lastly, we run Blomberg's K to test trait phylogenetic signal. The greater the soil acidity and less potential to soil water retention, the greater were the proportion of smaller leaves, tissue dry mass and density resulting in more resource conservative plant species and communities. Trait functions were tightly correlated among organs both at the plot and individual level, indicating a trend of morphological integration. Architectural traits were central in coordination, suggesting their key role at the integration of sap transport, mechanical support, and leaf display. Most of traits had a low phylogenetic signal and the statistically significant traits were normally associated with mechanical support/ sap transport. We conclude that the trait adjustments in response to soil parameters are an important mechanism to the coexistence of a high number of species in campo rupestre landscape.

Key words: Community weighted mean. Functional ecology. Harsh ecosystems. Phylogenetic signal. Rupestrian grassland. Species niche centroid. Trait network.

Sumário

1 Introduction

There are multiple mechanisms (i.e. filters) included in plant community assembly that drive species composition at local scales and hence are of great relevance to ecosystem functioning. The identification of these filters and prediction of species responses in future stage of communities have been considered the holy grail of ecology (Funk et al., 2016). This knowledge has important implications in conservation and management of natural environments (Lavorel & Garnier, 2002; Ackerly, 2004). One example is the selection of the appropriate species for restoration, or species able to survive the environmental stresses worsened by anthropic activity (Fernandes, 2016a). The trait-based approach uses plant functional traits to describe ecological requirements of species (Keddy, 1992; Spasojevic & Suding, 2012). This approach has been proven to be a fundamental tool to predict future stages of communities in terms of species composition, and magnitude of ecosystem processes associated with functional groups (e.g., Lavorel & Garnier, 2002; Westoby & Wright, 2006; Díaz et al., 2016). Here we use Violle et al. (2007) definition of functional traits defined as a characteristic measurable at the individual level that affects direct or indirectly the performance of a species.

Functional traits change along environmental gradients; thus, depending on habitat context a different phenotype trait will be displayed. Understanding patterns at community level help us to elucidate the main process of community dynamic (Götzenberger et al., 2012). Commonly, average trait value of communities is used as a proxy of an adaptative value (i.e. optimal trait value) in a specific condition (Laughlin & Messier, 2015). The main assumption of optimal trait value model is that the trait value of the most abundant species is associated with the highest fitness in that condition (Laughlin & Messier, 2015). Indeed, the optimal trait value model does not directly measure species fitness and assumes that there is just a single optimal trait value in a condition, excluding the possibility of alternative designs (Laughlin, Strahan, Adler, & Moore, 2018; but see, Marks & Lechowicz, 2006). In spite the weakness of this model, the understanding of the directional changes of optimal trait value along environmental gradients is the first step to access community dynamics and to provide information of the main drivers of community structure along environmental conditions (Laughlin & Messier, 2015). In this context, to record

trait patterns of community assembly is necessary to select traits that respond to environment changes (Rosado, Dias, & de Mattos, 2013).

In the trait-based context, the leaf economics spectrum (LES), wood spectrum (WS) and leaf size-twig size spectrum (SS) play a central role in ecological strategies species differentiation (Westoby, Falster, Moles, Vesk, & Wright, 2002; Wright et al., 2004; Chave et al., 2009; Reich, 2014; Messier, Lechowicz, McGill, Violle, & Enquist, 2017; Freschet, Violle, Bourget, Scherer-Lorenzen, & Fort, 2018). When analyzed simultaneously, the LES, WS and SS are broadly used to characterize plant ecological strategies among biomes and environmental gradients (Díaz et al., 2004, 2016; Poorter, 2008). The ecological differentiation associated with LES is related with a trade-off among two physiological functions related to acquisitive-conservative resource use strategies (Wright et al., 2004; Reich, 2014). In one extreme are species that shows organs traits with relatively few structural investments, low tissue density and matter content, and high carbon fixation rates (i.e. resource acquisition strategies). In the other extreme, are species that display organs traits with great amount of structural tissue, high tissue density and dry matter content, high lifespan, and low photosynthetic metabolism (i.e. resource conservation strategies) (Wright et al., 2004; Reich, 2014).

The WS is associated with physiological functions of xylem, which encompasses trade-offs between sap transport-mechanical support-transport safety (Chave et al., 2009). Wood is composed primarily by cells of: i) fibers, that is related to plant mechanical support; ii) transport vessels, that move water among plant organs; and, iii) parenchyma, that stores water. In woods with high fiber content the lumen area tends to be small, consequently tissue density should be high. In this dense wood, sap transport efficiency tends to be low, and so propensity of xylem cavitation. Therefore, dense wood has a safer water transport with a great mechanical support and is related with low growth rates (Chave et al., 2009; Ziemińska, Butler, Gleason, Wright, & Westoby, 2013). In the other hand, wood with high amount of transport vessels in relation to fibers tends to have less tissue density and mechanical support. Less dense wood tends to have a high sap transport, propensity to cavitation, and normally is associated with high growth rates (Ziemińska et al., 2013).

The SS are related with plant architecture and organ display. It has profound implications on coordination of central plant physiological functions of LES and WS: resource acquisition, sap

transport and mechanical support (Olson, Aguirre-Hernandéz, & Rosell, 2009; Messier et al., 2017). At the two extremes of the leaf size-twig size spectrum are species traits characterized by either: large leaves, branches and seeds or species with small leaves, low stature and small seeds (Corner, 1949; Díaz et al., 2016). From an integrative perspective Reich (2014) proposed a framework that connects LES, WS and SS, referred as plant economic spectrum (PES). He argues that plant functions at different organs should be related to cope with both, metabolic and biomechanical limitations (Grime, 1977; Kleyer & Minden, 2015). Thus, functions such as resource acquisition at an organ level should scale positively with resource acquisition and transport in other organs. The opposite is also true, have a slow metabolism in one organ will require be slow in other plant parts. Therefore, phenotype should be connected in a single fast-slow plant spectrum.

The LES, WS and SS have theoretical support of competitive-stress tolerant-ruderal (CSR) model proposed by Grime (1977). According with the CSR scheme, plant species would be classified among three primary strategies: i) competitor (C), species that show traits related of growth, rapid resources uptake and elongated organs such as leaves and branches that allow these species outcompete their neighbors; ii) stress tolerant (S), species with small leaves, dense tissues, slow growth metabolism, normally evergreen species that can persist in improvised resource environment; iii) ruderal (R), small stature species with tiny leaves, rapid metabolism, and frequently annuals. Plant species will thus be organized gathering distinct proportion of each of these three extremes of strategies. There is a strong empirical evidence that supports this species classification as reliable to describe ecological differentiation in a great range of spatial scales and habitats (Hodgson, Wilson, Hunt, Grime, & Thompson, 1999; Pierce et al., 2017; Negreiros, Le Stradic, Fernandes, & Rennó, 2014; de Paula et al., 2015).

The present study is framed on the investigation of community patterns in an old, climatically buffered, and infertile landscape (OCBIL). The OCBIL ecosystems were described by Hooper (2009) as a habitat assembling plant species with low dispersal capacity, plentiful strategies for resource acquisition, and persistent and old individuals derived from ancient lineages. Even with a restrict distribution worldwide, OCBILs are habitats that gather a high species richness and endemism. In Brazil, the rupestrian grassland (hereafter *campo rupestre* in Portuguese) resembles OCBILs in many aspects (see Hooper et al., 2016), such as: exceptional

plant diversity, since approximately 15% of vascular plant species of Brazil are gathered in *campo rupestre* habitats, restricted in less than 1% of the country area (Silveira et al., 2016; Fernandes et al., 2018); climatic stability and infertile soils as the main drivers of species adaptation/exaptation, resulting in a vast suite of traits related to resource uptake (Oliveira et al., 2015; Silveira et al., 2016); and biomass allocation trends, leading to presence of many sclerophyll species (Hopper, 2009; Negreiros et al., 2014). Despite the low nutritional value of the *campo rupestre* one of the main drivers of habitats distinguishment are the soil parameters. In which causes a remarkably local change in vegetation patterns. Even with a notably ecological importance, few studies analyzed the *campo rupestre* in a screening of functional approach to better understand plant community dynamics (Negreiros et al., 2014; Dayrell et al., 2018).

In order to further understand *campo rupestre* plant communities we aimed to: i) assess the role of soil proprieties on directional changes in the optimal trait value of functional traits related to LES, WS , SS and CSR ecological strategies. We expected to find in sites less favorable to plant development (i.e. low pH, less nutrients and water availability) species with relatively more stress tolerant strategies and conservative use of resources at whole plant level (Reich, 2014); ii) generate a trait network in order to test modularity of the evaluated trait spectra, and define the central traits. We expected that traits from all organs and spectra will be correlated in some extent, but traits related to the same functions will be more correlated independent of their organs (Reich, 2014). Also, we expected that central traits will be those that control the main physiological functions such as architectural traits (Messier et al., 2017). iii) to quantify the phylogenetic signal of evaluated traits. As our data set was composed by traits related to resource allocation, we expect to find a low phylogenetic signal. Therefore, species from distinct lineages should share similar traits, leading a trend of trait convergence across phylogeny of plants assemblage (persistent species; see Hopper, 2009).

2 Methods

2.1 Study site and sample design

The study was carried out at the southern portion of Espinhaço mountains range, in the municipality of Brumadinho, Minas Gerais (20°07'05.2"S 43°59'42.0"W). The spatial arrangement of the vegetation at study site resembles a mosaic rather than a linear gradient of structure and species composition (Viana & Lombardi, 2007). Contrasting habitats in terms of edaphic structure and geomorphological origins are side by side, (i.e. quartzite and ironstone *campo rupestre*). The plant survey was done in three *campo rupestre* habitats comprising: outcrop quartzite, quartzite grassland, and *canga* (Figure 1). *Canga* is a Brazilian term long used to describe the *campo rupestre* growing on ironstone (ferruginous) substrate (Schaefer, Cândido, Corrêa, Nunes, & Arruda, 2016). The vegetation of the four *campo rupestre* habitats is composed primarily by herbs, shrubs and small trees (Jacobi & Carmo, 2008). The climate is considerate mesothermic by Köppen-Geiger classification, with two seasons well defined: wet and hot summer and dry and cold winter. The altitudinal gradient of study site ranges from 900 to 1426 m.a.s.l. Due to proximity of sampled plots, we assume that solar radiation, precipitation, and daily temperature variation were the same for all sampled units.

In each of the four habitats, along a linear transect ten 10×10 m plots were demarcated ten meters apart, totalizing 40 sample plots (total sample area = 4000 m^2). Each habitat was at least 300 meters spaced out. All shrubs/shrub- like/small trees with diameter at soil height (DSH) greater than 10 millimeters were recorded and their total height (H, in cm) estimate from ground level to higher photosynthetic tissue were measured. All plant individuals were identified at species level whenever possible (111 species in total; Gomes et al., in preparation). The frequency of species presence, abundance in terms of number of individuals and density in terms of basal area were used to calculate the index of importance value (IVI) of each species in each one of the four habitats. We selected the more important species in terms of IVI of each habitat that summed count at minimum 80% of importance of the total community to perform the functional trait measurement (Garnier et al., 2004).

2.2 Soil sampling

In each plot we collected five samples of bulk soil (at the four corners and one in the center), at the depth ranging from 05-15 cm. We homogenized the five soil samples to comprise a composite sample to represent a plot soil sample. Thirteen physical and chemical parameters were measured, following the EMBRAPA procedures (de Paula & Duarte 1997). Phosphorous, (P, in mg.dm^{-3}), potassium (K, in mg.dm^{-3}), iron (Fe, in mg.dm^{-3}), manganese (Mn, in mg.dm^{-3}) were extracted by Mehlich reagent, while Calcium (Ca^{2+}, in cmol$_c$.dm^{-3}) and magnesium (Mg^{2+}, in cmol$_c$.dm^{-3}) were extracted by KCl reagent. Also, soil pH (in H$_2$O, aluminum (Al) saturation (in %), base saturation (in %), coarse sand (in %), clay (in %), silt (in %), and organic matter (OM, in dag.kg^{-1}) were also measured.
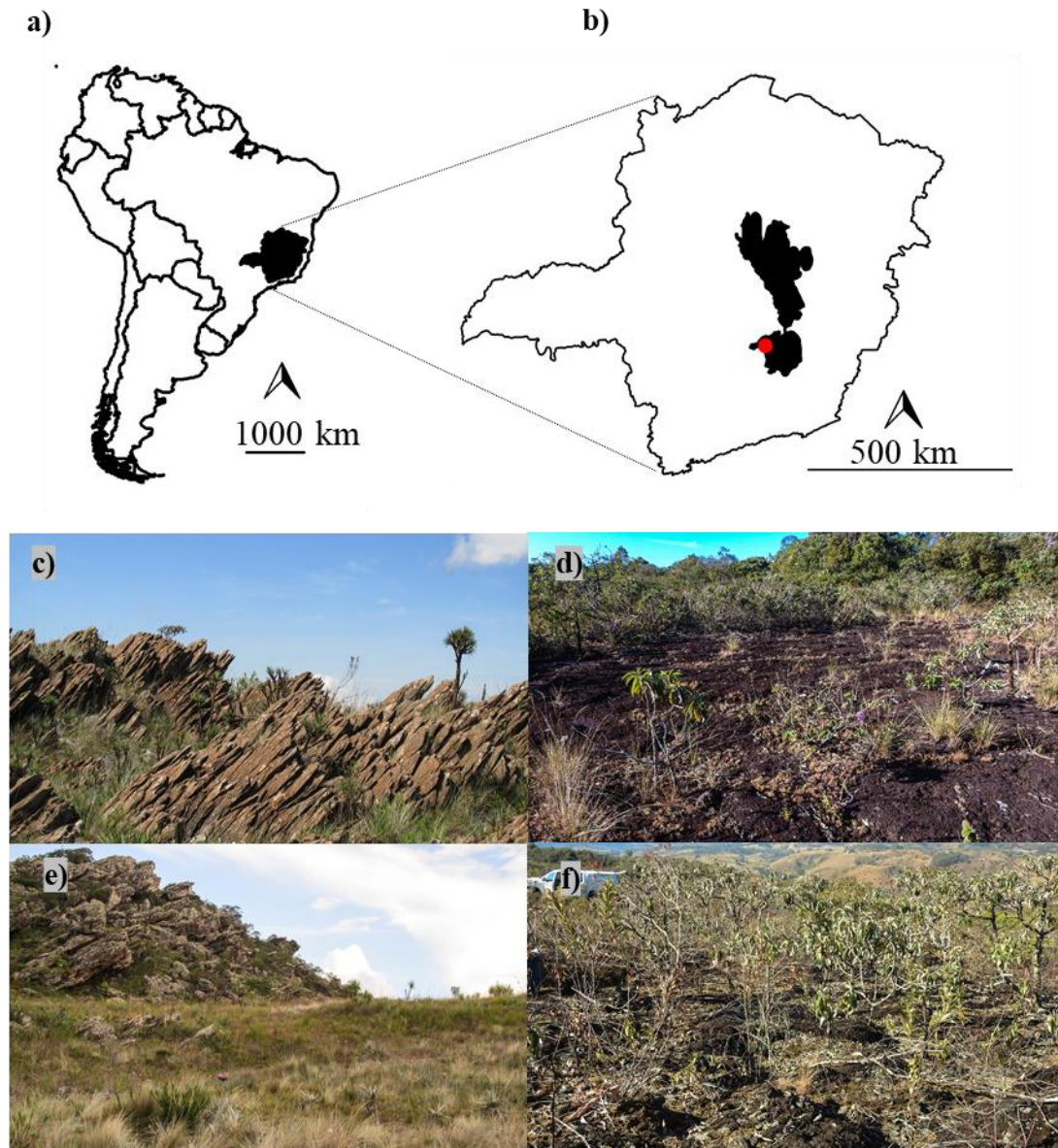
FIGURE 1 Overview of study habitats. a) South America, state of Minas Gerais in black. b) State of Minas Gerais, Espinhaço Mountain Range in black, red dot is where study was conducted. c) quartzite outcrop. d) canga couraçada. e) grassland quartzite. f) canga nodular. Photo credits: (c,e) D. Caminha Paiva, (d,f) G.W. Fernandes.

2.3 Plant trait measurements

To evaluate the LES, WS and SS we use those traits that are recognized to change according to soil nutritional status and water availability (Díaz et al., 2004; Negreiros et al., 2014).

We collected traits from three different organs (stem, petiole, and leaf) and architecture. All traits measurements were done following the procedures described by Pérez-Harguindeguy et al. (2013). In each habitat we collected at least six apparently healthy individuals of each species with diameter at soil height greater than ten millimeters. Every individual had a sun exposed branch with no herbivory and pathogen sign collected (length of at least 25 cm), labeled and packed in black plastic bag previously moistened and with moist paper towels inside of it. The sample was conducted in 2019, during the wettest months in the region (January and February) considered the growing season in the *campo rupestre* (Belo et al., 2013). Also, the sample occurred in the morning period (up to 10 am) in order to avoid the common high temperatures of the day and solar radiation that could lead to sample desiccation/deterioration.

At the laboratory we rehydrated the branches in 20-liter buckets filled with water during at least four hours. After rehydration, two fully expanded and apparently health leaves of each individual were taken to perform the functional measurements. We used the average of two leaves to estimate the leaf characteristic value *per* individual. We estimate chlorophyll (Chl, in $\mu g.cm^{-2}$) and flavonoid (Flav, in $\mu g.cm^{-2}$) content with Dualex (model DX4, Force-a) (Barthod, Cerovic, & Epron, 2007). Leaf and petiole fresh mass were estimated separately in a precision scale (precision of 0.001 g). Leaf thickness (LT, in mm) was estimated with a micrometer (Mitutoyo series 293, precision of 0.001 mm) avoiding leaf veins. Subsequently, leaves were scanned (at resolution of 200 dpi) to estimate their area (LA, in mm²) in the software ImageJ version 1.37. Petiole length (PL, in cm) was estimated with a digital caliper (precision of 0.01 cm). To analyze branch traits, we cut an approximately 4 cm of stem segment in the basal extremity of branch. After 40-60 min of rehydration we carried out the stem and bark measurements. In order to calculate wood and bark volume we estimated the volume of stem segment with and without bark, by the water displacement method (Pérez-Harguindeguy et al., 2013). Also, we measured fresh mass of both: bark and wood. Lastly, we estimated the total branch length, the number of leaves and petiole scars in the branch and the transversal area at the base of branch.

Leaves, petioles, stem segment and bark were then dried for at least 72 hours at 60° C in order to obtain dry mass. The following traits were estimated: specific leaf area (SLA, leaf area/leaf dry mass, in $mg.mm^{-2}$); leaf dry matter content (LDMC, leaf dry mass/leaf fresh mass, in %); leaf density (LD, 1/SLA × LT, in $g.cm^{-3}$); wood density (WD, wood dry mass/wood fresh volume, in

g.cm^{-3}); bark density (BD, bark dry mass/bark fresh volume, in g.cm^{-3}); wood dry matter content (WDMC, wood dry mass/ wood fresh mass, in %); bark dry matter content (BDMC, bark dry mass/bark fresh mass, in %); petiole dry matter content (PDMC, petiole leaf dry mass/petiole fresh mass, in %); branch leaf area per branch length ([BLABL, total number of branch leaves + petiole scars] $\times$ LA/branch length, in cm^2 cm^{-1}); leaf number per branch length (LNBL, [total branch leaf number + petiole scars]/branch length, in cm^{-1}); leaf area ratio (LAR, total number of branch leaves + petiole scars] $\times$ LA / whole branch dry mass, in cm^2.g^{-1}). Whole branch dry mass was estimated by: (sum of all petioles and leaves dry mass + branch volume (cm^3)) $\times$ density (wood and bark dry mass/ fresh volume, in g.cm^{-3}). Branch volume was estimated assuming a paraboloid shape (0.5 $\times$ branch transversal area $\times$ branch length); leaf mass fraction (LMF, total leaf mass in branch/branch total mass, or LAR/SLA, in g.g^{-1}); specific branch length (SBL, branch length/branch dry mass, in cm g^{-1}). The ecological meaning of each trait evaluated is summarized in Table 1.

2.4 CSR scheme

We performed a CSR analysis (competitor, stress-tolerant and ruderal classification (see, Grime 1977) according to Pierce et al. (2017) StrateFy spreadsheet. The input data of the CSR model correspond to SLA (in, mg.mm^{-2}), LDMC (in, %), and LA (in, mm^2) of mean trait value of each species.

2.5 Data analyses

All statistical analyses but PCA analysis were done using R-studio (version 1.2.1335). In order to define an environmental gradient of our study model we ran a principal component analysis (PCA) of soil properties using Systat (version 13.2). When necessary soil parameters were Log transformed to better approach a normal distribution of the data. The scores of the soil parameters in the two more important axis of PCA were our proxies to environmental differentiation at plot level.

TABLE 1 Abbreviation, unit and ecological meaning of measured functional traits of the species sampled in *campo rupestre* habitats, Brumadinho, Minas Gerais, Brazil. The number of species sampled for each functional trait are shown in parentheses after characteristic name.

Characteritic	Abbreviation–unit	Ecological meaning	References
Specific Leaf Area (43)	SLA – mg.mm^{-2}	Specific leaf area is associated with leaf production costs in terms of Carbon. Low values represent high investment in structural tissues, and conservative use of resources. High values are associated with low Carbon investments and is related with acquisitive use of resources.	Wright et al. (2004)
Leaf Area (43)	LA – mm²	Leaf area is related with light interception. Greater values are associated with more surface area to photosynthesis but are related with greater water loss. Low values intercept less light, but it decreases water loss.	Pérez-Harguindeguy et al. (2013)
Leaf Density (43)	LD – g.cm^{-3}	Leaf density is related with flux of water compounds in the leaf, and gas exchange between leaf and atmosphere. High values are associated low flux rates and more conservative use of resources. Low values allow a greater flux and therefore more acquisitive use of resources.	Witkowski & Lamont (1991)
Leaf Thickness (43)	LT – mm	Leaf thickness is associated with potential water storage inside leaves that allows plant to tolerate environmental stress.	Vendramini et al. (2002)
Leaf, Wood, and Petiole Dry Matter Content (43, 39, 39)	LDMC; WDMC; PDMC – %	Dry matter content is related with tissue quality. The greater the value the greater structural investments, sclerophyll, and more conservative use of resource.	Poorter et al. (2017)
Chlorophyll content (39)	Chl – µg.cm^{-2}	Chlorophyll content per unit of leaf area. It is related to photosynthetic metabolism. The greater values the more metabolic activity at the leaf level, and greater acquisitive use of resource.	Wright et al. (2004)
Flavonoids content (39)	Flav – µg.cm^{-2}	Flavonoid content per unit of leaf area. It is related with production of secondary	Wink (2016)

		metabolites and protection against pathogens, herbivores, and resistance to UV-B radiation.	
Wood Density (39)	WD – g.cm^{-3}	Wood density is related with water transport, resistance to cavitation, and mechanical support. Low values are related with greater water flux, less resistance to cavitation and mechanical support, normally associated with acquisitive use of resources. Greater values are related to a lower water flux, and more resistance to embolism and physical damage, thus conservative use of resource.	Chave et al. (2009)
Bark Density (39)	BD – g.cm^{-3}	Bark density is positively related with protection against hazards such as fires. Also is positively related with water storage and thus resistance to cavitation. Normally, scales negatively with wood density.	Poorter et al (2018)
Specific Branch Lenght (39)	SBL – cm g^{-1}	Specific branch length is related to construction costs of branch elongation. Greater values are associated with low biomechanical investments and greater investments in hydraulic support. Thus, is associated with low construction costs and rapid growth strategies.	Poorter (2008)
Leaf Mass Fraction (39)	LMF – %	Leaf mass fraction is the relative investments in leaves in relation to branch structures. Greater values are associated with higher light interception.	Poorter et al. (2018)
Petiole Lenght (39)	PL – cm	Petiole length is related to spatial positioning of leaves. Greater values are associated with greater light forage.	Poorter (2008)
Branch Leaf Area *per* Branch Length (39)	BLABL – cm^2.cm^{-1}	Branch lead area *per* branch length indicates the potential of light interception in the branch and the spatial positioning of leaves. Greater values are associated with greater potential to light interception but also can lead to a greater self-shading.	Poorter et al. (2018)

Leaf Number *per* Branch Length (39)	LNBL – cm⁻¹	Like BLABL leaf number *per* branch length also estimates how plant organized their leaves in the branch. High values are normally associated with smaller leaves and higher number of lateral buds.	Poorter et al. (2018)
Leaf Area Ratio (39)	LAR - cm².g⁻¹	Leaf area ratio is a parameter associated with growth rates. Low values are related with greater investments in branch structure in relation to leaf area, thus conservative use of resources. High values are associated with greater leaf surface in relation to structural investments, thus greater acquisitive resource use.	Lambers & Poorter (1992)
Height (43)	H – cm	Species maximum height is related with spatial positioning. Greater values are associated with more light interception.	Pérez-Harguindeguy et al. (2013)

To evaluate trait directional changes at the community level we estimated the Community Weighted Mean (CWM) of each trait measured and CSR classification (FD package) (Laliberté & Legendre, 2010). We pondered the CWM by the index of cover value of each species at plot level, estimated as a: [(*densp*/total density of all species) × 100 + (*domsp*/total dominance of all species) × 100]/2 (Cavassan, Cesar & Martins, 1984). *densp* represents the number of individuals of each species per plot, while *domsp* represents the basal area of each specie estimated by stem transversal area of each individual. Community weighted mean is a metric associated with functional composition of the mean trait of community (i.e. the dominant trait). When present in a certain environmental condition CWM is a proxy of the optimal trait value in terms of performance in that condition (Laughlin & Messier, 2015).Also, in order to evaluated how species habitats preference are associated with their traits we calculated species niche centroid (SNC), estimated as: the average of soil condition where a determinate species is present weighted by its index cover value.

To evaluate the relationship between traits and CSR strategies we ran Pearson correlation among them (*cor.test* function). Additionally, in order to evaluate the influence of soil characteristic in traits we carried out two liner regressions, one at plot level (community weighted

mean, CWM), and other at species level (species niche centroid, SNC) following ter Braak, Peres-Neto, & Dray (2018). For the first regression we use as independent variables the loadings of the two first axis of soil PCA and each CWM trait as a dependent variable. For the second regression, we used SNC as a dependent variable and mean trait value of that species as an independent variable. We combine these two tests for each trait and take the maximum *p* value to validate the regression. We run these two linear regressions because to infer about trait-environment associations is necessary to evaluated more than one species trait variation (ter Braak et al., 2018). For example, if a species with large leaves varied in abundance along an environmental condition, from a monodominance to just few individuals, it would be expected to observe a directional change in the leaf CWM independently of how other co-existing species with different leaf size respond to environment. However, the positive association between the example species and environmental condition could be due to other mechanisms than leaf size. Therefore, to avoid this possible spurious association between trait-environment it is important to access how the likely environmental conditions of all species that composed the evaluated community (i.e., species niche centroid, SNC) is associated with species trait (ter Braak et al., 2018). Therefore, if both regressions are significant: i) species mean trait value and species environmental preference (SNC); and, ii) environment associated and trait CWM we can validate the trait-environment association (ter Braak et al., 2018).

In order to define trait modularity and central traits we generated a trait network with the trait value at individual level. We analyzed trait network at individual level because species selection occurs at individual level and not at species level or community. Thus, to understand the role of physiological adjustments associated with environment it is important to consider intraspecific allocation patterns (Kleyer et al. 2019). The nodes in the network were represented by traits. The connectivity between nodes were the Spearman correlations coefficients among each pair of traits. We only used as connectivity significantly associations with correlations coefficients greater than 0.2. Correlations lower than 0.2 or non-significant were set to zero. We used the package *igraph* to generate the trait network (Csárdi & Nepusz (2006). The 2D plane of node distribution were organized by the default Kamada-Kawai layout that organize the node according to their correlation strength among traits. We used the function *betweenness* ( ) as an estimative of network centrality. Betweenness estimate the shortest way that all nodes get through a focal node. Hight values indicate that a trait has a great connectivity with other sub networks. To estimate the

network modularity, we use the function *cluster_optimal* ( ). This function measures the optimal structure of the subnetworks in the graph, by maximizing modularity of all possible nodes. Modularity is the tendency of the nodes to be arranged in subnetworks that has more connections within than among modules. In order to test for the significance of the modules in the observed network, we generated 1 000 network randomizations with the function *sample_degseq* ( ). For each new network a modularity test was carried out. We then, compare the observed modules with the 1 000 randomized modules with Z scores and *p* values in a confidence interval of 95%.

To evaluate the phylogenetic signal of each trait sampled and its relevance to community structure we generate a phylogenetic tree of the sampled species. We organized and updated species names using the package *plantminer* and function *taxize* (Szocs et al., 2019). To create a phylogenetic tree, we used the sampled species list and organized it with R20160415 angiosperms supertree (http://phylodiversity.net/phylomatic/). The undated nodes were corrected by *bladj* algorithm in phylocom software (version 4.2). We then compared the phylogenetic distribution of the plant species data and their respective trait (package *phytools* and function *phylosig*) (Revell, 2012). We carried out 10 000 randomizations to generate a Blomberg's K statistic, that assumes a Brownian motion model of trait evolution as a null model (Blomberg, Garland, & Ives, 2003). The Brownian motion model predicts that trait changes along phylogeny branches are random but close related species tends to share similar phenotypes due to close evolutionary relatedness. K statistics close to 1 indicate traits under Brownian motion model. K close to zero indicate a trend of different lineages to share the same trait (i.e., low phylogenetic signal), while K values greater than one represents trait conservation among lineages (i.e., high phylogenetic signal) (Blomberg et al., 2003).

3 Results

3.1 Soil proprieties

The two first axis of soil PCA (PC1 and PC2) explained 40.1% and 22.8 % of soil parameters variation, respectively (Figure 2). The first axis was better explained by Mg, Ca, Al saturation, base saturation, Mn, K, OM, and clay, while the second axis was better explained by coarse sand, P, silt, and pH. In general, the range of variation of soil proprieties was high, but still relatively low when compared with other vegetation types (see, Schaefer et al. 2016). Phosphorous, Ca, Mg, base saturation, OM, Mn, Fe, silt and clay had at least one order of magnitude in their range. Base saturation (min. 0.05 and max. 1.85, in %) and Ca (min. 0.00 and max. 1.49, in $cmol_c.dm^3$) had the greatest variation among the sampled plots (Table 2).

TABLE 2 Soil parameters of sampled in *campo rupestre* habitats, Brumadinho, Minas Gerais, Brazil. Mean ($\pm$SE), minimum and maximum values and transformation are shown.

| Parameters	Values	Minimum/Maximum	Transformation
pH (H_2O)	4.65 ± 0.05	4.09 / 5.37	-
P ($mg.dm^{-3}$)	0.91 ± 0.06	0.10 / 2.00	-
Ca ($cmol_c.dm^{-3}$)	0.46 ± 0.06	0.00 / 1.49	-
Mg ($cmol_c.dm^{-3}$)	0.11 ± 0.01	0.02 / 0.27	-
K ($cmol_c.dm^{-3}$)	25.35 ± 1.58	8.00 / 45.00	-
Al saturation ($cmol_c.dm^{-3}$)	58.18 ± 3.92	16.00 / 88.40	-
Base saturation (%)	0.64 ± 0.07	0.05/ 1.85	Log
Organic matter ($dag.kg^{-1}$)	3.98 ± 0.33	1.14 / 10.14	Log
Manganese ($mg.dm^{-3}$)	23.88 ± 4.31	1.10 / 106.80	Log
Iron ($mg.dm^{-3}$)	191.75 ± 12.81	63.80 / 411.40	-
Coarse Sand (%)	0.51 ± 0.02	0.10 / 0.76	-
Silt (%)	0.16 ± 0.01	0.04 / 0.47	Log
Clay (%)	0.18 ± 0.01	0.07 / 0.32	-

3.2 Overall species patterns

A total of 431 individuals belonging to 43 species and 17 families were sampled in the four habitat *campo rupestre* types. Asteraceae and Melastomataceae were the most well represented families, with 11 species each. In relation to conservation threat classification, *Chromolaena barbacensis* (Asteraceae), *Eriope macrostachya* (Lamiaceae) and *Vellozia variabilis* (Velloziaceae) are considered in least concern, while *Lychnophora pinaster* (Asteraceae) is classified as a near threatened according to IUCN (2019).

The most stress tolerant species according to the CSR classification was *Lychnophora pinaster* (Asteraceae) (C:S:R = 3.43:96.56:0.00 %). *Ageratum fastigiatum* (Asteraceae) (C:S:R = 12.99:43.05:38.95 %) an exotic species in *campo rupestre*, had the greatest values of ruderalism, as expected by "try harder" exotic species hypothesis (to further information regarding ecological strategies trends in biological invasions see discussion in, de Paula et al. 2015). *Palicourea rigida* (Rubiaceae) (C:S:R = 71.78:28.21:0.00 %) was the most competitive species but only occurred in the quartzite habitats (Figure 3). The functional traits of each species are shown in Table 3.
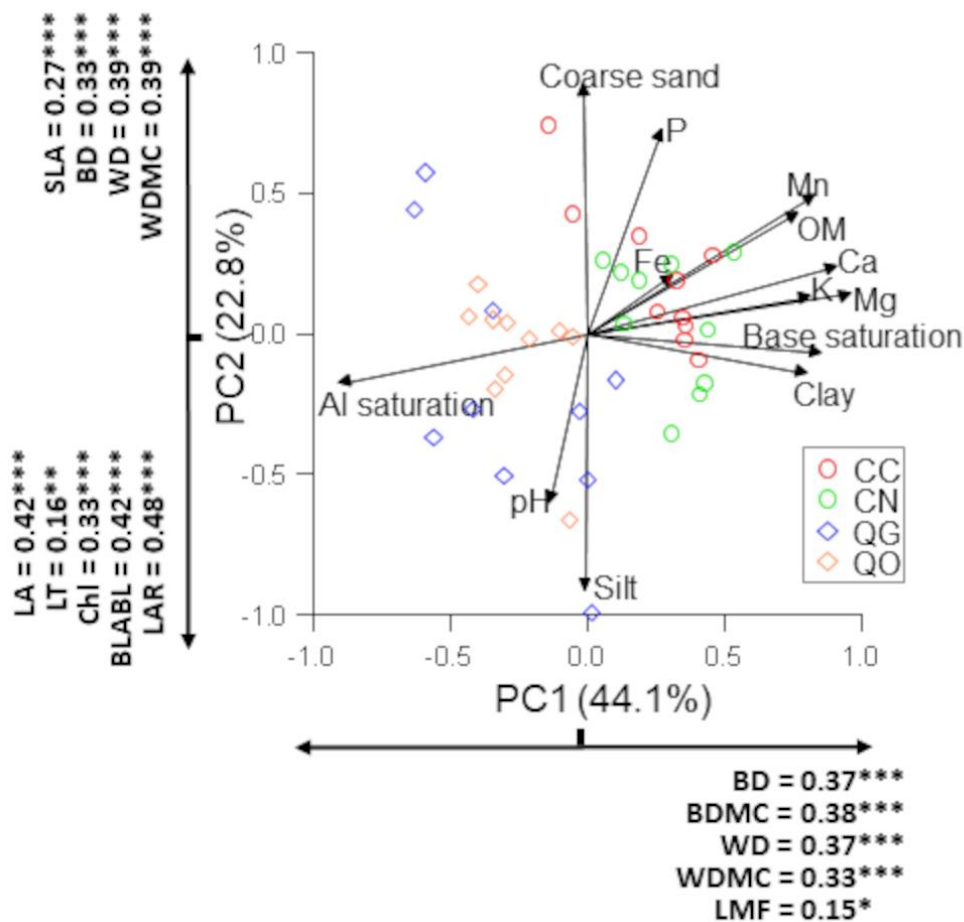
FIGURE 2 Principal component analysis of soil physical–chemical properties of campo rupestre habitats in the southern portion of Espinhaço mountains range, Minas Gerais, Brazil. CC canga couraçada, CN canga nodular, QG quartzitic grassland, QO quatzitic outcrop. Loadings of coarse sand, phosphorous (P), manganese (Mn), organic matter (OM), calcium (Ca), potassium (K), magnesium (Mg), base saturation, clay, silt, pH and Al saturation are shown. Significant trait-soil associations at the plot (CWM) and species level (SNC) are represented by the coefficient of determination between the main axis (PC1 and PC2) and CWM traits. LA = log-transformed leaf area, LT = leaf thickness, Chl = chlorophyll content, BLABL = log-transformed branch leaf area per branch length, LAR = leaf area ratio, SLA = log-transformed specific leaf area, BD = bark density, WD = wood density, WDMC = log-transformed wood dry matter content, and LMF = leaf mass fraction. * = p value <0.05; ** = p value <0.01; *** = p value <0.001.

a)

b)
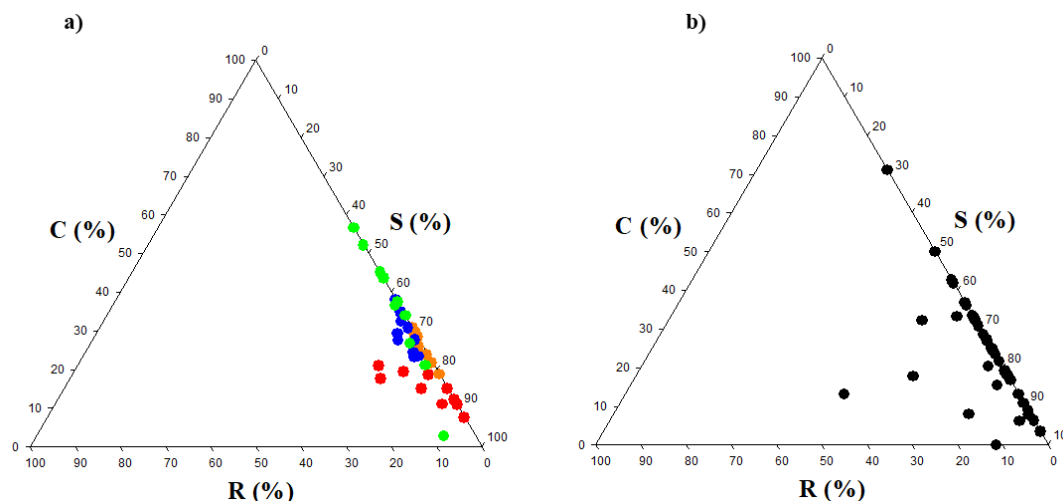
FIGURE 3 Overview of CSR scheme of ecological strategies, in campo rupestre habitats, Brumadinho, Minas Gerais, Brazil. Relative importance of competitiveness (C%), stress-tolerance (S%) and ruderalism (R%) are shown at: a) community level; and b) species level. In a) each dot represents a plot . Red: Canga couraçada; Orange: Canga nodular; Blue: Quartzite outcrop; Green: Quartzite grassland. In b) each dot represents a species.

3.3 Plant ecological patterns

The CSR strategies of species at *campo rupestre* shrub communities sampled were predominantly stress-tolerant, ranging mainly between stress-tolerant and competitiveness. Relatively low values of ruderalism proprieties were found among the sampled species, and just nine species showed some ruderalism (mean = 10.57±4.04). All trends of trait direction related with stress-tolerance/resource conservatism and competitiveness/resource acquisition, were consistent with the resource allocation and metabolic scaling hypotheses (Enquist, 2002). All trends of trait directional change are summarized in Figure 4.

We found several patterns of directional changes in CSR strategies and single traits along the PC2 soil PCA, that were more related to soil texture than PC1. In general, traits that reflects a greater tissue toughness, conservative of resources and less prone to acquire resources were related with soils with more coarse sand, phosphorus, acidity, and with less silt. Just WD, and BARKD

were significantly related with both, PC1 and PC2. The WDMC, BDMC, and FMF were significantly related with PC1. All significant regressions are shown in Figure 2.

In the network analysis we used data from 352 individuals belonging to 39 species. Three main modules of connectivity were found between evaluated traits, and were statistically significant (Z score = 2.239, p value < 0.012). All modules are related with plant functions and are not restricted by organs: i) resource acquisition-conservation, SLA, Chl, LT and LD; ii) sap transport-mechanical support, LDMC, PDMC, WD, BD, WDMC and BDMC; architecture iii) PL, LA, SBL, LNBL, LAR, LMF. In relation to betweenness six traits were more central than others, in parenthesis are the number of connections of each trait: SLA (13), LNBL (13), BLABL (11), PL (11), Chl (8), LD (8) (Figure 6). Flavonoid content was not correlated with other traits.

Regarding the phylogenetic signal, K value range from 0.29 to 0.67 indicates that in relation to a Brownian motion of evolution model, there is a random trend of trait distribution across plant lineages (Kraft et al. 2007). Wood density (K = 0.67), BD (K = 0.67), LD (K = 0.61), LDMC (K = 0.56), WDMC (K = 0.65), BDMC (K = 0.56), and PL (K = 0.61) were significant, which shows a moderate phylogenetic conservation of those traits (Table 5).
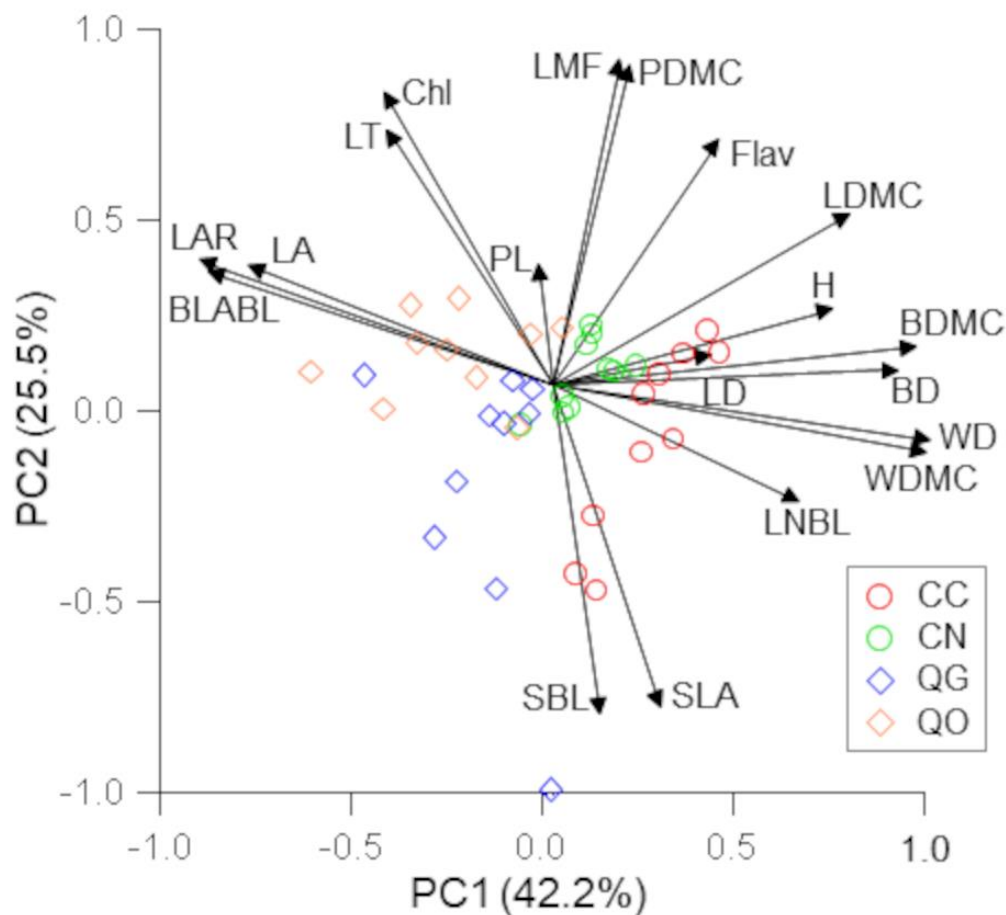
FIGURE 4 Principal component analysis of evaluated CWM functional traits of campo rupestre habitats, southern portion of Espinhaço mountains range, Minas Gerais, Brazil. CC = canga couraçada, CN = canga nodular, QG = quartzitic grassland, QO = quatzitic outcrop. Loadings of log-transformed specific leaf area (SLA), log-transformed leaf area (LA), leaf density (LD), leaf thickness (LT), flavonoid content (Flav), chlorophyll content (Chl), leaf dry matter content (LDMC), log-transformed wood dry matter content (WDMC), petiole dry matter content (PDMC), bark dry matter content (BDMC), wood density (WD), bark density (BD), specific branch length (SBL), leaf mass fraction (LMF), petiole length (PL), log-transformed branch leaf area per branch length (BLABL), leaf number per branch length (LNBL), leaf area ratio (LAR), and maximum height (H) are shown.

Table 3 Functional traits of 43 species sampled in *campo rupestre* habitats, Brumadinho, Minas Gerais, Brazil. Mean value for each species across all plots. C= competitiveness, in %; S= stress tolerance, in %; R= ruderalism, in %; SLA= specific leaf area, in mm^2.mg^{-1}; LA= leaf area, in mm^2; LD= leaf density, in g.cm^{-3}; LT= leaf thickness, in mm; Chl= chlorophyll content, in μg.cm^{-2}; Flav= flavonoid contented, in μg.cm^{-2}; LDMC= leaf dry matter content, in %; WDMC= wood dry matter content, in %; PDMC= petiole dry matter content, in %; BDMC=bark dry matter content, in %; WD= wood density, in g.cm^{-3}; BD= bark density, in g.cm^{-3}; SBL=specific branch length, in cm g^{-1}; LMF=leaf mass fraction, in g.g^{-1}; PL=petiole length, in cm; BLABL=branch leaf area *per* branch length cm^2 cm^{-1}; LNBL=leaf number *per* branch length cm^{-1}; LAR= leaf area ratio, in cm^2.g^{-1}; H= maximum height, in cm. Species nomenclature follows the Lista de Espécies da Flora do Brasil: http://floradobrasil.jbrj.gov.br/reflora

Species	C	S	R	SLA	LA	LD	LT	Chl	Flav	LDMC	WDMC
Actinocephalus bongardii	15.45	81.22	3.33	10.49	361.07	0.44	0.22	29.15	1.70	36.71	-
Ageratum fastigiatum	13.00	48.05	38.95	17.44	187.38	0.19	0.30	29.62	1.36	23.51	51.35
Banisteriopsis malifolia	32.38	67.62	0.00	8.25	2493.91	0.23	0.53	40.81	1.64	45.34	63.92
Baccharis reticularia	6.26	93.74	0.00	9.08	104.14	0.34	0.35	35.45	1.84	38.44	63.18
Baccharis serrulate	18.00	62.68	19.32	16.18	580.13	0.35	0.18	32.17	1.81	33.70	65.10
Campomanesiadamantium	27.58	72.42	0.00	4.29	2056.95	0.58	0.40	37.55	2.24	52.33	63.22
Chromolaena barbacensis	8.46	82.37	9.17	12.59	136.50	0.27	0.33	34.34	1.77	33.81	53.92
Chromolaena squalida	20.83	79.17	0.00	10.32	475.24	0.19	0.59	44.48	1.99	32.84	52.37
Diplusodon hirsutus	6.27	90.87	2.86	10.32	93.73	0.39	0.25	37.17	2.07	35.17	59.01
Eremanthus glomerulatus	33.69	66.31	0.00	7.37	1925.40	0.31	0.45	44.28	2.07	38.74	48.27
Eremanthus incanus	41.85	58.15	0.00	6.46	3826.11	0.45	0.36	42.20	2.12	38.69	52.72
Eriope macrostachya	33.38	63.92	2.70	10.30	765.72	0.18	0.55	43.84	2.04	26.43	51.05
Heteropterys umbellate	13.14	86.86	0.00	9.21	390.01	0.54	0.20	31.01	2.14	46.58	66.20
Hyptis proteoides	21.47	78.53	0.00	4.50	632.00	0.36	0.64	40.65	1.73	41.09	50.88
Jacaranda caroba	36.01	63.99	0.00	7.32	3070.52	0.25	0.56	35.07	2.12	43.05	45.77
Leandra aurea	37.12	62.88	0.00	5.60	3368.66	0.35	0.58	42.38	2.11	43.55	50.34
Lippia grata	8.92	91.08	0.00	6.71	197.76	0.37	0.42	41.16	2.08	44.60	65.72
Lippia lupulina	16.12	83.88	0.00	7.93	267.43	0.19	0.73	26.99	2.28	30.66	56.47
Lychnophora pinaster	3.44	96.56	0.00	6.41	73.54	0.59	0.27	-	-	48.22	66.51
Maytenus gonoclada	23.19	76.81	0.00	5.50	1020.63	0.43	0.43	55.43	1.86	42.49	50.78
Mimosa calodendron	24.83	75.17	0.00	5.40	1707.96	0.62	0.30	-	-	52.04	65.09
Microstachys corniculate	8.03	91.57	0.40	9.84	143.62	0.43	0.24	38.73	1.90	39.84	60.96
Microlicia martiana	0.00	93.40	6.60	12.19	7.04	0.42	0.23	-	-	37.76	55.72

Species	PDMC	BDMC	WD	BD	SBL	LMF	PL	BLABL	LNBL	LAR	H
Actinocephalus bongardii	-	-	-	-	-	-	-	-	-	-	145.00
Ageratum fastigiatum	18.53	24.31	0.52	0.19	6.39	0.90	5.03	11.02	6.05	1.85	195.00
Banisteriopsis malifolia	43.49	47.49	0.77	0.51	5.53	0.92	4.39	28.20	1.25	18.28	133.00
Baccharis reticularia	49.27	51.99	0.72	0.59	6.12	0.87	2.54	4.01	3.78	1.03	251.00
Baccharis serrulate	25.81	42.59	0.64	0.47	10.95	0.78	8.46	6.81	1.31	5.52	176.00
Campomanesia adamantium	45.50	47.66	0.62	0.52	7.80	0.92	6.42	19.94	0.99	13.48	77.00
Chromolaena barbacensis	38.55	35.29	0.61	0.37	9.02	0.84	2.30	4.48	3.18	1.35	165.00
Chromolaena squalida	37.30	28.43	0.56	0.29	8.57	0.80	5.83	6.78	1.41	4.33	156.00
Diplusodon hirsutus	39.70	38.80	0.68	0.44	5.77	0.86	1.36	4.07	4.34	0.93	223.00
Eremanthus glomerulatus	32.12	25.44	0.53	0.26	8.03	0.90	7.40	29.92	1.56	14.75	151.00
Eremanthus incanus	30.98	40.60	0.60	0.40	4.51	0.87	10.58	62.07	1.66	22.75	287.00
Eriope macrostachya	22.84	32.50	0.60	0.34	11.02	0.88	10.65	14.11	1.85	7.06	201.00
Heteropterys umbellate	44.68	50.32	0.79	0.63	8.57	0.89	3.25	5.67	1.63	3.70	118.00
Hyptis proteoides	41.42	37.43	0.50	0.40	13.77	0.82	5.22	7.50	1.19	5.35	151.00
Jacaranda caroba	35.62	45.22	0.44	0.52	8.33	0.94	9.63	22.15	0.75	20.78	153.00
Leandra aurea	35.08	39.42	0.60	0.45	5.90	0.89	15.87	29.49	0.90	20.03	134.00
Lippia grata	38.27	50.00	0.72	0.53	8.26	0.84	5.62	3.83	2.04	1.91	293.00
Lippia lupulina	-	45.67	0.66	0.49	28.91	0.92	-	9.08	3.49	2.55	126.00
Lychnophora pinaster	-	45.92	0.79	0.44	8.88	0.91	-	7.09	9.59	0.73	200.00
Maytenus gonoclada	39.64	43.88	0.59	0.52	8.06	0.92	5.15	13.69	1.46	8.37	215.00
Mimosa calodendron	52.56	46.69	0.78	0.53	8.49	0.90	10.95	12.03	0.75	12.55	96.00
Microstachys corniculate	33.44	32.45	0.64	0.37	7.65	0.84	2.55	2.32	1.67	1.41	187.00
Microlicia martiana	-	36.55	0.67	0.40	19.48	0.76	-	0.41	7.07	0.07	80.00

Species	C	S	R	SLA	LA	LD	LT	Chl	Flav	LDMC	WDMC	PDMC
Miconia pepericarpa	24.44	75.56	0.00	6.17	1449.99	0.43	0.38	48.02	1.75	48.37	51.91	41.77
Mimosa pogocephala	28.78	71.22	0.00	7.29	1938.35	0.54	0.26	-	-	46.58	61.30	32.18
Mikania sessilifolia	23.68	76.32	0.00	6.44	538.93	0.28	0.56	44.53	2.15	31.46	48.46	24.79
Miconia theaezans	36.22	63.78	0.00	4.99	2772.32	0.42	0.48	45.18	1.96	40.85	52.28	37.75
Myrcia splendens	18.31	81.69	0.00	6.13	801.51	0.50	0.33	42.74	2.09	49.49	58.35	41.00
Ossaea congestiflora	30.76	69.24	0.00	5.02	1396.16	0.20	0.99	50.90	2.15	36.26	52.34	36.72
Palicourea rigida	71.79	28.21	0.00	6.36	21143.43	0.39	0.41	41.82	2.01	30.66	24.51	-
Periandra mediterrânea	21.67	78.33	0.00	6.30	1022.54	0.34	0.46	43.29	1.90	46.59	62.81	44.54
Peixotoa tomentosa	36.59	63.41	0.00	6.50	4181.14	0.29	0.55	38.82	1.79	49.16	61.76	40.58
Pleroma heteromallum	50.10	49.90	0.00	7.62	4321.27	0.19	0.72	40.14	1.82	31.98	39.47	22.75
Solanum subumbellatum	18.82	81.18	0.00	6.33	724.71	0.29	0.54	47.78	2.03	44.96	52.52	35.57
Stachytarpheta glabra	27.02	72.98	0.00	9.40	511.47	0.29	0.37	36.31	2.48	27.63	63.07	-
Symphyopappus angustifolius	12.44	87.56	0.00	7.93	163.08	0.39	0.33	35.63	1.69	33.17	55.40	35.70
Trembleya laniflora	24.77	75.23	0.00	5.40	1373.70	0.31	0.73	51.81	1.88	46.32	43.25	39.70
Trixis vauthieri	32.38	55.83	11.79	13.31	1829.59	0.20	0.39	32.81	1.97	33.71	59.25	23.32
Vellozia compacta	17.99	82.01	0.00	6.16	554.47	0.42	0.40	36.31	1.79	41.10	-	-
Vellozia intermedia	32.36	67.64	0.00	6.75	2171.24	0.42	0.39	37.85	1.98	41.92	-	-
Vellozia variabilis	33.43	66.57	0.00	6.49	2024.99	0.36	0.44	46.28	1.82	38.84	-	-
Vochysia thyrsoidea	31.00	69.00	0.00	3.25	3998.93	0.47	0.66	55.23	2.01	38.43	36.48	30.30

Species	BDMC	WD	BD	SBL	LMF	PL	BLABL	LNBL	LAR	H
Miconia pepericarpa	42.26	0.61	0.47	5.32	0.86	8.26	9.40	0.69	11.17	213.00
Mimosa pogocephala	47.02	0.70	0.56	8.61	0.85	8.70	25.22	1.28	14.76	105.00
Mikania sessilifolia	32.23	0.50	0.35	12.61	0.87	3.38	8.88	1.63	4.91	179.00
Miconia theaezans	35.32	0.62	0.40	6.52	0.76	12.26	14.25	0.54	16.13	121.00
Myrsine lancifolia	45.27	0.60	0.51	5.21	0.95	5.27	20.85	4.01	5.65	189.00
Myrcia splendens	47.71	0.67	0.56	4.99	0.84	5.79	12.02	1.81	6.88	182.00
Ossaea congestiflora	38.81	0.61	0.43	12.93	0.87	4.11	13.46	1.04	10.55	67.00
Palicourea rigida	19.23	0.27	0.17	6.26	0.88	-	114.79	0.55	42.62	73.00
Periandra mediterrânea	47.51	0.77	0.56	9.10	0.96	2.35	19.73	1.96	8.68	67.00
Peixotoa tomentosa	47.93	0.69	0.52	6.62	0.82	7.89	34.24	0.82	22.95	159.00
Pleroma heteromallum	32.08	0.45	0.35	8.28	0.87	13.48	109.66	2.74	26.27	196.00
Solanum subumbellatum	38.01	0.56	0.41	7.42	0.91	5.14	13.14	1.81	6.43	88.00
Stachytarpheta glabra	33.98	0.65	0.35	7.87	0.89	-	5.80	1.15	4.80	148.00
Symphyopappus angustifolius	35.24	0.67	0.36	9.09	0.83	4.19	2.78	1.47	1.89	191.00
Trembleya laniflora	36.35	0.50	0.33	6.75	0.84	11.37	14.09	1.01	10.32	117.00
Trixis vauthieri	25.24	0.61	0.24	5.33	0.92	6.46	165.82	9.49	15.83	215.00
Vellozia compacta	-	-	-	-	-	-	-	-	-	161.00
Vellozia intermedia	-	-	-	-	-	-	-	-	-	90.00
Vellozia variabilis	-	-	-	-	-	-	-	-	-	112.00
Vochysia thyrsoidea	33.28	0.42	0.30	5.52	0.87	13.13	70.86	1.78	16.84	287.00

4 Discussion

There was a clear plant trait syndrome differentiation between soil physical/chemical characteristics in the *campo rupestre* (Figure 2 and 5), corroborating the hypothesis (i) that the ecological strategy of vegetation in *campo rupestre* is mainly associated with conservative use of resources. This hypothesis predicts that, trait patterns along LES, WS and SS are driven by soil parameters in *campo rupestre* (Negreiros et al., 2014; Silveira et al., 2016; Fernandes, 2016b). In general, in the iron substrate habitats we observed plots with potentially lower water availability (inferred by higher concentration of coarse sand and clay). In contrast, in the quartzite substrate, especially in the grassland habitat, we observed a greater tendency to water retention in the soil (inferred by less coarse sand and more silt). In lower water retention habitats, the vegetation possessed denser tissues and smaller leaves, leading to more stress-tolerant communities. In habitats with greater tendency to retain water, plants had larger of leaves and more photosynthetically active tissues, leading to communities composed by relatively more competitive plants. The observed patterns of trait display are in accordance with the fast-slow plant economic spectrum (Reich, 2014). The PES predicts a tendency of plants that features a conservative use of resources in one organ will require to be slower in other functions, and the contrary is also true, be acquisitive at organ level will require to have a fast metabolism in all plant physiological functions (i.e. an integrated response) (Grime, 1977; Enquist, 2002; Reich, 2014; Poorter, Castilho, Schietti, Oliveira, & Costa, 2017).

4.1 Importance of soil physical proprieties

The straight association between ecological strategies, and coarse sand and silt indicates that water availability could be potentially more important than nutrient concentration for the development of plant species in *campo rupestre*. A possible explanation relays in the fact that *campo rupestre* ecosystem has extreme low nutrient concentration (Negreiros et al., 2009; Messias, Leite, Neto, Kozovits, & Tavarez, 2013; Fernandes et al., 2016ab; Schaefer et al., 2016). The low nutritional status of *campo rupestre* is mainly caused by its resistant and poor nutrient parent rock

and its highly lixiviate soils (Benites, Schaefer, Simas & Santos, 2007; Schaefer et al., 2016). Negreiros et al. (2014), proposed that soil texture, pH and water retention, but no nutrient concentration, should be the main edaphic drives to cause habitat variation in *campo rupestre*. The presence of more nutrients it is not necessarily associated with nutrient availability to plant uptake, once nutrient absorption depends on water flux from soil to plant root system (Lambers & Oliveira, 2019). Therefore, to fully appreciate the role of plant ecological dynamics in these harsh habitats it is important to analyze not only soil nutritional status, and broader properties of soil, but also plant nutrient and water uptake.

Nutrient concentration was relatively higher in the ironstone habitat soil compared to the quartzite habitat soils. However, we also found a greater proportion of clay in those iron rich habitats. Concentration of clay is directly related with soil water retention, once the small sized particles that compose clay have more small soil pores that create a large suction tension hampering water movement in the soil and to the plant (i.e., highly capillarity effect) (Yang et al., 2014; Lambers & Oliveira, 2019). Additionally, in some ironstone plots a greater proportion of coarse sand was observed. Coarse sand is related with water drainage, hindering water soil retention. Thus, water availability to plant use is potentially diminished under greater concentration of coarse sand (Bernard, Kroener, Vontobel, Kaestner, & Carminati, 2016; Lambers & Oliveira, 2019). In the other hand, the greater proportion of silt and less concentration of coarse sand in quartzite habitats may favor water retention and absorption by plants (Lambers & Oliveira, 2019). Also, the highly dense graminoid vegetation that is usually present in more grassy habitats can better stabilize soil due to root structure. In turn, the most stabilized soils can potentially enhance water storage in their structure and water availability for the plants. The differential water soil retention is long known to affect plant strategies and niche partition (e.g., Silvertown, Araya, Gowing, 2015). Species tends to specialize in niche space where they best perform once they are susceptible to trade-offs of water use efficiency (Silvertown et al., 2015). From this perspective, habitats with low water availability will tend to select species with greater water use conservation, and the opposite array of traits is also true to habitats with greater water availability. Therefore, water flux and storage in soils may be one of the main drivers of plant ecological specialization in *campo rupestre*.
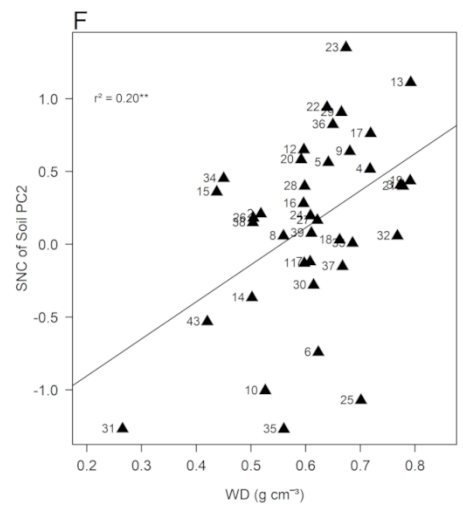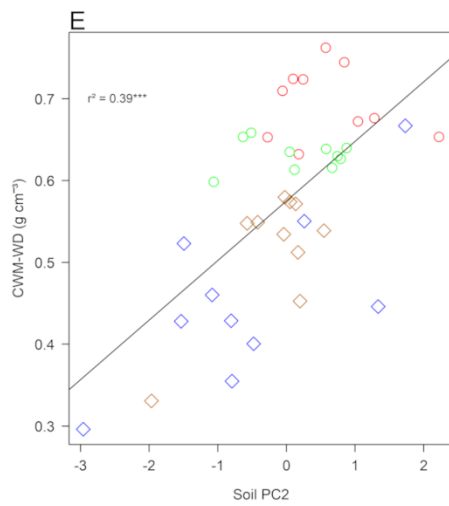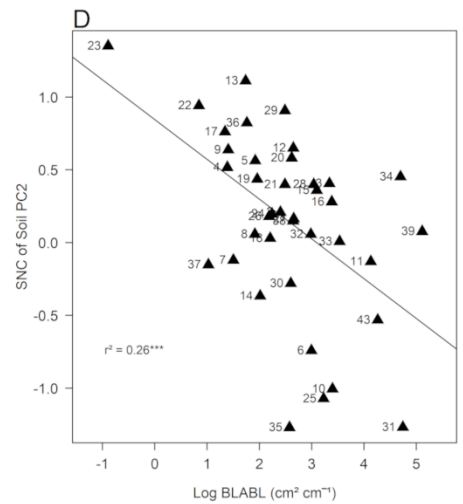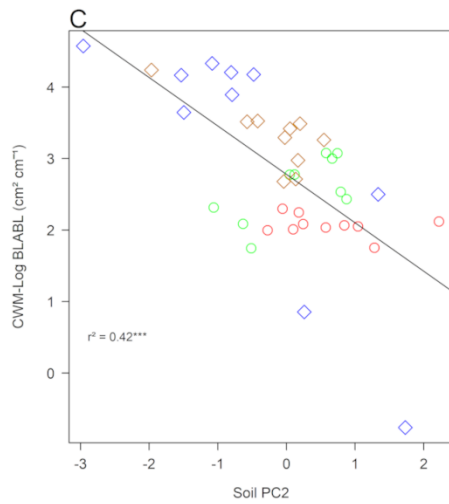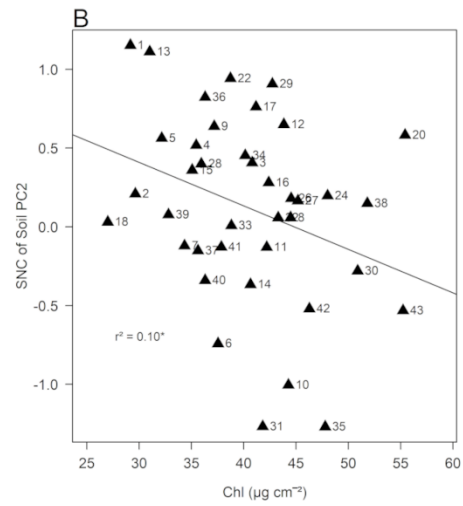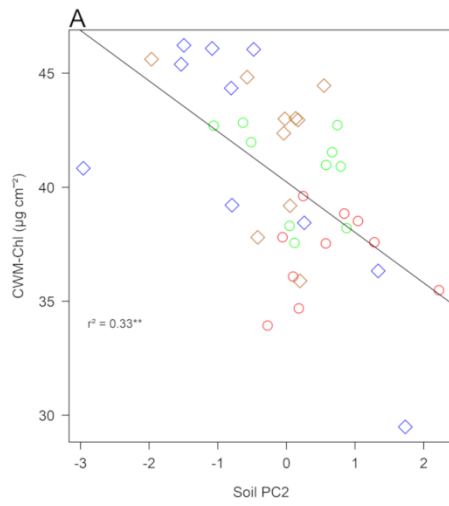
FIGURE 5 Significant linear regressions of CWM key traits × soil PC2 axis, and SNC × mean trait values of shrub species, in the campo rupestre habitats, southern portion of Espinhaço mountains range, Minas Gerais, Brazil. r² are shown. * = p value <0.05, ** = p value <0.01, *** = p value <0.001. Chl = chlorophyll content, WD = wood density and BLABL = Branch leaf area per branch length. Red circles = canga couraçada plots, green circle = canga nodular plots, blue diamond = quartzitic grassland plots, orange diamond = quartzitic outcrop plots. Triangle and respective number = species, where *1 = Actinocephalus bongardii, 2 = Ageratum fastigiatum, 3 = Banisteriopsis malifolia, 4 = Baccharis reticularia, 5 = Baccharis serrulata, 6 = Campomanesia adamantium, 7 = Chromolaena barbacensis, 8 = Chromolaena squalida, 9 = Diplusodon hirsutus, 10 = Eremanthus glomerulatus, 11 = Eremanthus incanus, 12 = Eriope macrostachya, 13 = Heteropterys umbellata, 14 = Hyptis proteoides, 15 = Jacaranda caroba, 16 = Leandra aurea, 17 = Lippia grata, 18 = Lippia lupulina, 19 = Lychnophora pinaster, 20 = Maytenus gonoclada, 21 = Miconia pepericarpa, 22 = Miconia theaezans, 23 = Microlicia martiana, 24 = Microstachys corniculata, 25 = Mikania sessilifolia, 26 = Mimosa calodendron, 27 = Mimosa pogocephala, 28 = Myrsine lancifolia, 29 = Myrcia splendens, 30 = Ossaea congestiflora, 31 = Palicourea rigida, 32 = Periandra mediterranea, 33 = Peixotoa tomentosa, 34 = Pleroma heteromallum, 35 = Solanum subumbellatum, 36 = Stachytarpheta glabra, 37 = Symphyopappus angustifolius, 38 = Trembleya laniflora, 39 = Trixis vauthieri, 40 = Vellozia compacta, 41 = Vellozia intermedia, 42 = Vellozia variabilis, 43 = Vochysia thyrsoidea.*

4.2 Ecological trade-offs and synergies

Our data set illustrates plant biomass allocation in different soil conditions. This pattern is in accordance with Reich's (2014) plant economic spectrum hypothesis and architectural traits trade-off. In turn, both plant economic spectrum and constrains of architectural traits are in accordance with biomechanical and metabolic scaling conceptual frameworks (see Díaz et al., 2016; Messier et al., 2017). These frameworks support the view that plant functions are integrated at whole plant level either by metabolic and/or biophysical constrains, and this would restrict trait array in few possibilities. Traits are not independently formed, and very often the investment in one trait is constrained by formation of another trait (Kleyer & Minden, 2015; Laughlin & Messier, 2015). In this sense, biomechanical view predicts that biomass allocation and plant form should be either: associated in synergy, and investment in one trait should be accompanied by investment in other trait; or, the allocation in one trait should be related with a trade-off in other function (Enquist, 2002; Kleyer & Minden, 2011). For example, greater leaf density may constrain petiole dry mass values due to a biomechanical propriety, once light petioles cannot sustain a high leaf biomass. In this way, a plant would face a synergy related to resource allocation. Similarly, from a metabolic point of view, high metabolic leaves must be highly nutrient, and water supplied, in order to maintain their metabolic activity. Thus, it would be expected that roots, stems and petioles would

be associated with functions that allows a greater water flux. The observed coordination of functions among organs in our data set, reinforce the idea of investments in one kind of function at organ level is only affordable when other organs share similar functions (Westoby & Wright, 2006; Reich, 2014; Dwyer & Laughlin, 2017). Otherwise, experimental studies at this end are called for.

The PCA based on traits and CWM and SNC regressions shows that plots related to soils with lower water retention capacity were composed by traits related with functions such as resource conservation, mechanical support (Figures 4 and 5). Traits of density tissue and dry matter content in leaves and branches were highly positive correlated. High dry matter content and tissue density are associated with highly organized cells with thick cuticle cell walls, and small cell interspaces (Witkowski & Lamont 1991; Westoby et al., 2002; Chave et al., 2009). In leaves, high cell packaging difficult leaf gas exchange and water transport, slowing down growth metabolism (Niinemets, 2001; Reich, 2014). Similarly, high values of WD and WDMC are related with more structural tissue (fibers) and less vessels area and parenchyma in stem (Ziemińska et al., 2013). Consequently, is expected a higher water transport safety due to diminished vessels lumen area, thus decreasing the propensity of drought induced xylem cavitation (Preston, Cornwell, & DeNoyer, 2006; Chave et al., 2009; Ziemińska et al., 2013). These plots had plants with a great number of leaves per branch length but with a relatively smaller total leaf surface area. Larger leaves tend to have a thick boundary layer when compared to small leaves. The thicker boundary layer is the greater is the tendency of increase leaf temperature. Thus, to avoid degradation of photosynthetic molecules plants need to diminish leaves surface temperature. An alternative to do that is by increasing leaf transpiration. However, in hot and watery limited environments, an increase in leaf transpiration without increase photosynthesis can be dangerous to plant performance. Therefore, produce various and smaller leaves can be advantageous in habitats with less water availability because of decrease of surface area (Westoby et al., 2002). Also, these leaves accumulate a greater proportion of mass, reinforcing strategies of conserved water use. Lastly, it was observed a greater concentration of Flav on leaves in these plots. High Flav indicates communities more resistant to UV-B radiation as well as to some herbivores and pathogens (Coley, Bryant, & Chapin, 1985). Together, the above described trait syndromes, indicate a tendency of diminishing water movement in vessels and loss at leaf surface. The lower water flux is related with a slow metabolism and growth rates (Preston et al., 2006; Chave et al., 2009; Reich, 2014).

Consequently, it is likely to an increased pay-back time and plant life span in those plots (Marba, Duarte, & Agustí, 2007).

Habitats on soils likely to retain more water were associated with more resource acquisitive functions, higher metabolic activity and traits related to softer tissues. Larger, thicker and potentially more photosynthetically active leaves were organized in lighter branches (Figures 4 and 5). Greater leaves are likely to increase surface leaf area per branch length. The relatively greater water demand due to greater leaf surface area could explain that less dense branches associated with it; namely, bigger vessels should be related with bigger leaves (Chave et al., 2009; Reich, 2014; Kleyer & Minden, 2015; Poorter et al., 2017). Greater leaves might be associated with elongated branches (and therefore, greater rates of stem elongation and low tissue density) to increase leaf spacing and avoid self-shading (Westoby et al., 2002; Poorter, 2008). However, in our data set, SBL and LA were not correlated indicating that this association may be more relevant for plant phenotype in less sun exposed habitats (Westoby et al. 2002; Poorter, 2008). Additionally, both high LD and LT are strategies related with plant development in stressed locations with low water availability (Vendramini et al., 2002). However, species with high LT tend to be more water dependent than sclerophyllous species (Witkowski & Lamont, 1991). In terms of ecological strategies, plants with high LT or LD could be characterized as a slow growing species, that invests more in tissue durability than in metabolic activity (Niinemets, 2001; Vendramini et al., 2002). However, we found that LT was positively related with Chl content and traits associated with competitiveness strategy. Indeed, LT is positively related cell number per unit of area, thus could scale positively with Chl content if mesophyll cells are associated with photosynthetic metabolism (Niinemets, 1999). Therefore, the greater water availability to plants, the greater is the tendency of leaf investments in relation to area and thickness, less investments in stems support and greater investments in photosynthetic tissues (Olson et al., 2009).

4.3 Central traits and modularity

The trait patterns of trade-offs and synergies described at plot level (from PCA and CWM analysis) were in accordance with our network analysis at individual level. Traits from different

organs related to functions of resource acquisition and water transport were positive correlated. Traits from mechanical support and resource conservation were positively correlated. We observe that traits of LES, WS and SS were arranged in a great network highly correlated. However, the modularity test shows that three major groups were formed. Traits from the same functions tend to be more correlated within than among functions. Thus, structural and conservative traits were tightly correlated. While, acquisitive and sap transport traits were more correlated. This modularly arrangement agrees with the hypothesis (ii) of trait network organization, in which all organs and trait spectra would be correlated but within function the association will be stronger (Westoby, 2002; Reich, 2014; Kleyer et al., 2019). The trait modularity pattern indicates that form and functions in different organs tend to be integrated and their effects should scale positively in plant phenotype.

We observed traits from LES and SS as the more central traits in linking traits modules. From those LNBL, SLA, BLABL, PL shows a greater centrality; thus, environmental pressure on these traits will lead to changes in biomass allocation, organ display, and plant functions. Messier et al. (2017), also found architectural traits as a main integrator of plants phenotype. Indeed, several physiological functions are coordinated by architectural traits. These functions include organ display, mechanical support and sap transport. The coordination of these function is associated with trade-offs of resource allocation, in which is again in accordance of biomechanical restriction and metabolic scaling in above session described. In water limited, poor nutrient and highly sunny environments, such as *campo rupestre* investments in one kind of strategy will only be reasonable if all organs share similar functions (Dwyer et al., 2017). For example, an increase in BLABL will lead to a greater investments of branch leaf area in relation to branch mass, leading to a positive scale with LAR and LA. Simultaneously, it will be done less investments in stems and bark, in order to allow water flux from root to leaf. Leading to a decrease in BD, WD, BDMC and WDMC values, that favor water movement. Also, larger leaves cannot be too heavy; thus, LD will decrease, and LT will tend to increase with increasing values of BLABL. By contrast, lower values of BLABL will be associated with the opposite array of traits. Therefore, due to the greater importance of architectural traits to link forms and functions in individual plant phenotype, it is reinforced again the trend of plant in *campo rupestre*, and possibly in harsh environments in general, to have a positive and coordinated integration among organs (see Dwyer et al., 2017).

It is worth to note that PL and LNBL that does not respond to environment at plot level had a great importance in trait-trait coordination at individual level. This result highline the importance to observe trait × trait integration to evaluated plant response to environmental changes (Kleyer & Minden, 2015). Physiological adjustments to functions such as growth and persistence not necessary respond to extrinsic factors. However, they are intrinsic related with a whole plant metabolism and thus can respond indirectly to the environment.
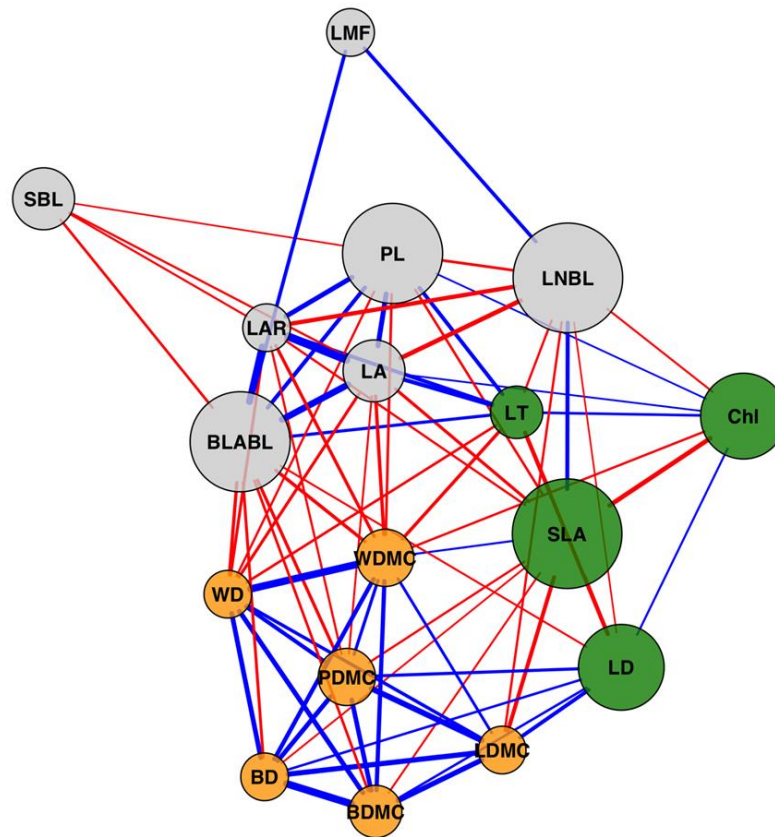
FIGURE 6 Trait network at individual level in campo rupestre habitats, Brumadinho, Minas Gerais, Brazil. The more central traits in the 2D plane do more connections with other traits. Only significant correlations from 0.2 to 0.9 are show. Blue and red lines represent positive and negative correlations, respectively. The thicker the line greater is the correlation. Node size are pondered by betweenness. Grey nodes are related to architecture, green nodes represent acquisition-conservative functions, and yellow nodes represents support-transport functions. SLA = specific leaf area, LA = leaf area, LD = leaf density, LT = leaf thickness, Chl = chlorophyll content LDMC = leaf dry matter content, WDMC = wood dry matter content, PDMC = petiole dry matter content, BDMC = bark dry matter content, WD = wood density, BD = bark density, SBL = specific branch length, LMF = leaf mass fraction, PL = petiole length, BLABL = branch leaf area per branch length, LNBL = leaf number per branch length, and LAR = leaf area ratio are shown.

TABLE 5 Blomberg's K for phylogenetic signal of evaluated traits in campo rupestre habitats, Brumadinho, Minas Gerais, Brazil. Significant values (p value < 0.05) are in bold.

	K	*p*
Competitiveness	0.50	0.181
Stress-tolerance	0.44	0.418
Ruderality	0.40	0.618
Specific Leaf Area	0.50	0.207
Leaf Area	0.62	0.191
Leaf Density	**0.61**	**0.017**
Leaf Thickness	0.52	0.119
Chlorophyll	0.52	0.132
Flavonoid	0.51	0.163
Leaf Dry Matter Content	**0.56**	**0.033**
Wood Dry Matter Content	**0.65**	**0.014**
Petiole Dry Matter Content	0.64	0.428
Bark Dry Matter Content	**0.56**	**0.049**
Wood Density	**0.67**	**0.007**
Bark Density	**0.67**	**0.005**
Specific Branch Lenght	0.29	0.946
Leaf Mass Fraction	0.48	0.278
Petiole Lenght	**0.61**	**0.039**
Branch Leaf Area per Leaf Length	0.44	0.464
Leaf Number per Branch Length	0.47	0.337
Leaf Area Ratio	0.57	0.085
Maximum Height	0.39	0.730

4.4 Traits phylogenetic signal

We found a conservative phylogenetic signal in some key functional traits with a random pattern of distribution (Table 3). These data only corroborate partially the hypothesis (iii) that predicts a low phylogenetic signal due to nature of the analyzed traits that lies in resource allocation in fast/slow strategies. It is worth to note, that all traits that showed phylogenetic signal, but PL, where related with tissue quality. This evidence indicated a possible trend of functional

convergence in terms of resource allocation, across plants lineage of the *campo rupestre* that results in a similar response to environmental filters (Kraft, Cornwell, Webb, & Ackerly, 2007). In other words, the same trait expression may be observed across plants from very different lineages, reinforcing a tendency of *campo rupestre* shrub vegetation and, probably OCBILs in general, to show similar responses to the same problem: protection of photosynthetic apparatus from strong winds, high solar radiation and low water availability (Hopper, 2009; Silveira et al., 2016).

5 Conclusions

Along with the study of Negreiros et al. (2014) we are one of the first studies that evaluated the harsh and highly threatened mountaintop *campo rupestre* habitats by a functional approach. The main response of *campo rupestre* shrub communities in relation to trait patterns favored a convergence in relation to a conservative use of resource. Our data set evidenced trade-offs between traits related to plant economics and leaf size-twig size spectrum that are associated with species performance and, spatial partitioning along soil environment. The differential trait syndrome among habitats highlines the importance of analyzing multiple dimensions of attributes to understand allocation patterns and ecological trade-off. We observe a pivotal role of architectural traits to connect form and functions at different organs, and we highline that trait covariation is a good proxy of plant performance and fitness. Therefore, covariation should be included in studies of community assembly. We show that most of traits phylogenetic conserved showed a low signal, indicating a possible functional convergence in relation to resource/acquisition and architectural traits across plant lineages of *campo rupestre*. Lastly, our results help to generate insights of patterns of trait and species distribution based on their ecological requirements in OCBILs habitats worldwide.

Acknowledgments

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