

**Diversity and life-forms of a woody-herbaceous community on the quartzite rocky complexes in the Brazilian Iron Quadrangle**  
**Diversidad y formas de vida de una comunidad leñosa-herbácea en los complejos rocosos de cuarcita del Quadrilátero Ferrífero brasileño**

Wesley Alves Silva<sup>1</sup>

Pedro Manuel Villa<sup>1,2</sup>

Carlos Ernesto Gonçalves Reynaud Schaefer<sup>3</sup>

Walnir Gomes Ferreira-Júnior<sup>4</sup>

Prímula Viana Campos<sup>1</sup>

Izabela Ferreira Fialho<sup>1</sup>

Andreza Viana Neri<sup>1</sup>

1. Universidade Federal de Viçosa, Departamento of Plant Biology, Laboratory of Ecology and Evolution of Plants, Campus Universitário, 36570-900, Viçosa-MG, Brazil; wesleyalvesbiologo@gmail.com, andreza.neri@ufv.br, primula.vc@gmail.com, izaaff.7@gmail.com

2. Fundación para la Conservación de la Biodiversidad, 7101, Mérida, Mérida, Venezuela; villautana@gmail.com

3. Universidade Federal de Viçosa, Departament of Soil, Campus Universitário, 36570-900, Viçosa-MG, Brazil; carlos.schaefer@ufv.br

4. Instituto Federal de Educação, Ciência e Tecnologia do Sul de Minas Gerais, Campus Machado, Rodovia MG-453, km<sup>3</sup>, 37750-000 Machado, MG, Brazil; walnir.ferreira@gmail.com

Received 24-IV-2018

Corrected 19-IX-2018

Accepted 22-II-2019

**Abstract**

Although *campos rupestres* are iconic rock outcrops with a high biogeographic value in Brazilian highlands, little is known about the drivers responsible for the plant community pattern. We studied the diversity and life forms of the woody and herbaceous components occurring along different phytophysiognomies of the quartzite rocky complexes in highlands of the Quadrangle, Minas Gerais State, Brazil. A total of 130 plots were allocated in three phytophysiognomies along the pedogeomorphological gradient: i) herbaceous *campo rupestre*; ii) upper and lower strata of montane forest (capão florestal) and iii) scrub. Overall, 4 446 individuals were sampled, distributed among 218 species, especially from families: Asteraceae, in general; Myrtaceae, in the woody community; and Poaceae and Cyperaceae, in the herbaceous community. Species diversity, life forms, and abundance showed differences between phytophysiognomies. The most frequent life form was phanerophyte (montane forest and scrub), followed by hemicryptophyte (herbaceous *campo rupestre*). Our study reveals marked differences in the floristic composition, species richness, and life form spectrum among phytophysiognomies on a local scale. Such differences probably indicate that there is a high environmental heterogeneity at a small spatial scale.

**Key words:** *campo rupestre*, highlands, phytophysiognomies, richness; rock outcrop.

## Resumen

Aunque los *campos rupestres* son afloramientos rocosos icónicos con un alto valor biogeográfico en las tierras altas de Brasil, se sabe poco sobre los modeladores responsables de los patrones de comunidades vegetales. Estudiamos la diversidad y las formas de vida de los componentes leñosos y herbáceos que se encuentran a lo largo de diferentes fitofisionomías de los complejos rocosos de cuarcita en las tierras altas del Cuadrilátero Ferrífero brasileño, Estado de Minas Gerais, Brasil. Se realizaron un total de 130 parcelas en tres fitofisionomías a lo largo del gradiente pedogeomorfológico: i) *campo rupestre* herbáceo; ii) estratos superior e inferior del bosque montano (*capão florestal*) y iii) matorral. En general, se muestrearon 4 446 individuos, distribuidos en 218 especies, especialmente de familias: Asteraceae y Myrtaceae en la comunidad de leñosas; y Poaceae y Cyperaceae, en la comunidad herbácea. La diversidad de especies, las formas de vida y la abundancia mostraron marcadas diferencias entre las fitofisionomías. La forma de vida más frecuente fue la fanerófita (bosque de montaña y matorral), seguida de hemicriptófita (*campo rupestre* herbáceo). Nuestro estudio revela diferencias marcadas de la composición florística, la riqueza y el espectro de las formas de vida entre fitofisionomías en los complejos rocosos a escala local. Tales diferencias probablemente indican que existe una alta heterogeneidad ambiental en pequeñas escalas espaciales.

**Palabras clave:** afloramiento rocoso, campo rupestre, fitofisionomías, riqueza, tierras altas.

## Introduction

High altitude rocky complexes represent important centers of plant endemism in South America (i.e., *tepui*s, *campo rupestre*); mainly driven by high environmental heterogeneity at small spatial scales (e.g., Barthlott, Mutke, Rafiqpoor, Kier, & Kreft, 2005; Fernandes, 2016). Rocky complexes, known as *campo rupestre*, are important terrestrial hotspots (Alves Silva, Oliveira, & Medeiros 2014; Silveira et al., 2015), and are found on the high peaks of the main mountain ranges, that mainly occur in the Espinhaço Range mountain in Southeastern Brazil (Giulietti, Pirani, & Harley, 1997; Alves et al., 2014). These singular landscapes occur mainly on quartzite and ironstone formations, mostly above 900 m (a.s.l.) and up to 2 033 m (Benites, Schaefer, Simas, & Santos, 2007; Silveira et al., 2015). They can occur in association with different surrounding vegetation types, such as Cerrado (Neotropical savanna) and Atlantic Forest, as well as in Caatinga, Cerrado and Atlantic Forest transition (central and Northern of the Espinhaço Range). The study of plant communities in these rocky complexes is becoming increasingly relevant since they have been recently proposed as one of the world's Old Climatically-Buffered Infertile Landscapes (OCBILs), and due to its high local endemism (e.g., Echternacht, Trovó, Oliveira, & Pirani, 2011; Silveira et al., 2015; Pontara, Bueno, Rezende, Oliveira-Filho, Gastauer, & Meira-Neto, 2018). *Campo rupestre* is described primarily as a more or less continuous grassy-shrubby vegetation mosaic with scattered rocky outcrops of quartzite that harbor small shrub and sub-shrub patches (Giulietti, Pirani, & Harley, 1997). Patches of transitional vegetation such as cerrado, and relictual montane forests also occur within the *campo rupestre* landscape, also known as *capão florestal* (montane forest) and scrub (Alves et al. 2014). Thus, some studies have shown that high environmental heterogeneity (i.e., local

topography and soils) determine plant communities assembly forming patches mosaic (Giulietti et al., 1997; Conceição & Giulietti, 2002; Fernandes, 2016). For instance, the vegetation cover at the Espinhaço Range consists of a mosaic of phytophysionomies, that encompasses i) forest formations associated with water catchments or lowland areas, ii) distinct savannah phytophysionomies; and iii) grassland formations (Silveira et al., 2015). However, there are still a limited number of studies that evaluate changes in floristic diversity and composition between phytophysionomies distributed along the same environmental gradient at a local scale.

The high altitude Brazilian rocky complexes comprises the largest areas of *campos rupestres*, which is the centre of diversity for many angiosperm groups and houses almost 15 % of the Brazilian vascular flora in an area corresponding to only 0.78 % of the country's land surface (Silveira et al., 2015). For instance, approximately 30 % of plant species of the Espinhaço Range are endemic to *campos rupestres* (Giulietti et al., 1997). Furthermore, one of the main issues raised when addressing rupestrian vegetation research is its biodiversity, which is not homogeneously distributed, with disproportionately high levels of diversity and endemism at local and regional scales (Fernandes, 2016; Silveira et al., 2015). In this heterogeneous environment the floristic spectra change in the different habitats, where the grasslands had a higher percentage of hemicryptophytes followed by chamaephytes; and the scrub boundaries are more phanerophytic (Caiafa & Silva, 2005; Conceição & Pirani, 2007).

In this context, understanding how the species diversity and species composition patterns of *campo rupestre* are distributed throughout different phytophysionomies represents an important challenge for improving the methods of conservation, restoration and management in high altitude rocky complexes. For example, most studies that discuss the premises for *campo rupestre* conservation are mainly based on grasslands, and we believe that conservation strategies should be planned along the phytophysionomical gradient, and a first step is describing patterns of diversity. For this reason, we analyzed the changes in the diversity and life forms of the woody-herbaceous community along a phytophysionomical gradient on the quartzite rocky complexes in the Brazilian Iron Quadrangle. In order to evaluate the ecological patterns of species diversity along the phytophysionomical gradient, we asked the following research questions: i) How does floristic composition, species diversity and life forms change between phytophysionomies? ii) Is there some decoupling in the richness and floristic composition between lower and upper strata of montane forest and scrub phytophysionomies? iii) What are the changes for community dissimilarity between phytophysionomies in quartzite rocky complexes, and iv) What are the changes for strata dissimilarity of montane forest and scrub phytophysionomies?

## Materials and methods

**Study area:** The study was conducted in a quartzite rocky complex area located in a conservation unit (20°10'10.98'' - 20°10'34.45'' S & 43°34'07.95'' - 43°36'50.39'' W). The area is located in the Eastern boarder of the Iron Quadrangle and encompasses the municipalities of Santa Bárbara and Ouro Preto, Minas Gerais State, Brazil. Climate in the region is (Cwa) according to Köppen classification, subtropical with dry winters and hot summers. Mean annual precipitation is 1 300 mm and mean annual temperature is 20 °C (Silva, 2013).

Three main phytophysognomies were studied along the pedogeomorphological gradient: i) herbaceous *campo rupestre* on Typical Dystrophic Regolith Neosol; ii) scrubs on Umbric Dystrophic Tb Haplic Cambisol; and iii) montane forest patch (*capão florestal*) on Typical Dystrophic Tb Fluvic Neosol.

**Vegetation sampling:** Sampling was performed from July 2011 through March 2012. Since the gradient is characterized by the presence of several phytophysognomies, we stratified the landscape, using plot sizes that were adequate to each predominant life form in each area. In the herbaceous *campo rupestre* we established eighty plots ( $1 \times 1$  m) for abundance sampling. For woody vegetation 20 plots ( $5 \times 5$  m) were randomly distributed along the scrub, and 15 plots ( $10 \times 10$  m) along the montane forest. In the scrub, all individuals presenting circumference at soil height (CSH)  $\geq 3$  cm were sampled, while in the montane forest sampling was performed of all individuals presenting circumference at 1.30 m from the soil (CBH)  $\geq 10$  cm. The number of plots in the montane forest was low because it was restricted in the only patch with limited area within the analyzed gradient. In scrub and montane forest we sampled the upper and lower vegetation strata separately (for more detail see Silva, 2013). Within each plot in the scrub and montane forest we delimited 20 and five plots ( $1 \times 1$  m) respectively to sample the lower stratum vegetation (Braun-Blanquet, Lalucat, & de Bolòs, 1979). In each plot, individuals per species were counted and identified to the species level and tagged for measurement. For species and family classification, the *Angiosperm Phylogeny Group III* system (APG III, 2009) was used.

**Life form:** The sampled species were classified according to Raunkiaer's life-form (Raunkiaer, 1934). The results were then graphically illustrated representing biological and vegetational spectra. When the number of individuals of each life-form is counted, instead of species, each class can be weighted by its abundance, resulting in the vegetation's biological spectrum (Raunkiaer, 1934).

**Quantification of biodiversity indices:** Measures of taxonomic diversity were calculated for each plot from the three phytophysognomies. Measures included species richness, Pielou's evenness and Shannon-Wiener's diversity index (Magurran, 2004). All diversity indices were calculated using the 'vegan' package (Oksanen et al., 2017) in the software R 3.2.2. (R Core Team, 2016).

**Data and statistical analyses:** Variables were tested for normal distribution with the Shapiro-Wilk test by evaluating the Q-Q plot (Crawley, 2013). To compare the means of the variables between phytophysognomies (i.e. richness, diversity indices, abundance) we used Kruskal-Wallis' test (for non-normally distributed data) followed by Dunn's test (Dinno, 2017). All these analyses were performed with the "stats" and "dunn.test" packages (Dinno, 2017). To verify whether the biological spectra differed among areas, we used the  $\chi^2$  (chi-square) test (Campos, Villa, Nunes, Schaefer, Porembski, & Neri, 2018).

We analyzed differences in species richness between the three phytophysognomies by using both sampled-based and individual-based rarefaction and extrapolation curves with the first Hill number (species richness,  $q = 0$ ) (Chao et al., 2014; Colwell et al., 2012; Jost, 2007). We analyze the difference in individual-based rarefaction and extrapolation curves between vegetation of the lower and upper strata of both montane forest and scrub phytophysognomies. Extrapolations were made from presence/absence data, being higher than twice the sample size (Colwell et al., 2012). Sample and

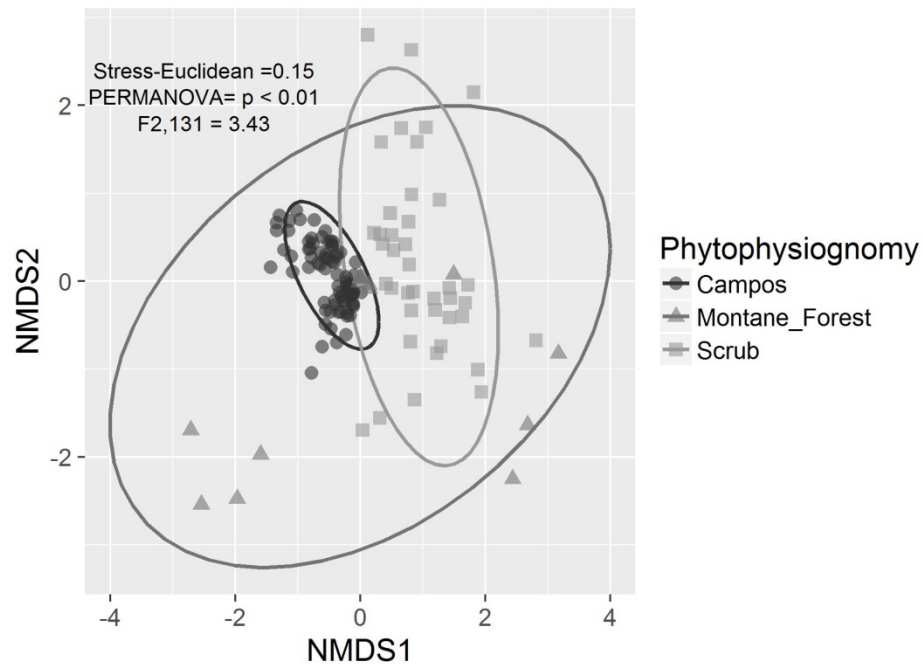
individual-based rarefaction/extrapolations were computed using the ‘iNEXT’ package (Hsieh, Ma, & Chao, 2016). Rarefaction was estimated as the mean of 100 replicated bootstrapping runs to estimate the 95 % confidence intervals. Whenever the 95 % confidence intervals did not overlap, species numbers differed significantly at  $P < 0.05$  (Colwell et al., 2012).

Non-metric multidimensional scaling (NMDS) was performed to examine differences between the sampled phytophysiognomies in terms of species composition, by assessing Euclidean dissimilarities. We performed the NMDS using the metaMDS function of the ‘vegan’ package (Oksanen et al., 2017). We also performed a permutational multivariate analysis of variance (PERMANOVA, 9 999 permutations) to determine the differences in species composition, by using the ‘adonis’ routine from the ‘vegan’ package (Oksanen et al., 2017). We examined the species composition similarity between phytophysiognomies, such similarity being represented by the mean pairwise similarity between plots in the same phytophysiognomy, and between strata (lower and upper) of montane forest and scrub phytophysiognomies. We furthermore used the abundance-weighted Bray-Curtis dissimilarity index between different phytophysiognomies plots (Villa et al., 2018a). To compare the means of the dissimilarities between strata by phytophysiognomy (i.e., montane forest and scrub) we used Student’s T-Test (Crawley, 2013).

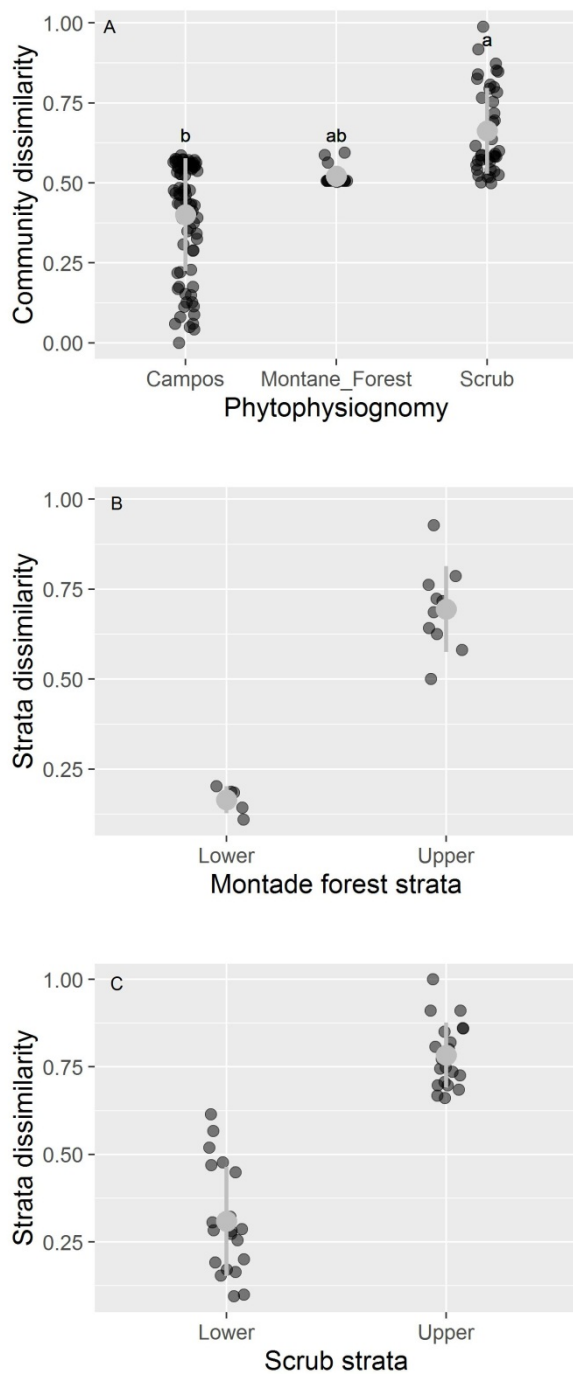
## Results

**Floristic composition:** Overall, 4 446 individuals were sampled, among 218 species, 112 genera, and 55 families. The richest families were: Asteraceae (27 species), Myrtaceae (22 species), Melastomataceae (17 species), Poaceae (13 species), Fabaceae and Rubiaceae (12 species each), Cyperaceae (eight species), Erythroxylaceae (six species), Convolvulaceae, Lauraceae, Malpighiaceae and Verbenaceae (five species each). Altogether, these families represented 62.79 % of the species sampled.

The NMDS showed that species composition varied considerably among phytophysiognomies, mainly among herbaceous *campo rupestre* with montane forest and scrubs (Permanova,  $P < 0.01$ ,  $F_{2,131} = 3.43$ ; stress = 0.15, Fig. 1). The NMDS ordination of species composition allowed for the distinction of three different groups, with the two principal dimensions explaining most of the variance among plots. On the other hand, we observed that species dissimilarity among *campos* (Bray-Curtis index ~ 0.30) and scrub (Bray-Curtis index ~ 0.70) phytophysiognomies plots was different. Montane forest presented intermediate values (Bray-Curtis index ~ 0.50) without difference with relation to *campos* and scrub (Fig. 2A). Species composition dissimilarity presented differences ( $P < 0.05$ ) between strata in both montane forest and scrub phytophysiognomies (Fig. 2B, Fig. 2C).



**Fig. 1.** Non-metric multidimensional scaling (NMDS) based on species composition on the quartzite rocky complexes in the municipalities of Santa Bárbara and Ouro Preto, Minas Gerais State, Brazil. Herbaceous *campo rupestre* is identified as Campos.



**Fig. 2.** Plant community dissimilarity of the species in different phytophysionomies of the quartzite rocky complexes, Iron Quadrangle, Minas Gerais State, Brazil. The dark gray circles represent the plots in A. different phytophysionomies, and in different strata, B. montane forest and C. The gray point and range indicates mean values and standard deviations. Different letters indicate significant differences ( $p < 0.05$ ) among the sampled phytophysionomies.

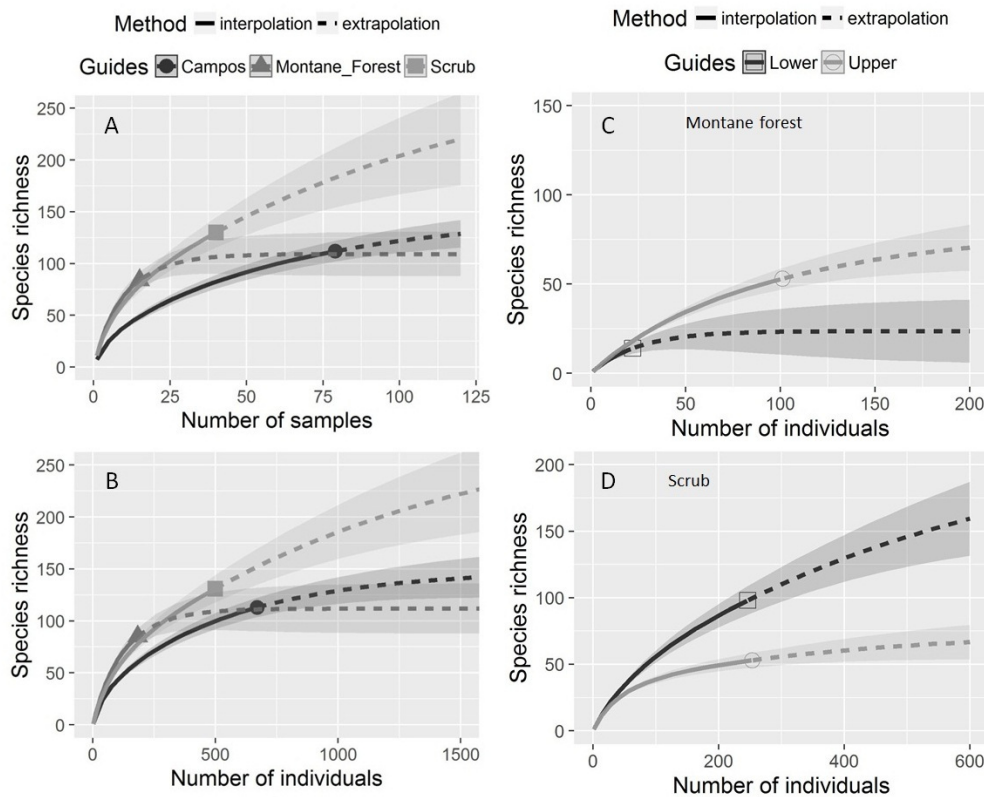
In herbaceous *campo rupestre* 3 413 individuals were sampled, among 107 species, 56 genera and 31 families. Asteraceae (22 species), Poaceae (nine species), Fabaceae and Cyperaceae (seven species each), Myrtaceae and Rubiaceae (five species each) were the richest families, representing 51.04 % of the species sampled in this phytophysionomy.

In the upper scrub stratum, 625 individuals were sampled, distributed among 52 species, 35 genera and 25 families. Myrtaceae was the richest family (10 species), followed by Melastomataceae (six species) and Fabaceae (five species). In the lower scrub stratum, 229 individuals were sampled, covering 73 species, 35 genera and 25 families. In this sampling, Poaceae (nine species), Melastomataceae (nine species), Hypericaceae (nine species), Rubiaceae (six species), Myrtaceae (four species), Asteraceae (eight species) and Fabaceae (three species) were the main families.

In the upper montane forest stratum, 141 individuals were sampled, encompassing 40 species, 25 genera and 24 families. The richest families were Myrtaceae (14 species) and Anacardiaceae (two species). In the lower montane forest stratum, 38 individuals were sampled, 13 species, 13 genera and 11 families. The richest families were: Fabaceae (eight species), Melastomataceae (six species), Aspleniaceae and Poaceae (five species each), Peraceae and Rubiaceae (four species each).

**Species diversity and abundance pattern:** We observe contrasting richness pattern between phytophysiognomies with differences using both sample-based and individual-based rarefaction and extrapolation curves (Fig. 3). Thus, rarefaction and extrapolation curves showed higher species richness in scrubs than in herbaceous *campo rupestre* with montane forest phytophysiognomies. Likewise, species richness curves showed significant differences between forest strata of montane forest and scrubs (Fig. 3).

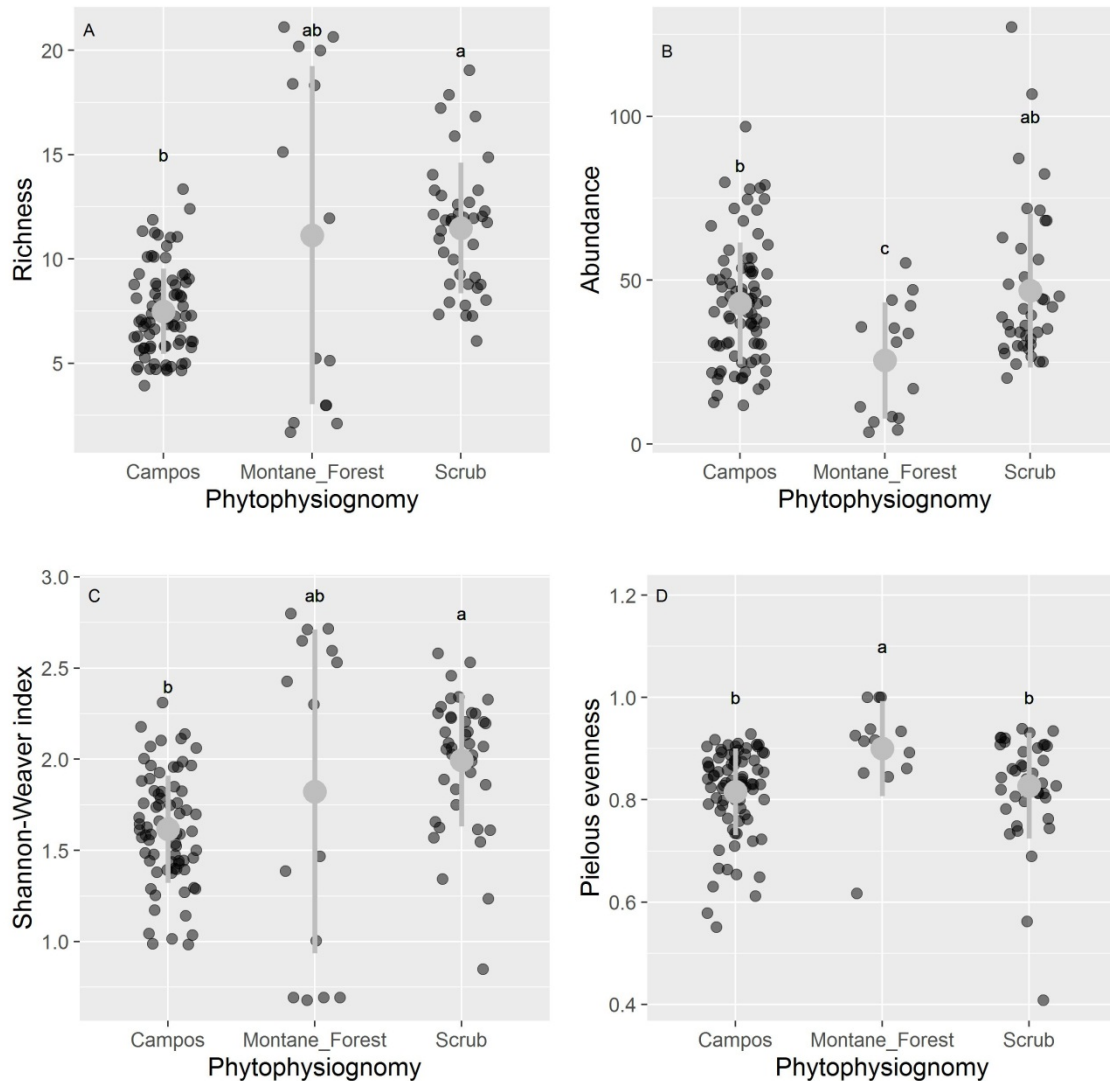
Species richness ( $\chi^2 = 34.36$ ,  $df = 2$ ,  $P < 0.001$ ), Shannon diversity index ( $\chi^2 = 24.62$ ,  $df = 2$ ,  $P < 0.01$ ), Pielou evenness ( $\chi^2 = 16.21$ ,  $df = 2$ ,  $P < 0.01$ ), and abundance ( $\chi^2 = 9.03$ ,  $df = 2$ ,  $P < 0.01$ ) showed differences between phytophysiognomies (post hoc Dunn's test  $P < 0.05$ , Fig. 4).



**Fig. 3.** Individual-based and sampled-based rarefaction (solid lines) and extrapolation curves (dashed lines) for the sampled areas in three phytophysiognomies (A-B), and Individual-based rarefaction and extrapolation curves in vertical richness distribution

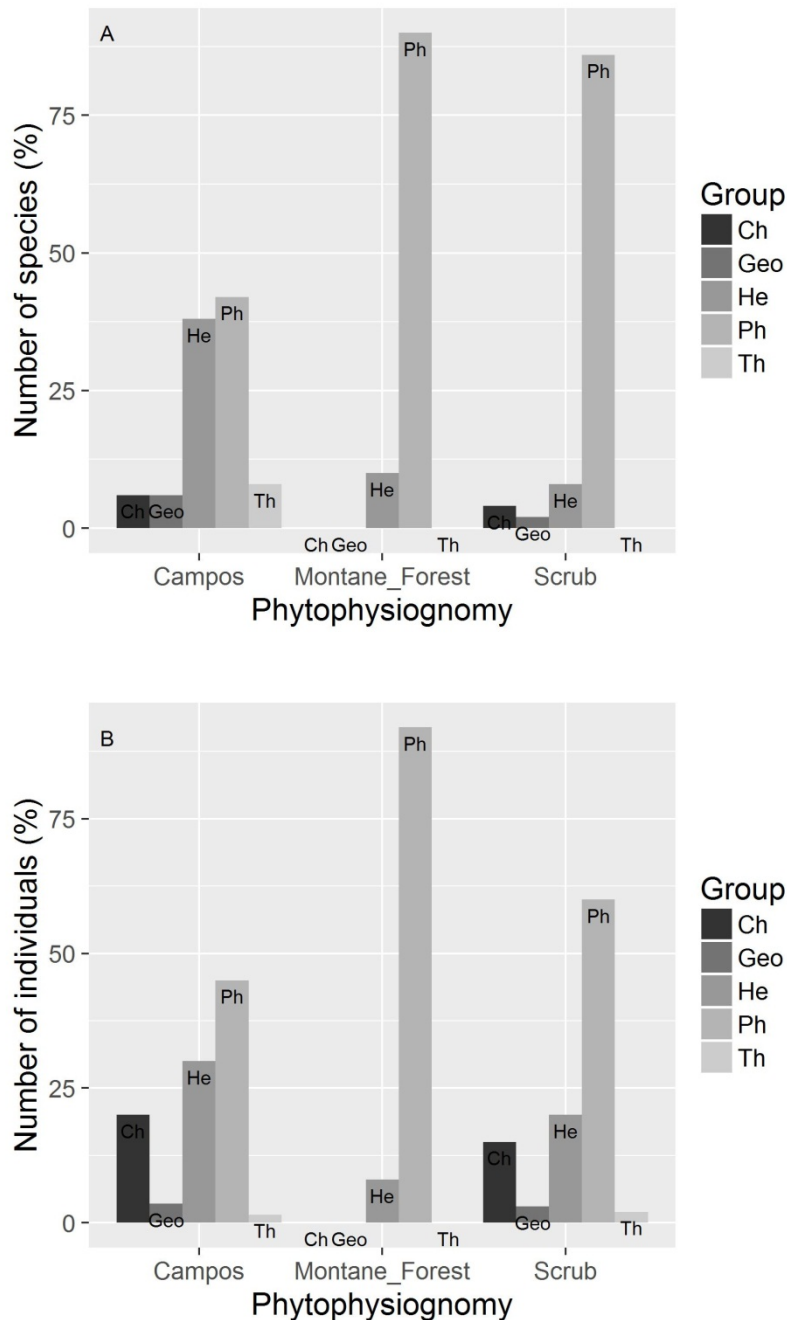


(lower and upper stratum) of diversity in C. montane forest and D. scrub. Herbaceous *campo rupestre* is identified as Campos. Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95 % confidence intervals. The filled circles represent the plots of herbaceous *campo rupestre*, triangles represent the montane forest patches and squares represent the scrubs. The empty circles and squares represent upper and lower respectively for both montane forest and scrub.



**Fig. 4.** A. Differences in species richness, B. abundance, C. Shannon-Weaver diversity and D. Pielou's evenness along different phytophysiognomies of the quartzite rocky complexes, Iron Quadrangle, Minas Gerais State, Brazil. Herbaceous *campo rupestre* is identified as Campos. The dark gray circles represent the plots in different phytophysiognomies. The gray point and range indicates mean values and standard deviations. Different letters indicate significant differences ( $p < 0.05$ ) among the sampled phytophysiognomies.

**Life forms:** There were significant differences in the proportion of the number of species ( $df = 8$ ;  $\chi^2 = 342.99$ ;  $p < 0.001$ ) and individuals ( $df = 8$ ;  $\chi^2 = 1\,157.59$ ;  $P < 0.001$ ) in all the life form between phytophysiognomies (Fig. 5). Among the sampled species, 140 were considered phanerophytes, 41 hemicryptophytes, 29 chamaephytes, five therophytes and three geophytes. Phanerophytes were the most abundant species and individuals ones, with 2 364 individuals, followed by hemicryptophytes (1 443 individuals), therophytes (265 individuals), geophytes (213 individuals) and chamaephytes (161 individuals).



**Fig. 5.** A. Biological spectrum and B. vegetation spectrum sampled along different phytophysiognomies of the quartzite rocky complexes, Iron Quadrangle, Minas Gerais State, Brazil. Herbaceous *campo rupestre* is identified as Campos. Phanerophytes (Ph),

hemicytrophites (He), chamaephytes (Ch), therophytes (Th) and geophytes (Geo) are indicated.

## Discussion

**Floristic composition:** Our results showed that species composition varied considerably among phytophysognomies. Asteraceae, the richest families in our study, were consistent with other floristic surveys performed in *campos rupestres* of the Iron Quadrangle and Espinhaço range (Conceição & Pirani, 2007; Mourão & Stehmann, 2007). Poaceae and Fabaceae was also among the most important ones. The success of these families may be due to their ability to colonize poor and shallow soils under high insolation, which are important environmental filters in these rocky complexes (e.g., Silveira et al., 2015; Zappi, Moro, Meagher, & Lughadha, 2017). Regarding distant ironstone, such as the Carajás Mountain, in the state of Pará, Northern Brazil, Fabaceae was reported to be the most important family in the shrubby ironstone *campo rupestre* (Nunes, 2009). In the Iron Quadrangle flora assessed in the present study, Fabaceae also appears frequently among the richest families. This species diversity pattern might be due to the genetic diversity, which results in morphological adaptations to several different environmental stresses (Oliveira, Souza, & Loiola, 2012), e.g. tolerance to desiccation and the ability to grow in dry open areas (Kellogg, 2001).

We observed that species similarity among herbaceous *campo rupestre* phytophysognomies plots was low in comparison to montane forest and scrubs. The biophysical drivers associated with the high environmental specificity of plant species probably explains the great differences in floristic similarity between rupestrian grasslands within the Espinhaço Mountains (Alves et al., 2014; Silveira et al., 2015). In this sense, recent studies show how both lack of nutrients and shallow soil substrate determine vegetation physiognomy (Alves et al., 2014), and are of critical importance to plant distributions in *campo rupestre* (Alves et al., 2014; Fernandes, 2016; Zappi et al., 2017). They also conclude that the use of environmental contrasts (geologically different substrates, open versus forested vegetation) provides a useful framework for investigating diversity patterns in *campo rupestre*.

**Species diversity and abundance pattern:** Our study area showed high species richness in relation to a small spatial scale, coinciding with similar patterns observed in other Brazilian highlands (Tinti, Schaefer, Nunes, Rodrigues, Fialho, & Neri, 2015; Neri et al., 2016; Campos et al., 2018). Thus, despite a smaller sample area, the montane forest showed high diversity (richness and Shannon index) compared with the other phytophysognomies. This pattern is probably due to a more heterogeneous vertical distribution of vegetation (lower and upper strata) compared to herbaceous *campo rupestre* that present a homogenous distribution, suggesting stability in the abundance of their species (Battilani, Scremin-Dias, & Souza, 2005). Likewise, according to the extrapolation using an individual-based approach for the montane forest, it is presumed that the species richness could be much higher in that same spatial scale.

Conversely, Shannon and Pielou's evenness indices showed no regular pattern, which does not differ between phytophysognomies, despite the marked differences in species richness. This pattern of diversity may presumably be related to a greater relative uniformity in the species abundance distribution due to resource constraints (i.e., water,

nutrients) and spatial distribution. Furthermore, this diversity pattern has recently been demonstrated for highlands in Southeastern Brazil, where it is inferred that communities are relatively stable regarding the distribution of their abundances (Campos et al., 2018). This assumption is based on the premise that recently *campo rupestre* was considered one of the world's old climatically-buffered infertile landscapes with high levels of local endemism (Silveira et al., 2015).

Phytosociological analysis in the upper scrub strata showed *Eremanthus erythropappus* to be the predominant species. In the ecological succession process, *E. erythropappus* is considered a pioneer species, as it is the precursor of field invasions and colonizes poor, sandy and even rocky soils (Messias, Leite, Neto, & Kozovits, 2012). In the montane forest some of these species are frequently found in semi-deciduous seasonal forest formations in the Iron Quadrangle region (Spósito & Stehmann, 2006).

Our result showed that the lower and upper strata diversity and similarity of the scrub and montane forest were decoupled. The low diversity found in these phytophysognomies may be related to low light availability, because the montane forest presents a closed canopy and irregular height. Plants with high emergence velocity and high initial growth rates have advantages in using environment resources (Gustafson, Gibson, & Nickrent, 2004). Thus, we expect there to be low light availability in the understory of a closed canopy (Nicotra, Chazdon, & Iriarte, 1999), and consequently low species richness and abundance under such conditions. Other studies have found that the compositional decoupling between canopy and recruitment communities is primarily associated with soil factors (e.g., Anderson, Morrison, Rugemalila, & Holdo, 2015). On the other hand, some studies have shown that plant coverage increases species richness and diversity but not species evenness (e.g., Sanaei, Ali, Chahouki, & Jafari, 2018), which may be related to the high canopy density of the vegetation through niche differentiation, and hence may promote species coexistence through niche facilitation (Grytnes & Birks, 2002; Sanaei et al., 2018). An alternative and complementary way to analyze these diversity patterns in rocky complexes, could be through species abundance distribution and species-area relationship analysis to elucidate the processes that maintain diversity (Villa et al., 2018b).

**Life forms:** Phanerophytes were the most representative life form in our study, which is consistent with other studies on Brazilian quartzite (Conceição & Giulietti, 2002; Conceição & Pirani, 2007), granite (Caiafa & Silva, 2005; Neri et al., 2016; Campos et al., 2018), and ironstone (Mourão & Stehmann, 2007). The high number of phanerophytes found in our study area was mainly due to sampling the upper stratum of the montane forest and scrub. In the herbaceous *campo rupestre*, the hemicryptophytes stood out, mainly represented by Poaceae and Cyperaceae. This life form is can survive under unfavorable climatic conditions (e.g. winter; dry season), since their buds are protected by scales or by dry leaves from the previous season.

In the montane forest and scrub, phanerophytes represented a significant number of species and individuals. Among the phanerophytes observed in these phytophysognomies, there are some that are also frequent in forest phytophysognomies, in both the Cerrado and the Atlantic Rainforest; e.g. *E. erythropappus*, *E. incanus*, *Guatteria vilosissima*, *Myrcia splendens*, *Tapirira guianensis* and *Vismia brasiliensis* (Messias et al., 2012). The dominance of this life form in these environments can be explained by the greater soil depth, the occurrence of fissures in the rocks which enable rooting of higher species, and also by the slightly higher amounts of certain nutrients in these microhabitats (Vincent & Meguro, 2008).

Additionally, the higher water retention capacity enables a higher intake of the small amounts of nutrients available.

Our study reveals marked differences in floristic composition, richness, and life form spectra between phytophysionomies on the quartzite rocky complexes in the southeast Brazilian Iron Quadrangle. Such differences probably indicate that there is a high environmental heterogeneity at small spatial scales. We suggest future studies evaluate the effect of environmental drivers on the diversity changes along *campo rupestre* gradients, beyond a floristic evaluation.

## Acknowledgments

We thank FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais) for the scholarships granted to the first and fourth authors, and Companhia Vale do Rio Doce for grant and support given during the research. The author A.V. Neri thanks CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico - Document: 206814/2014-3) for postdoctoral scholarships.

## REFERENCES

Alves, R. J. V., Silva, N. G., Oliveira, J. A., & Medeiros, D. (2014). Circumscribing campo rupestre megadiverse brazilian rocky montane savannas. *Brazilian Journal Biology*, 74, 355-362.

Anderson, T. M., Morrison, T., Rugemalila, D., & Holdo, R. (2015). Compositional decoupling of savanna canopy and understory tree communities in Serengeti. *Journal of Vegetation Science*, 26, 385-394.

APG III (Angiosperm Phylogeny Group III). (2009). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. *Botanical Journal of the Linnean Society*, 161, 105-121.

Barthlott, W., Mutke, J., Rafiqpoor, M. D., Kier, G., & Kreft, H. (2005) Global centers of vascular plant diversity. *Nova Acta Leopoldina*, 92, 61-83.

Battilani, J. L., Scremin-Dias, E., & Souza, A. L. T. (2005). Fitossociologia de um trecho da mata ciliar do rio da Prata, Jardim, MS, Brasil. *Acta Botanica Brasilica*, 19, 597-608.

Benites, V., Schaefer, C. E. G. R., Simas, F. N. B., & Santos, H. G. (2007). Soils associated with rock outcrops in the brazilian mountain ranges Mantiqueira and Espinhaço. *Revista Brasileira de Botânica*, 30, 569-577.

Braun-Blanquet, J., Lalucat, J., & de Bolòs, O. (1979). *Fitosociología; Bases para el estudio de las comunidades vegetales*. Madrid, España: Blume press.

Caiafa, A. N., & Silva, A. F. (2005). Composição florística e espectro biológico de um Campo de Altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais - Brasil. *Rodriguésia*, 56, 163-173.

Campos, P. V., Villa, P. M., Nunes, J. A., Schaefer, C. E. R. G., Porembski, S., & Neri, A. V. (2018). Plant diversity and community structure of a Brazilian Páramos from

Southeastern Brazil. *Journal of Mountain Science*, 15, 1186-1198.

Conceição, A. A., & Giulietti, A. M. (2002). Composição florística e aspectos estruturais de campo rupestre em dois platôs do Morro do Pai Inácio, Chapada Diamantina, Bahia, Brasil. *Hoehnea*, 29, 37-48.

Conceição, A. A., & Pirani, J. R. (2007). Diversidade em quatro áreas de campos rupestres na Chapada Diamantina, Bahia, Brasil: espécies distintas, mais riquezas similares. *Rodriguésia*, 58, 193-206.

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S. Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, 5, 3-21.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monograph*, 84, 45-67.

Crawley, M. J. 2013. The R Book (2<sup>nd</sup> Ed.). London, United Kingdom: John Wiley & Sons, Ltd.

Dinno, A. (2017). “*dunn.test*” package: *Dunn's test of multiple comparisons using rank sums*. Retrieved from <http://CRAN.R-project.org/package=dunn.test>. RStudio package version 1.0.14.

Echternacht, L., Trovó, M., Oliveira, C. T., & Pirani, J. R. (2011). Areas of endemism in the Espinhaço Range in Minas Gerais, Brazil. *Flora*, 206, 782-791.

Fernandes, G. W. (2016). The Megadiverse Rupestrian Grassland. In G.W. Fernandes (Ed.), *Ecology and Conservation of Mountaintop Grasslands in Brazil* (pp. 1-14). Minas Gerais, Brazil: Springer International Publishing Switzerland.

Giulietti, A. M., Pirani, J. R., & Harley, R. M. (1997). Espinhaço Range region, eastern Brazil. In S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, A. C. Hamilton (Eds.), *Centres of plant diversity: a guide and strategy for their conservation* (pp. 397-404). Cambridge, UK: Information Press, Oxford.

Gustafson, D. J., Gibson, D. J., & Nickrent, D. L. (2004). Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology*, 18, 451-457.

Grytnes, J. A., & Birks, H. J. B. (2002). The influence of scale and species pool on the relationship between vascular plant species richness and cover in an alpine area in Norway. *Plant Ecology*, 169, 273-284.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). *iNEXT: iNterpolation and EXTrapolation for species diversity* (Version 2.0.12). Retrieved from <https://cran.r-project.org/web/packages/iNEXT/iNEXT.pdf>.

- Jacobi, C. M., Carmo, F. F., Vincent, R. C., & Stehmann, J. R. (2007). Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodiversity Conservation*, 16, 2185-2200.
- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427-2439.
- Kellogg, E. A. (2001). Evolutionary history of the grasses. *Plant Physiology*, 125, 1198-1205.
- Magurran, A. E. (2004). *Measuring biological diversity*. Oxford, United Kingdom: Wiley-Blackwel.
- Messias, M. C. T. B., Leite, M. G. P., Neto, J. A. A. M., & Kozovits, A. R. (2012). Fitossociologia de campos rupestres quartzíticos e ferruginosos no Quadrilátero Ferrífero, Minas Gerais. *Acta Botanica Brasilica*, 26, 230-242.
- Mourão, A., & Stehmann, J. R. (2007). Levantamento da Flora do Campo Rupestre sobre Canga Hematítica Couraçada remanescente na Mina do Brucutu, Barão de Cocais, Minas Gerais, Brasil. *Rodriguésia*, 58, 775-786.
- Neri, A. V., Borges, G. R. A., Neto-Meira, J. A. A. M., Magnago, L. F. S., Trotter, I. M., Schaefer, C. E. G. R., & Porembski, S. (2016). Soil and altitude drives diversity and functioning of Brazilian Páramos (Campo de Altitude). *Journal of Plant Ecology*, 10, 771-779
- Nicotra, A. B., Chazdon, R. L., & Iriarte, S. V. B. (1999). Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, 80, 1908-1926.
- Nunes, J. A. (2009). *Florística, estrutura e relações solo-vegetação em gradiente fitofisionômico sobre canga, na Serra Sul, Flona de Carajás, Pará* (Doctoral Thesis). Universidade Federal de Viçosa, Minas Gerais, Brazil.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. M., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2017). *Vegan: Community Ecology Package* (Version 2.4-3). Retrieved from <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Oliveira, A. C. P., Souza, A. S. P. R. F., & Loiola, M. I. B. (2012). Composição florística de uma comunidade savânica no Rio Grande do Norte, Nordeste do Brasil. *Acta Botanica Brasilica*, 26, 559-569.
- Pontara, V., Bueno, M. L., Rezende, V. L., Oliveira-Filho, A. T., Gastauer, M., & Meira-Neto, J. A. A. (2018) Evolutionary history of campo rupestre: an approach for conservation of woody plant communities. *Biodiversity Conservation*, 27, 1-20.
- R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>.

Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography*. Oxford, United Kingdom: Clarendon Press.

Sanaei, A., Ali, A., Ali, M., & Chahoukia, M. A. Z. (2018). Plant coverage is a potential ecological indicator for species diversity and aboveground biomass in semi-steppe rangelands. *Ecological Indicators*, 93, 256-266.

Silva, W. A. (2013). *Gradiente vegetacional e pedológico em complexo rupestre de quartzito no Quadrilátero Ferrífero, Minas Gerais, Brasil* (Master Thesis) Universidade Federal de Viçosa, Minas Gerais, Brazil.

Silveira, F. A. O., Negreiros, D., Barbosa, N. P. U., Buisson, E., Carmo, F. F., Carstensen, D. W., Conceição, A. A., Cornelissen, T. G., Echternacht, L., Fernandes, G. W., Garcia, Q. S., Guerra, T. J., Jacobi, C. M., Lemos-Filho, J. P., Le Stradic, S., Morellato, L. P. C., Neves, F. S., Oliveira, R. S., Schaefer, C. E., Viana, P. L., & Lambers, H. (2015). Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil*, 403, 129-152.

Spósito, T. C., & Stehmann, J. R. (2006). Heterogeneidade florística e estrutural de remanescentes florestais da Área de Proteção Ambiental ao Sul da Região Metropolitana de Belo Horizonte (APA Sul-RMBH), Minas Gerais, Brasil. *Acta Botanica Brasilica*, 20, 347-362.

Tinti, B. V., Schaefer, C. E. R. G., Nunes, J. A., Rodrigues, A. C., Fialho, I. F., & Neri, A. V. (2015). Plant diversity on granite/gneiss rock outcrop at Pedra do Pato, Serra do Brigadeiro State Park, Brazil. *Check List*, 11, 1-8.

Vincent, R. C., & Meguro, M. M. (2008). Influence of soil properties on the abundance of plants species in ferruginous rocky soils vegetation, Southeastern Brazil. *Revista Brasileira Botânica*, 31, 377-388.

Villa, P. M., Martins, S. V., Oliveira Neto, S. N., Rodrigues, A. C., Martorano, L., Delgado, L., Cancio, N. M., & Gastauerg, M. (2018a) Intensification of shifting cultivation reduces forest resilience in the northern Amazon. *Forest Ecology Management*, 430, 312-320.

Villa, P., de Siqueira Cardinelli, L., Magnago, L., Heringer, G., Venâncio Martins, S., Viana Campos, P., Rodrigues, A., Viana Neri, A., & Alves Meira-Neto, J. (2018b). Relación especie-área y distribución de la abundancia de especies en una comunidad vegetal de un inselberg tropical: efecto del tamaño de los parches. *Revista de Biología Tropical*, 66, 937-951.

Zappi, D. C, Moro, M. F., Meagher, T. R., & Lughadha, E. N. (2017). Plant Biodiversity Drivers in Brazilian Campos Rupestres: Insights from Phylogenetic Structure. *Frontiers in Plant Science*, 8, 1-15.