

Seasonality drives herbaceous community beta diversity in lithologically different rocky outcrops in Brazil

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Background and aims – Seasonality exerts strong controlling forces on species diversity in herbaceous species communities, however, this control process remains poorly understood in tropical lithologically different rocky outcrops. We aim to investigate the effect of seasonality and the variability of soil properties on changes in the herbaceous species richness and species composition of two different herbaceous species communities on rocky outcrops in Brazil. We hypothesize that seasonality, determined by variation in precipitation, and soil fertility, determined by variability in nutrient-related soil properties, drives species diversity (i.e., richness and beta diversity) patterns of herbaceous communities at local scale.

Methods – To investigate how the variation between dry and wet seasons affects species richness and beta diversity, we studied plots on rocky outcrops of Iron Quadrangle (40 plots, 1 × 1 m) and Carajás (20 plots, 1 × 1 m).

Key results – We observed similar richness patterns between seasons, without significant differences between sites, using rarefaction and extrapolation curves. However, we observed significant differences in beta diversity between seasons. Our results indicate that seasonality determines the temporal variation of the herbaceous species composition, but not species richness. Likewise, our tested models indicated that seasonality shape beta diversity in the studied rocky outcrops.

Conclusions – The predictable seasonal precipitation is closely related to the community composition on this type of rocky outcrop formation, where there typically is a marked seasonal water deficit pattern, with increased deficit during the dry season. We presume that seasonality is an important driver in determining plant community assembly at local scale on the studied rocky outcrops.

Keywords – Beta diversity; campo rupestre; environmental seasonality; seasonal precipitation.

INTRODUCTION

Temporal environmental fluctuations, such as climatic seasonality, exert strong controlling forces on species diversity patterns from different ecological communities (Ferreira et al. 2017; Bao et al. 2019; Duong et al. 2019; Villa et al. 2019a). Therefore, understanding how seasonal environmental variation determines plant community diversity has been

one of the central aspects of ecological studies (e.g., Bao et al. 2017; Poorter et al. 2019). Seasonal climatic conditions (i.e., precipitation) generally determine the temporal dynamics of germination and dormancy (Silveira et al. 2016; Tonkin et al. 2017), and the amount of water available for plants to grow and establish is an important limiting factor in several global ecosystems (e.g., Ulrich et al. 2014; Le Bagousse-Pinguet et al. 2017; Bao et al. 2018). Specific

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ly, the temporal variation in precipitation can substantially affect species composition and richness patterns in different plant communities (e.g., Klanderud et al. 2015; Le Bagousse-Pinguet et al. 2017; Bao et al. 2018), particularly for water-dependent herbaceous species with short life cycles (Royo & Ristau 2013; Bao et al. 2017). Conversely, seasonality provides the necessary conditions for the regeneration of plant species (Poorter et al. 2019; Rozendaal et al. 2019). Compared to stable systems, predictable seasonal precipitation can promote high species turnover (Tonkin et al. 2017), particularly beta diversity (Shimadzu et al. 2013; Bao et al. 2017, 2018). Beta diversity is a measure of the temporal or spatial variation of species composition (Tuomisto 2010; Anderson et al. 2011). The simplest definition of taxonomic beta diversity, and one of the most used, is that it is the percentage of dissimilarity in the species composition of two communities (Koleff et al. 2003). However, most studies on species composition variation have used spatial analysis along environmental gradients, and studies on temporal variations are scarce (Ruhí et al. 2017).

The rocky outcrops in Brazil, known as campos rupestres, are hotspots of terrestrial species diversity (Alves et al. 2014; Fernandes 2016). Although this region occupies less than 1% of the Brazilian territory, it hosts nearly 15% of the national flora (Silveira et al. 2016) and nearly 40% of the species are narrow endemics (ca. 2000 species), many of which are threatened with extinction (Martinelli & Moraes 2013). Campos rupestres comprises a mosaic of plant communities that have adapted to the landscape heterogeneity of mountain ranges with varying levels of tolerance to edaphoclimatic factors (Negreiros et al. 2014; Fernandes 2016). The vegetation faces specific environmental conditions of high stress due to shallow nutrient-poor soils with low water-holding capacity, which leads to low water availability and drought-induced growth limitation (Benites et al. 2007; Jacobi et al. 2007; Fernandes 2016; Figueira et al. 2016; Schaefer et al. 2016; Silveira et al. 2016). The diversity of habitat types is also considerable and the region contains peculiar landscapes occurring mainly on quartzite and ironstone formations (Benites et al. 2007; Silveira et al. 2016). The rocky outcrops are also recognized as ecosystems with marked environmental seasonality (Silveira et al. 2016). Due to changes in climate, mountains are suitable systems for identifying changes in diversity patterns (Pecl et al. 2017). Tropical mountains have higher temperatures at low elevations and overall wetter conditions than temperate mountains (McCain & Grytnes 2010). However, most studies about changes in species composition and diversity in plant communities of Brazilian rocky outcrops have analysed environmental gradients (e.g., Alves et al. 2014; Nunes et al. 2015; Mota et al. 2018; Alves-Silva et al. 2019), while temporal differences in the composition of the herbaceous community remain poorly understood.

In this study, we investigated the effects of seasonal differences in precipitation and variability in soil fertility on species richness and beta diversity of two different herbaceous plant communities in the Brazilian campos rupestres. For that reason, we sampled herbaceous species on an ironstone outcrop in the Carajás National Forest (Pará state) and a quartzite outcrop in the Iron Quadrangle (Minas Gerais state). We established the following two research questions:

(1) How do the species richness and beta diversity of each site change between the dry and the wet season? (2) What are the effects of seasonal differences in precipitation (i.e., between the dry and the wet season) and variability in soil fertility on species richness and beta diversity? We hypothesize that seasonality, determined by variation in precipitation, and soil fertility, determined by variability in nutrient-related soil properties, drives species diversity (i.e., richness and beta diversity) patterns of herbaceous communities at local scale.

MATERIALS AND METHODS

Study sites

The study was carried out at two different Brazilian campos rupestres. (1) The ironstone outcrop formation, canga (lateritic capping), known as Serra Sul (738–762 m a.s.l.), located in the Carajás National Forest (6°24'37.7"S, 50°21'31.0"W) conservation unit in south-eastern Amazonia, Pará state, Brazil. The ironstone canga (ferruginous campo rupestre islands) covers approximately 9031 ha (2.28%) of the total FLONA area of 395,827 ha (Nunes et al. 2015). (2) A quartzite outcrop formation in a private nature reserve at Fazenda da Capanema (20°13'41.4"S, 43°36'48.7"W). This site is located on the eastern border of the Iron Quadrangle, Minas Gerais state, Brazil. We selected sampling areas at each site that were as homogeneous as possible. Additionally, this criterion allows for controlling for possible effects of fine spatial scale differences and analysing the direct effects of seasonality and soil fertility.

Climate and soil characteristics

The climate in Carajás National Forest is tropical, hot and humid (type "Aw" in the Köppen climate classification) (Alvares et al. 2014) with a dry season between May and October that receives 14.5% of the total annual rainfall and an average of 50 mm precipitation per month (INMET 2020; supplementary file 1A). The rainy season, between November and April, receives an average of 244 mm precipitation per month and 79% of the total annual rainfall (Lopes et al. 2013). The mean annual temperature ranges from 23.5°C at 835 m a.s.l. to 26.2°C at 203 m a.s.l. (Silva et al. 1996). The position of the Intertropical Convergence Zone and the intensity of convection in the Amazon are two major factors driving differences in regional and seasonal precipitation (Lopes et al. 2013). In addition, moist trade winds from the tropical Atlantic and evapotranspiration from the Amazon rainforest also contribute to the precipitation (Alizadeh et al. 2017).

The climate in the Iron Quadrangle is subtropical with a dry winter and a hot summer (type "Cwa" in the Köppen climate classification) (Alvares et al. 2014), and is strongly influenced by altitude. This region has a dry season between April and September with an average of 32 mm precipitation per month and a rainy season between October and March with an average of 200 mm precipitation per month (INMET 2020; supplementary file 1B). Throughout the year, the region experiences considerable temperature variability, reaching below 10°C in winter and above 30°C in summer (Vincent 2004; Ferrari et al. 2016). Seasonal moisture variation in the soil of the campo rupestre is indicative of severe

water deficiency during the winter/dry season (Ferrari et al. 2016). Ferrari et al. (2016) also pointed out that the first 30 cm of topsoil has the highest water deficiency, reaching values close to zero.

The soil in Carajás rocky outcrop is acidic and has low phosphorus content (Nunes et al. 2015). The ironstone areas, comprises a friable soil that rarely exceeds 5 cm of horizon A. In some areas, the soil is formed from old abandoned termite mounds, forming micropockets of organic soil that fill fractures and dissolution depressions in the canga (Schaefer et al. 2016). The Iron Quadrangle quartzite formation, the soil is also very acid and extremely oligotrophic and high levels of exchangeable Al. In general, both areas represent a harsh condition with low levels of nutrients and low water availability due to the shallow soil (Schaefer et al. 2016).

These rocky outcrops have been recently proposed as one of the world's old climatically buffered infertile landscapes (OCBILs), which have reduced water and nutrient availability and contain shallow soils (Silveira et al. 2016).

Soil properties measurements

In order to measure the soil properties within each plot by season and site, a surface soil sample was collected (up to 10 cm depth). Soil properties of the samples were measured in the Soil Analysis Laboratory of the Federal University of Viçosa, following standard protocols (EMBRAPA 1997). The following parameters were assessed: available exchangeable P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, Al, exchangeable acidity (H + Al), pH (H₂O), organic matter (OM), sum of exchangeable bases (SB), effective cation exchange capacity (t), cation exchange capacity acidity (T), potential index (m), bases saturation index (V), and Na saturation index (ISNa). Soil data was in part locally available or could otherwise be obtained from the harmonized world soil database (HWSD version 1.2; FAO et al. 2012).

Vegetation sampling

We carried out vegetation sampling in 20 plots (1 × 1 m) in Carajás and 40 plots (1 × 1 m) in the Iron Quadrangle. We sampled each plot twice, once during the dry season and once during the wet season. In the Carajás ironstone outcrop, the plants were sampled in July 2007 and January 2008, while in the Iron Quadrangle quartzite outcrop, the plant sampling was carried out in July 2011 and February 2012. In each plot, the number of individuals of each species was counted (Braun-Blanquet 1979). The species were also classified according to Raunkiaer's biological spectrum (e.g., Campos et al. 2018; Alves-Silva et al. 2019).

Data analyses

Differences in species richness between the two sampled areas were evaluated using individual-based data to estimate rarefaction and extrapolation curves using the first Hill number (Chao et al. 2014), and extrapolations were made based on abundance data for the 1 × 1 m plots (Colwell et al. 2012). Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals (i.e., Campos et al. 2018;

Alves-Silva et al. 2019). These estimates were obtained using the 'iNEXT' package (Hsieh et al. 2016).

We performed principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity matrix among seasons to explore the effects of seasonality on the patterns of species composition. PCoA is run on distance matrix (Monte-Carlo, 999 permutations) and can directly represent the relationships among samples to determine differences in species composition. The PCoA was performed using the 'vegan' package in R (Oksanen et al. 2018). We used permutation multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the 'adonis' routine, available within the vegan package (Oksanen et al. 2018).

To assess beta diversity, we used the betadisper function in vegan, based on the applied multivariate analysis of dispersal (PERMDISP) method (Anderson 2006). We used distance to group centroids to assess variability in species composition, based on the Bray-Curtis metric, on the abundance data (Monte-Carlo, 9999 permutations). In this analysis, the greater the dispersal of the data points, the greater the heterogeneity of the groups. We tested for differences in beta diversity between seasons for each site using PERMANOVAs (Anderson 2001). All data and statistical analyses were conducted in R version 3.2.2 (R Core Team 2017). Finally, we used the two-way cluster analyses using Bray-Curtis dissimilarity based on abundance data using the PC-ORD software (i.e., Villa et al. 2019b) to identify similarity patterns for the species between seasons.

We used principal components analysis (PCA) on the correlation matrix to reduce the number of redundant soil properties (e.g., Schmitz et al. 2020) in each site (fig 2), using the 'FactoMineR' package (Husson et al. 2017). Thus, we reduced the correlations among local soil variables using the first PCA axis for mainly the variability of nutrient-related soil properties (PCA1) (e.g., Schmitz et al. 2020). To explain the main effects of variability of nutrient-related soil properties (PCA1) and seasons on species richness and beta diversity, we constructed linear mixed effect models (LMM) after having evaluated normality (Crawley 2013). The models were tested for each site to explain local effects of seasonality and soil variability. We observed that soil texture does not vary between seasons and was not an important predictor between tested models. Predictor variables were grouped into two categories, i.e., the variability of nutrient-related soil properties as a continuous variable and the season as a categorical variable that has two levels (i.e., dry and wet season). The univariate and interaction effect of the predictors on richness and beta diversity was evaluated, and the plots were considered as a random factor, and the PCA axis predictor and seasons as a fixed factor. All models were calculated using the packages 'lme4' (Bates et al. 2015, 2017) in the platform R version 3.6.0 (R Core Team 2019).

RESULTS

The first two axes of PCA explained ~ 53% of the variation in soil data in Carajás (fig. 1A). The first axis (PCA1) explained 35.8% of the variation in soil data and correlated positively with variability of fertility-related soil properties,

such as sum of exchangeable bases ($R = 0.96$, $p < 0.05$), Ca ($R = 0.97$, $p < 0.05$), effective cation exchange capacity ($R = 0.83$, $p < 0.05$), and negatively with aluminium saturation index ($R = -0.91$, $p < 0.05$; supplementary file 2). The second axis (PCA2) explained 17.6% of the variation in soil data (fig. 1A), and correlated positively with pH ($R = 0.69$, $p < 0.05$). Meanwhile, the first two axes of PCA explained ~ 56% of the variation in soil data in Iron Quadrangle (fig.

1B), where the first axis was correlated positively with effective cation exchange capacity ($R = 0.84$, $p < 0.05$), cation exchange capacity acidity ($R = 0.81$, $p < 0.05$), but negatively with pH ($R = -0.79$, $p < 0.05$) and Ca ($R = 0.78$, $p < 0.05$; supplementary file 3).

We observed similar richness patterns between seasons without significant differences using both individual-based rarefaction and extrapolation curves (fig. 2A–B). However,

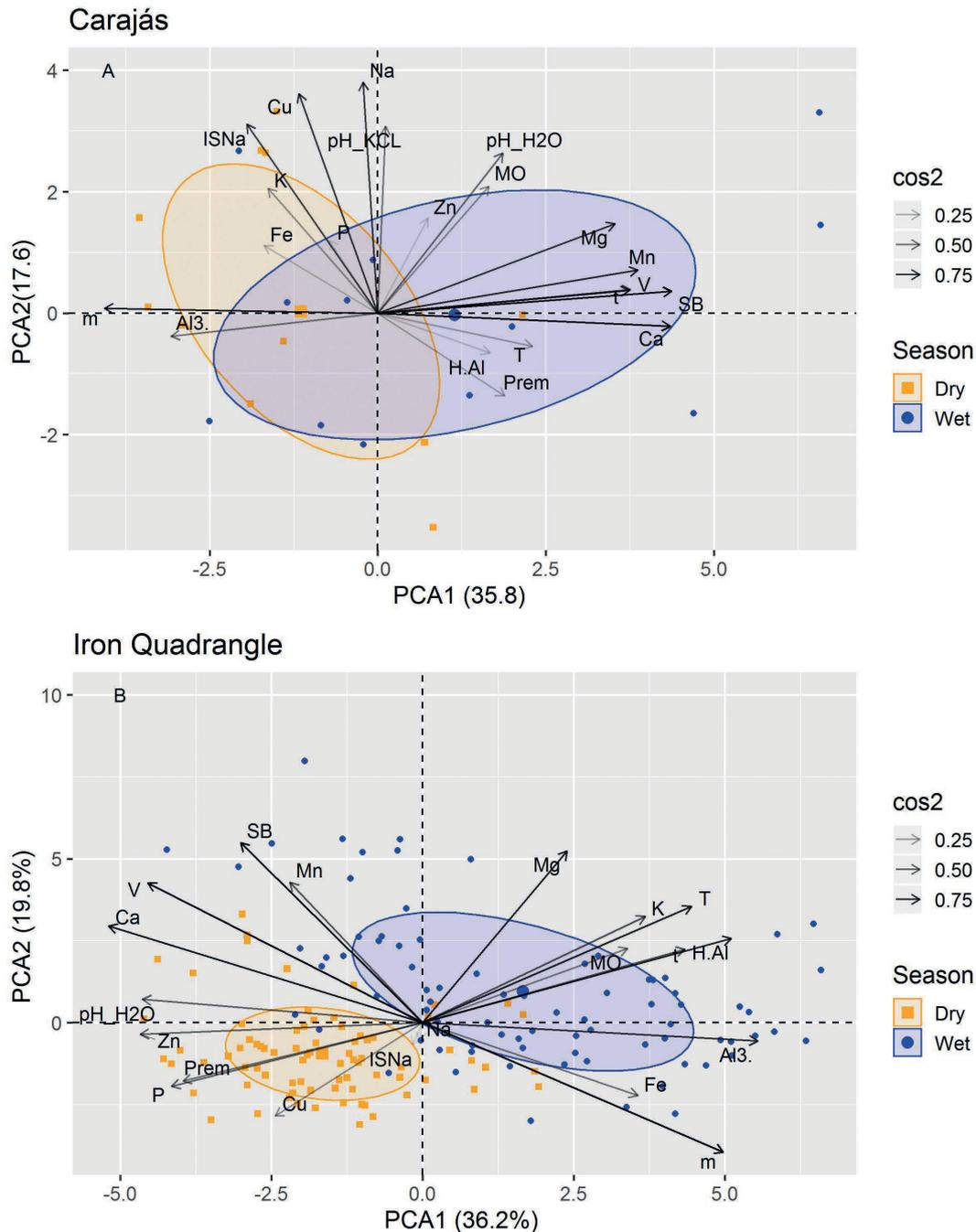


Figure 1 – Principal Component Analysis (PCA) for the soil properties of different seasons and sites. For analysis: available exchangeable P, K, Ca, Na, Mg, Fe, Cu, Mn, Zn, Al, exchangeable acidity (H + Al), pH (H₂O), organic matter (OM), sum of exchangeable bases (SB), effective cation exchange capacity (t), cation exchange capacity acidity (T), aluminium saturation index (m), bases saturation index (V), and Na saturation index (ISNa) were included. Cos2 means the relative contribution of the variables represented by the vectors.

there are notable differences in the number of species at both sites between the wet and the dry season, especially for the chamaephytes and therophytes (fig. 3).

Species compositions showed significant differences between dry and wet seasons at both sites, in Carajás (PERMANOVA: $F_{1,38} = 6.70$, $p < 0.001$; fig. 4A) and in Iron Quadrangle (PERMANOVA: $F_{1,77} = 14.54$, $p < 0.001$; fig. 4C), forming two groups on the first axis. According to the first two PCoA axes, seasonality explains 36.13% and 38.12% of the variance in species for the Carajás and Iron Quadrangle site, respectively (fig. 4). From this analysis, most of the sample points for the dry season clustered together in the multidimensional space, with less distance from the centroid, compared to a more dispersed pattern for the wet season. We did not observe changes in beta diversity between seasons at the Carajás site (PERMANOVA: $F_{1,38} = 1.41$, $p < 0.24$; fig. 4B) or the Iron Quadrangle (PERMANOVA: $F_{1,77} = 5.78$, $p < 0.10$; fig. 4D).

The two-way cluster analyses broadly divided the plant species into two groups based on season, which can be clearly seen by the two main branches of the dendrogram at both sites, in Carajás (fig. 5) and in Iron Quadrangle (fig. 6).

Despite the lack of differences in beta diversity between the two sites, the models indicate that beta diversity is main-

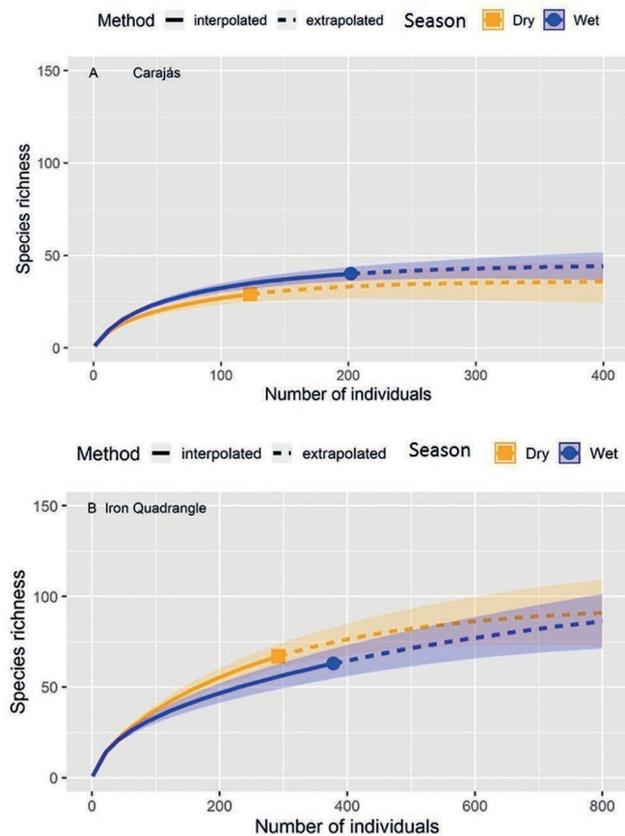


Figure 2 – Individual-based (solid lines) and extrapolation curves (dashed lines) for the sampled plots in quartzite Iron Quadrangle, Minas Gerais, Brazil (A), and in canga in Carajás, Pará, Brazil (B) during different seasons (wet and dry). The lines represent the mean values and the shaded area represents the 95% confidence intervals.

Table 1 – Candidate mixed effect models predicting the effect of variability of nutrient-related soil properties (PCA1) and seasons on beta diversity with Gaussian error distribution (linear mixed effects model - lmer).

The models were tested for each site to explain local effects of seasonality and soil variability. The p-value of each predictor is given as: * $p < 0.001$.

| Response variable | Fixed effects | Estimate | SE | t |
|-------------------|---------------|----------|-------|-------|
| Beta diversity | ~PCA1 | 0.01 | 0.019 | -0.30 |
| Carajás | ~Season | 0.51 | 0.035 | 4.31* |
| Beta diversity | ~PCA1 | 0.13 | 0.01 | 7.09 |
| Iron Quadrangle | ~Season | 0.53 | 0.023 | 4.98* |

ly explained by seasonality within both sites, but without an effect on species richness, and there is no effect of variability of nutrient-related soil properties (table 1).

DISCUSSION

Our results indicate that seasonality (i.e., changes between dry and wet season) determines the temporal variation of beta diversity of the studied rocky outcrops. This indicates that the predictable seasonal precipitation is closely linked to the community composition on this type of rocky outcrop formation, where there typically is a marked seasonal pattern of water deficit (Silveira et al. 2016). Likewise, it was possible to observe how seasonality can promote similar

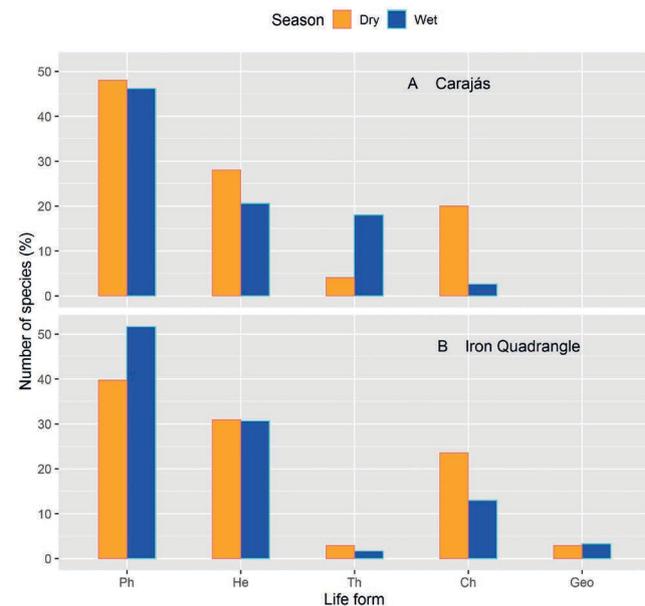


Figure 3 – The number of species per life form found during both seasons (dry and wet) in Carajás, Pará, Brazil (A) and Iron Quadrangle, Minas Gerais, Brazil (B). Phanerophytes (Ph), hemicryptophytes (He), therophytes (Th), chamaephytes (Ch), and geophytes (Geo).

beta diversity patterns between seasons at each site. In different rocky outcrops, there are plant communities that are well adapted to extreme environmental conditions, mainly to water and nutrient deficits, as well as shallow soils (Lüttge 1997; Gröger & Huber 2007). These species have different mechanisms and adaptive strategies to tolerate scarce substrates and water, as well as the high temperatures due to the bare rock surface (i.e., Lüttge 1997). Several studies in America and Africa show that the vegetation on rocky outcrops is dominated by succulents, geophytic and xerophytic species, and drought-tolerant species and drought-avoiding species such as therophytes (Lüttge 1997; Gröger & Huber 2007). Our results allow us to confirm the hypothesis that seasonality, based on changes between a dry and a wet season, determines species composition and beta diversity, but not species richness. However, soil fertility determined by variability of nutrient-related soil properties has no effect on species composition and beta diversity.

Some plants that are not drought-resistant use drought avoidance as a mechanism to allocate more energy to survival during certain periods, to germinate and grow sufficient aerial biomass during a short period of time, and to conclude

their entire life cycle before the end of wet season. For example, therophytes that germinate after the beginning of the wet season can develop in a short period of time while the humidity is relatively high (Lüttge 1997; Gröger & Huber 2007; Villa et al. 2018). Likewise, geophytes are another group of plants that exhibit this mechanism. They store resources in their underground organs (rhizomes, tubers, bulbs) in order to survive periods of drought and to protect them against excessive water loss (Lüttge 1997). Conversely, a classic example of a tolerance strategy in plants is desiccation tolerance, which allows plants to almost completely dehydrate their tissues and cellular protoplasm (between 85 and 95% of the total water content of the plant), and dehydrated and rehydrated between the dry and wet seasons (Dinakar et al. 2012). Reactive photosynthetic activity is usually reactivated within a few days after the onset of precipitation and rehydration of the plants (Lüttge 1997; Dinakar et al. 2012).

In this study, we found that, despite the lack of differences in species richness between dry and wet season, there are notable differences in beta diversity. We assume that fine-scale variations in species composition change considerably due to the influence of water availability, resulting

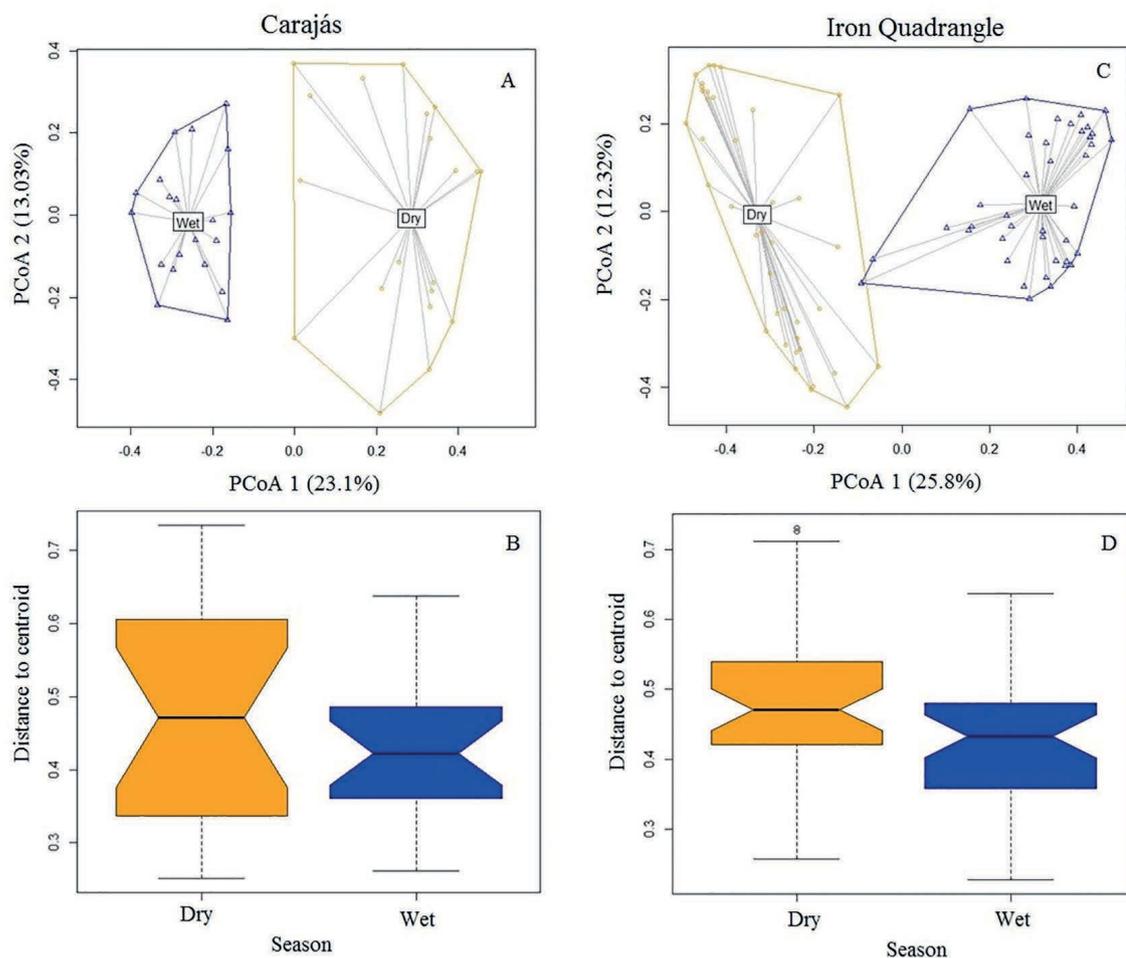


Figure 4 – Principal coordinate analysis (PCoA) based on the Bray-Curtis dissimilarity metric (A, C), and differences in beta diversity (B, D) between sampled plots in quartzite Iron Quadrangle, Minas Gerais, Brazil, and in canga in Carajás, Pará, Brazil during different seasons (wet and dry).

in the coexistence of a higher number of species (Bao et al. 2018). Therefore, seasonal environmental variation, such as precipitation, can also be a determining factor in the availability of resources (i.e., water) and the coexistence of herbaceous community species in the same space (e.g., Ulrich et al. 2014; Le Bagousse-Pinguet et al. 2017; Bao et al. 2018). Therefore, it is possible that the availability of water may be considered an important abiotic filter shaping species composition at a fine-scale in the rocky outcrops studied.

Species richness did not show differences between seasons, which is more likely due to species redundancies in the two studied sites, and this pattern may be a response to high environmental stress, mainly the reduced water and nutrient availability (Silveira et al. 2016). However, we found considerable differences in the community composition between seasons. In this sense, we attribute this change in community composition to the predictable effect of seasonally variable precipitation. Moreover, the low water storage capacity of the soil in the rocky outcrops is an additional environmental

filter determining the temporal dynamics of the plant communities' diversity.

Our results provide evidence that seasonality shapes the temporal beta diversity in herbaceous communities. However, most of the studies on Brazilian rocky outcrops have analysed changes in woody community composition along environmental gradients, and among habitats and phytogeographies within the campo rupestre s. lat. (e.g., Alves et al. 2014; Nunes et al. 2015; Prata et al. 2018; Silva et al. 2019). On the other hand, the majority of studies on plant communities on rocky outcrops, using an environmental gradient approach, have analysed the direct effects of physico-chemical parameters of the soil on the community diversity and structure (e.g., Nunes et al. 2015; Neri et al. 2016). Overall, these studies concluded that the spatial variation of resources in these edaphic environments is one of the main factors affecting woody species diversity. However, few studies have evaluated these ecological patterns within the herbaceous communities that represent some of the most important phy-

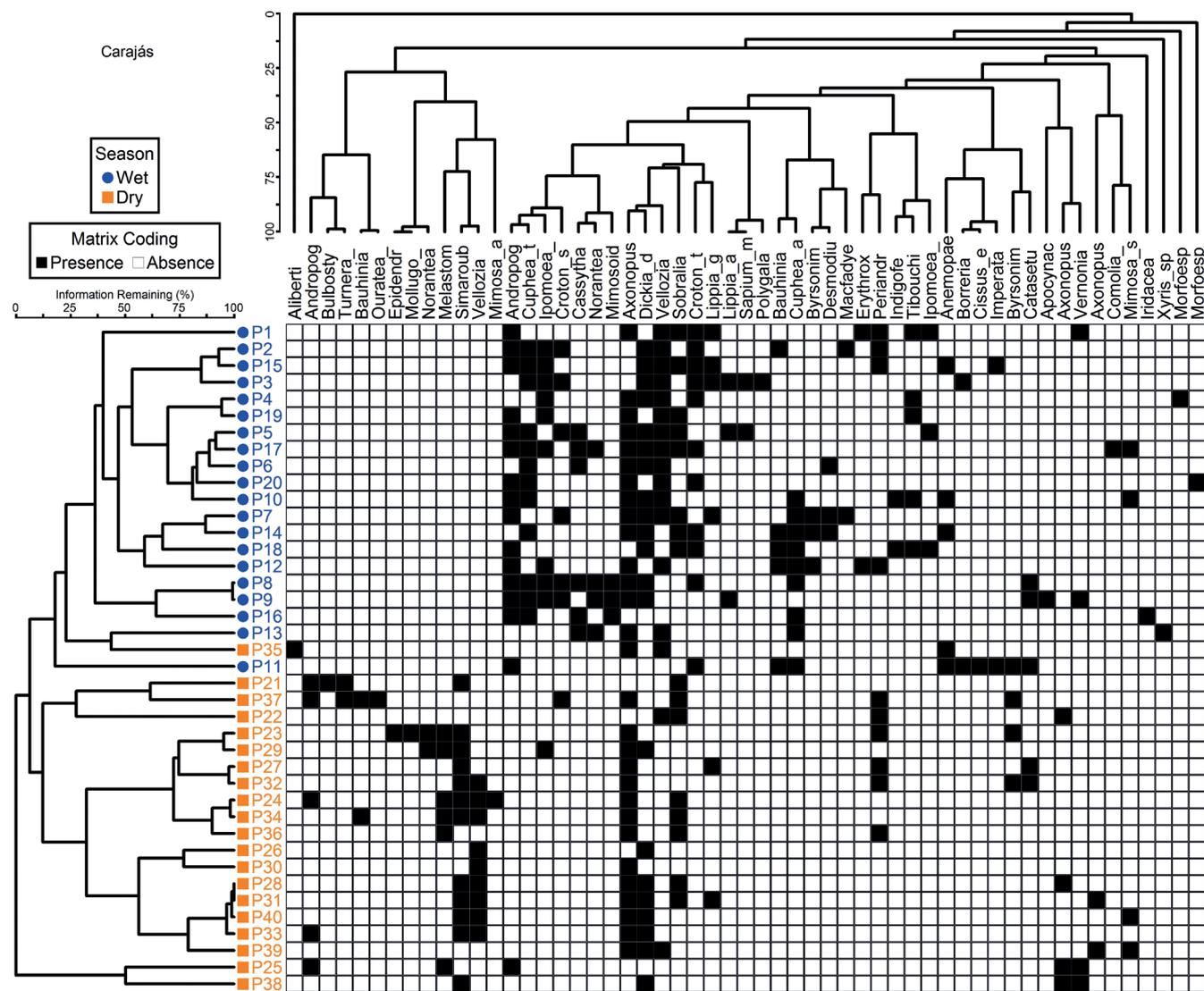


Figure 5 – Distribution of 55 species within 40 sampled plots installed in Carajás, Pará, Brazil, and distribution using two-way cluster dendrogram based on the Bray-Curtis dissimilarity metric.

tophysognomies of the campos rupestres. In fact, these communities are responsible for a large part of the diversity and endemism of these ecosystems (Alves et al. 2014; Fernandes 2016). In contrast, our study reveals that soil fertility does not explain the temporal variation in species richness and composition of herbaceous communities.

Therefore, we emphasize that, when studying the diversity of herbaceous communities, one should consider both spatial variations using the environmental gradients approach, as well as seasonal environmental variation. It has been reported that in rocky outcrops (i.e., campos rupestres, inselbergs), where there is a considerable water deficit, annual short cycle species (i.e., ephemeral plants) are common (Silveira et al. 2016; Villa et al. 2018). These plants have developed an adaptive strategy to avoid the dry season and we

presume that they are responsible for the considerable species turnover during the dry season, when these ephemeral species are absent, thus determining the high beta diversity.

The high beta diversity may reflect a higher habitat heterogeneity, which can be induced by seasonal environmental changes (Heino et al. 2015; Tonkin et al. 2017; Bao et al. 2019), and species establish according to their degree of ecological tolerance (Pott & Silva 2015; Tonkin et al. 2017). We presume that despite the lack of difference in beta diversity between the seasons, and the effect of seasonality on beta diversity, it is observed that the environmental heterogeneity promoted by seasonality may lead to an increase in the number of coexisting species. In this context, seasonality probably causes divergence of the community composition (high beta diversity) by increasing environmental filtering (Myers et

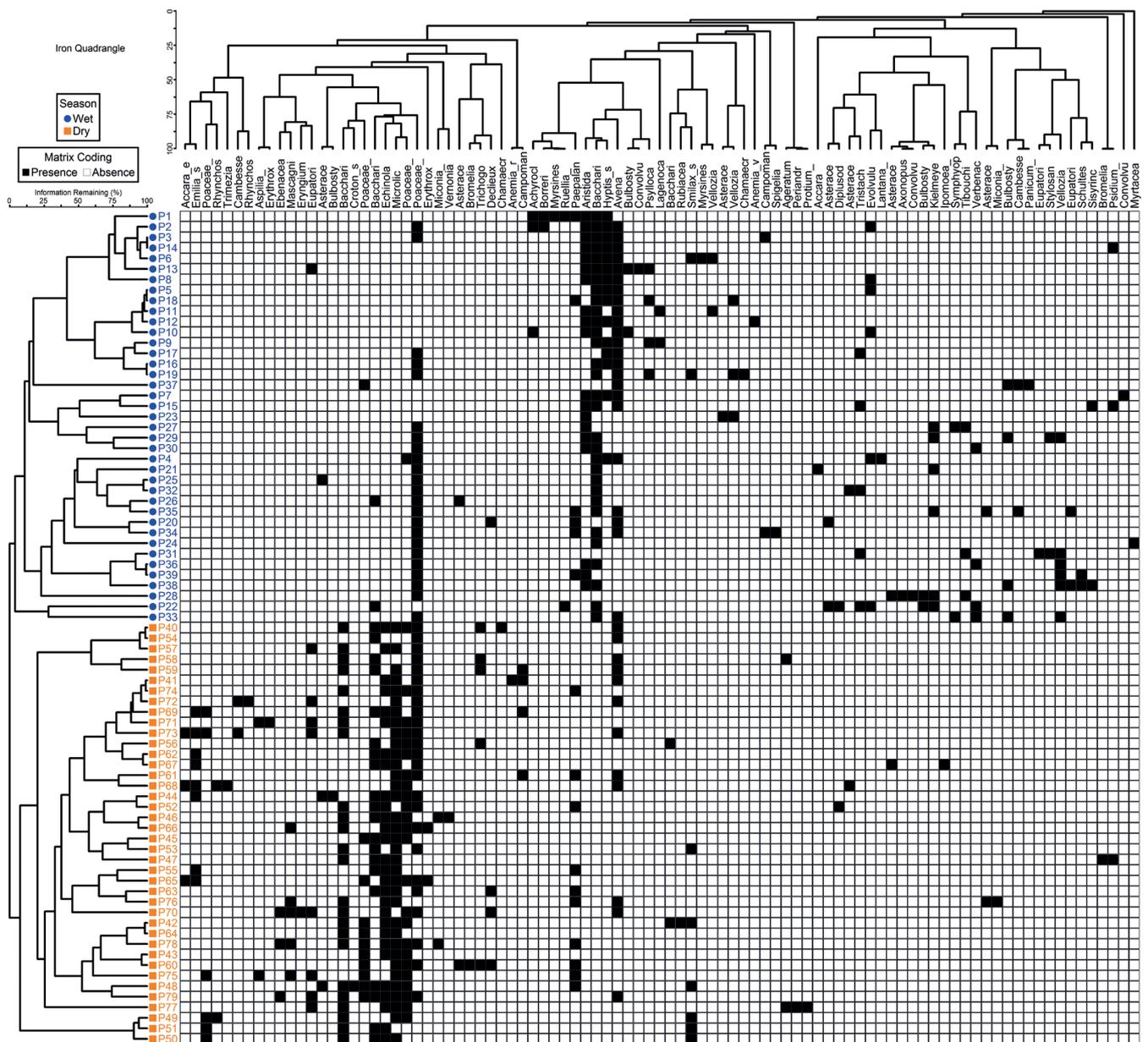


Figure 6 – Distribution of 91 species within 79 sampled plots installed in quartzite Iron Quadrangle, Minas Gerais, Brazil, and distribution using two-way cluster dendrogram based on the Bray-Curtis dissimilarity metric.

al. 2015; Bao et al. 2019). For example, the seasonality of precipitation can regulate the water availability in the soil, which, in turn, regulates species richness and the abundance of seedlings from the seed bank (Bao et al. 2017).

CONCLUSION

The herbaceous species composition and beta diversity is considerably different between seasons on the two rocky outcrops studied. However, species richness did not differ between seasons at either site, which had similar species turnovers that maintained the differences in species composition. Our result corroborates the hypothesis that seasonality determined by changes between the dry and the wet season determines beta diversity, but not species richness. However, soil fertility determined by variability of nutrient-related soil properties has no effect on species composition and beta diversity. Finally, we suggest that future studies on herbaceous community assemblies in lithologically different rocky outcrops should evaluate the temporal effect of the environment, such as the seasonal variation of precipitation; as well as the species responses to the temporal resource variability.

SUPPLEMENTARY FILES

Five supplementary files are associated with this paper:

Supplementary file 1: Precipitation patterns of study sites during the survey period.

<https://doi.org/10.5091/plecevo.2020.1668.2155>

Supplementary file 2: Spearman correlation coefficients between soil properties and PCA axes from Carajás, Pará, Brazil.

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Supplementary file 3: Spearman correlation coefficients between soil properties and PCA axes from Iron Quadrangle, Minas Gerais, Brazil.

<https://doi.org/10.5091/plecevo.2020.1668.2159>

Supplementary file 4: List of species from canga in Carajás, Pará, Brazil.

<https://doi.org/10.5091/plecevo.2020.1668.2161>

Supplementary file 5: List of species from quartzite Iron Quadrangle, Minas Gerais, Brazil.

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REFERENCES

Alizadeh K., Matthias I., Rodríguez-Zorro P.A., Hermanowski B., da Costa M.L., Behling H. (2017) Forest-savanna boundary shift on the plateau of Serra Sul dos Carajás (southeastern Amazonia) since the mid-Holocene; driving forces and limiting factors. *Quaternary International* 449: 12–21. <https://doi.org/10.1016/j.quaint.2017.07.001>

- Alvares C.A., Stape J.L., Sentelhas P.C., de Moraes G.J.L., Sparovek G. (2014) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22(6): 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Alves R.J.V., Silva N.G., Oliveira J.A., Medeiros D. (2014) Circumscribing campo rupestre – megadiverse Brazilian rocky montane savanas. *Brazilian Journal of Biology* 74(2): 355–362. <http://doi.org/10.1590/1519-6984.23212>
- Alves Silva W., Villa P.M., Schaefer C.E.G., Ferreira-Júnior W.G., Campos P.V., Fialho I.F., Neri A.V. (2019) Diversity and life-forms of a woody-herbaceous community on the quartzite rocky complexes in the Brazilian Iron Quadrangle. *Revista de Biologia Tropical* 67(3): 357–369.
- Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26(1): 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson M.J. (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62(1): 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>
- Anderson M.J., Crist T.O., Chase J.M., Vellend M., Inouye B.D., Freestone A.L., Sanders N.J., Cornell H.V., Comita L.S., Davies K.F., Harrison S.P., Kraft N.J.B., Stegen J.C., Swenson N.G. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14(1): 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Bao F., Elsey-Quirk T., Assis M.A., Pott A. (2017) Seed bank of seasonally flooded grassland: Experimental simulation of flood and post-flood. *Aquatic Ecology* 52: 93–105. <https://doi.org/10.1007/s10452-017-9647-y>
- Bao F., Elsey-Quirk T., Assis M.A., Arruda R., Pott A. (2018) Seasonal flooding, topography, and organic debris interact to influence the emergence and distribution of seedlings in a tropical grassland. *Biotropica* 50(4): 616–624. <https://doi.org/10.1111/btp.12550>
- Bao F., Villa P.M., Rodrigues A.C., Schmitz D., Assis M.A., Arruda R., Pott A. (2019) Topography and seasonality promote taxonomic beta diversity of seedlings in a tropical wetland. *Oecologia Australis* 23: 917–925. <https://doi.org/10.4257/occo.2019.2304.15>
- Bates D., Mächler M., Bolker B., Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bates D., Maechler M., Bolker B., Walker S., Christensen R.H.B., Singmann H., Dai B., Scheipl F., Grothendieck G., Green P. (2017) 'lme4' package: Linear mixed-effects models using eigen and S4. Available at <https://cran.r-project.org/web/packages/lme4/lme4.pdf> [accessed 11 May 2020].
- 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. *Brazilian Journal of Botany* 30: 569–577. <http://doi.org/10.1590/S0100-84042007000400003>
- Braun-Blanquet J. (1979) Fitosociología. Bases para el estudio de las comunidades vegetales. Madrid, H. Blume Ediciones.
- Campos P.V., Villa P.M., Nunes J.A., Schaefer C.E.G.R., Poremsbki S., Neri A.V. (2018) Plant diversity and community structure of Brazilian Páramos. *Journal of Mountain Science* 15: 1186–1198. <https://doi.org/10.1007/s11629-017-4674-7>
- 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 Monographs* 84(1): 45–67. <https://doi.org/10.1890/13-0133.1>

- 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(1): 3–21. <https://doi.org/10.1093/jpe/rtr044>
- Crawley M.J. (2013) *The R Book*. Second edition. London, Wiley.
- Dinakar C., Djilianov D., Bartels D. (2012) Photosynthesis in desiccation tolerant plants: Energy metabolism and antioxidative stress defense. *Plant Science* 182: 29–41. <https://doi.org/10.1016/j.plantsci.2011.01.018>
- Duong T.T., Nguyen H.Y., Le T.P., Nguyen T.Q., Tran T.T.H., Le N.D., Dang D.K., Vu T.N., Panizzo V, McGowan S. (2019) Transitions in diatom assemblages and pigments through dry and wet season conditions in the Red River, Hanoi (Vietnam). *Plant Ecology and Evolution* 152(2): 163–177. <https://doi.org/10.5091/plecevo.2019.1627>
- EMBRAPA – Empresa Brasileira de Pesquisa Agropecuária (1997) *Manual de métodos de análises de solo*. Second edition. Rio de Janeiro, Ministério da Agricultura e do Abastecimento. [In Portuguese].
- FAO, IIASA, ISRIC, ISSCAS, JRC (2012) *Harmonized world soil database (version 1.2)*. Rome, Italy & Laxenburg, Austria, FAO & IIASA.
- Fernandes G.W. (2016) The megadiverse rupestrian grassland. In: Fernandes G.W. (ed.) *Ecology and conservation of mountaintop grasslands in Brazil*: 3–14. Cham, Springer International Publishing. https://doi.org/10.1007/978-3-319-29808-5_1
- Ferrari L.T., Schaefer C.E.G.R., Fernandes R.B.A., Mendonça B.A.F., Gjorup D.F., Corrêa G.R., Senra E.O. (2016) Thermic and hydric dynamics of ironstone (Canga) and quartzite rupestrian grasslands in the Quadrilátero Ferrífero: The ecological importance of water. In: Fernandes G.W. (ed.) *Ecology and conservation of mountaintop grasslands in Brazil*: 71–85. Cham, Springer International Publishing. https://doi.org/10.1007/978-3-319-29808-5_4
- Ferreira M.S., Delpupo G.G.V., Vieira M.V., Silva R.C. (2017) Climate-driven variation in space use by the neotropical marsupial *Metachirus nudicaudatus*. *Oecologia Australis* 21(4): 450–454. <https://doi.org/10.4257/oeco.2017.2104.09>
- Figueira J.E.C., Ribeiro K.T., Ribeiro M.C., Jacobi C.M., Franc A. H., Neves A.C.O., Conceição A.A., Mourão F.A., Souza J.M., Miranda C.A.K. (2016) Fire in rupestrian grasslands: plant response and management. In: Fernandes G.W. (ed.) *Ecology and conservation of mountaintop grasslands in Brazil*: 415–448. Cham, Springer International Publishing. https://doi.org/10.1007/978-3-319-29808-5_18
- Gröger A., Huber O. (2007) Rock outcrop habitats in the Venezuelan Guayana lowlands: their main vegetation types and floristic components. *Brazilian Journal of Botany* 30(4): 599–609. <https://doi.org/10.1590/S0100-84042007000400006>
- Heino J., Melo A.S., Bini L.M. (2015) Reconceptualising the beta diversity environmental heterogeneity relationship in running water systems. *Freshwater Biology* 60(2): 223–235. <https://doi.org/10.1111/fwb.12502>
- Hsieh T.C., Ma K.H., Chao A. (2016) ‘iNEXT’: iNterpolation and EXTrapolation for species diversity (Version 2.0.12). Available at <https://cran.r-project.org/web/packages/iNEXT/iNEXT.pdf> [accessed 11 May 2020].
- Husson F., Lê S., Pagès J. (2017) *Exploratory Multivariate Analysis by Example Using R*. Second edition. New York, Chapman & Hall/CRC.
- Instituto Nacional de Meteorologia – INMET (2020) Available at <http://www.inmet.gov.br/portal/> [accessed 4 May 2020].
- Jacobi C.M., Do Carmo F.F., Vincent R.C., Stehmann Jr. (2007) Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodiversity and Conservation* 16: 2185–2200. <https://doi.org/10.1007/s10531-007-9156-8>
- Klanderud K., Vandvik V., Goldberg D. (2015) The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLOS ONE* 10(6): e0130205. <https://doi.org/10.1371/journal.pone.0130205>
- Koleff P., Gaston K.J., Lennon J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology* 72(3): 367–382. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>
- Le Bagousse-Pinguet Y., Gross N., Maestre F.T., Maire V., de Bello F., Fonseca C.R., Kattge J., Valencia E., Leps J., Liancourt P., Avolio M. (2017) Testing the environmental filtering concept in global drylands. *Journal of Ecology* 105(4): 1058–1069. <https://doi.org/10.1111/1365-2745.12735>
- Lopes M.N.G., De Souza E.B., Ferreira D.B.S. (2013) Climatologia Regional da Precipitação no Estado do Pará. *Revista Brasileira de Climatologia* 12: 84–102. <https://doi.org/10.5380/abclima.v12i1.31402>
- Lüttge U. (1997) *Physiological ecology of tropical plants*. Berlin & Heidelberg, Springer Verlag. <https://doi.org/10.1007/978-3-540-71793-5>
- Martinelli G., Moraes M.A. (2013) *Livro Vermelho da Flora do Brasil*. First Edition. Rio de Janeiro, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.
- McCain C., Grytnes J.-A. (2010) Elevational gradients in species richness. *Encyclopedia of Life Sciences (eLS)*: 1–10. <https://doi.org/10.1002/9780470015902.a0022548>
- Mota G.S., Luz G.R., Mota N.M., Silva Coutinho E., Veloso D.M., Das. M., Fernandes G.W., Nunes Y.R.F. (2018) Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in southeastern Brazil. *Flora* 238: 32–42. <https://doi.org/10.1016/j.flora.2017.03.010>
- Myers J.A., Chase J.M., Crandall R.M., Jimenez I. (2015) Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology* 103(5): 1291–1299. <https://doi.org/10.1111/1365-2745.12436>
- Negreiros D., Le Stradig S., Wilson Fernandes G., Rennó H.C. (2014) CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. *Plant Ecology* 215: 379–388. <https://doi.org/10.1007/s11258-014-0302-6>
- 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(5): 771–779. <https://doi.org/10.1093/jpe/rtw088>
- Nunes J.A., Schaefer C.E.G.R., Ferreira-Junior W.G., Neri A.V., Correa G.R., Enright N.J. (2015) Soil-vegetation relationships on a banded ironstone ‘island’, Carajás Plateau, Brazilian Eastern Amazonia. *Anais da Academia Brasileira de Ciências* 87(4): 2097–2110. <https://doi.org/10.1590/0001-376520152014-0106>
- Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlenn D., Minchin P.R., O’Hara R.B., Simpson G.L., Solyomos P. et al. (2018) *Vegan: Community ecology package*. R package version 2.0-7. Available at <https://cran.r-project.org/web/packages/vegan/index.html> [accessed 11 May 2020].
- Peel G.T., Araújo M.B., Bell J.D., Blanchard J., Bonebrake T.C., Chen I.C., Clark T.D., Colwell R.K., Danielsen F., Evengård B., Falconi L., Ferrier S., Frusher S., Garcia R.A., Griffiths R.B., Hobday A.J., Janion-Scheepers C., Jarzyna M.A., Jennings S., Lenoir J., Linnetved H.I., Martin V.Y., McCormack P.C., Mc-

- Donald J., Mitchell N.J., Mustonen T., Pandolfi J.M., Pettorelli N., Popova E., Robinson S.A., Scheffers B.R., Shaw J.D., Sorte C.J.B., Strugnell J.M., Sunday J.M., Tuanmu M.N., Vergés A., Villanueva C., Wernberg T., Wapstra E., Williams S.E. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355 (6332): eaai9214. <https://doi.org/10.1126/science.aai9214>
- Poorter L., Rozendaal D.M.A., Bongers F., Almeida-Cortez J.S., Zambrano A.M., Álvarez F.S., et al. (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution* 3: 928–934. <https://doi.org/10.1038/s41559-019-0882-6>
- Pott A., Silva J.S.V. (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I., Assine M.L. (eds) Dynamics of the Pantanal Wetland in South America. *The Handbook of Environmental Chemistry* vol. 37: 111–131. https://doi.org/10.1007/698_2015_352
- Prata E., Teixeira A., Joly C., Assis M. (2018) The role of climate on floristic composition in a latitudinal gradient in the Brazilian Atlantic Forest. *Plant Ecology and Evolution* 151(3): 303–313. <https://doi.org/10.5091/plecevo.2018.1407>
- R Core Team (2017) R: A language and environment for statistical computing. Version 3.2.2. Vienna, Austria, R Foundation for Statistical Computing. Available at <https://www.R-project.org/> [accessed 11 May 2020].
- R Core Team (2019) R: A language and environment for statistical computing. Version 3.6.0. Vienna, Austria, R Foundation for Statistical Computing. Available at <https://www.R-project.org/> [accessed 11 May 2020].
- Royo A., Ristau T. (2013) Stochastic and deterministic processes regulate spatio-temporal variation in seed bank diversity. *Journal of Vegetation Science* 24(4): 724–734. <https://doi.org/10.1111/jvs.12011>
- Rozendaal D.M.A., Bongers F., Aide T.M., Alvarez-Dávila E., Ascarrunz N., Balvanera P., et al. (2019) Biodiversity recovery of Neotropical secondary forests. *Science Advances* 5(3): eaau3114. <https://doi.org/10.1126/sciadv.aau3114>
- Ruhí A., Datry T., Sabo J.L. (2017) Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conservation Biology* 31(6): 1459–1468. <https://doi.org/10.1111/cobi.12906>
- Schaefer C.E.G.R., Corrêa G.R., Candido H.G., Arruda D.M., Nunes J.A., Araujo R.W., Rodrigues P.M.S., Fernandes Filho E.I., Pereira A.F.S., Brandão P.C., Neri A.V. (2016) The physical environment of rupestrian grasslands (campos rupestres) in Brazil: Geological, geomorphological and pedological characteristics, and interplays. In: Fernandes G.W. (ed.) Ecology and conservation of mountaintop grasslands in Brazil: 15–53. Cham, Springer International Publishing. https://doi.org/10.1007/978-3-319-29808-5_2
- Schmitz D., Schaefer C.E.R.G., Putzke J., Francelino M.R., Ferrari F.R., Corrêa G.R., Villa P.M. (2020) How does the pedoenvironmental gradient shape non-vascular species assemblages and community structures in Maritime Antarctica? *Ecological Indicators* 108: 105726. <https://doi.org/10.1016/j.ecolind.2019.105726>
- Shimadzu H., Dornelas M., Henderson P.A., Magurran A.E. (2013) Diversity is maintained by seasonal variation in species abundance. *BMC Biology* 11: 98. <https://doi.org/10.1186/1741-7007-11-98>
- Silva M., Secco R., Lobo M. (1996) Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. *Acta Amazonica* 26(1–2): 17–44. <https://doi.org/10.1590/1809-43921996261044>
- Silva W.A., Villa P.M., Schaefer C.E.G.R., Ferreira Júnior, W.G., Campos P.V., Fialho I.F., Neri A.V. (2019) Diversity and life-forms of a woody herbaceous community on the quartzite rocky complexes in the Brazilian Iron Quadrangle. *Revista de Biologia Tropical* 67: 357–369.
- 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. (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil* 403: 129–152. <https://doi.org/10.1007/s11104-015-2637-8>
- Tonkin J.D., Bogan M.T., Bonada N., Rios-Touma B., Lytle D.A. (2017) Seasonality and predictability shape temporal species diversity. *Ecology* 98(5): 1201–1216. <https://doi.org/10.1002/ecy.1761>
- Tuomisto H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33(1): 2–22. <https://doi.org/10.1111/j.1600-0587.2009.05880.x>
- Ulrich W., Soliveres S., Maestre F.T., Gotelli N.J., Quero J.L., Delgado-Baquerizo M., et al. (2014) Climate and soil attributes determine plant species turnover in global drylands. *Journal of Biogeography* 41(12): 2307–2319. <https://doi.org/10.1111/jbi.12377>
- Villa P.M., de Siqueira Cardinelli L., Magnago L.F., Heringer G., Martins S.V., Campos P.V., Rodrigues A.C., Neri A.V., Meira-Neto J.A.A. (2018) 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(2): 937–951. <https://doi.org/10.15517/RBT.V66I2.33424>
- Villa P.M., Pérez-Sánchez A.J., Nava F., Acevedo A., Cadenas D.A. (2019a) Local-scale seasonality shapes anuran community abundance in a cloud forest of the tropical Andes. *Zoological Studies* 58: 17. <https://doi.org/10.6620/ZS.2019.58-17>
- Villa P.M., Martins S.V., Rodrigues A.C., Vieira N., Bonilla M.A., Ali A. (2019b) Testing species abundance distribution models in tropical forest successions: implications for fine-scale passive restoration. *Ecological Engineering* 135: 28–35. <https://doi.org/10.1016/j.ecoleng.2019.05.015>
- Vincent R.C. (2004) Florística, Fitossociologia e relações entre a vegetação e o solo em áreas de campos ferruginosos no Quadrilátero Ferrífero, Minas Gerais. Ph.D. thesis, Universidade de São Paulo, São Paulo, Brazil.

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