UNIVERSIDADE FEDERAL DE SÃO CARLOS
DEPARTAMENTO DE CIÊNCIAS AMBIENTAIS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS AMBIENTAIS

PADRÕES FILOGENÉTICOS DE COMUNIDADES VEGETAIS EM UM GRADIENTE ALTITUDINAL NA SERRA DO CIPÓ, MINAS GERAIS, BRASIL

JACQUELINE SALVI DE MATTOS

São Carlos – SP
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“The love for all living creatures is the most noble attribute of man.”

“O amor por todas as criaturas que vivem é o atributo mais nobre do ser humano.”

– Charles Darwin

RESUMO

DE MATTOS, J.S. Padrões filogenéticos de comunidades vegetais em um gradiente altitudinal na Serra do Cipó, Minas Gerais, Brasil. 2019. 97f. Dissertação de Mestrado em Ciências Ambientais – Universidade Federal de São Carlos, São Carlos, 2019.

Desde o ínicio dos estudos da ecologia, cientistas se preocupam em explorar como comunidades naturais se estruturam no espaço o no tempo. Montanhas costumam ser ótimos sistemas para estudar essaes padrões de diversidade e também como os fatores ambientais podem atuar nessa estruturação. A diversidade filogenética incorpora a história evolutiva das espécies, e juntamente de outros métodos de distribuição de espécies pode ajudar na investigação de padrões biogeográficos. No presente trabalho nós utilizamos quatro métricas de diversidade filogenética e espacial (riqueza filogenética de espécies, variabilidade filogenética de espécies, escore de sobrerepresentação específica e divergência geográfica de nós) e sua relação com filtros ambientais, utilizando o gradiente de altitude da Serra do Cipó, MG, como objeto de estudo e testando a influência do conservadorismo de nicho e da alopatria de nós. Estudamos a flora vascular dos campos rupestres da Serra do Cipó, localizada na Cadeia do Espinhaço, sudeste do Brasil. Colocamos 180 quadrados de 1m² em cinco áreas ao longo do gradiente de altitude (variando de 800 a 1400m) e coletamos todas as espécies de angiospermas presentes nos mesmos. Coletamos também propriedades do solo, declividade e valores de altitude. A variabilidade filogenética de espécies diminuiu com a altitude, enquanto a riqueza filogenética de espécies aumentou. Assim, o número de espécies e a agregação filogenética aumentou em áreas mais elevadas. Ambas as métricas tiveram relações significativas com variáveis edáficas, como pH, Nitrogênio, Fósforo e Potássio, assim nos levando a afirmar que a intensidade dos filtros ambientais também aumentou com a altitude. Enquanto isso, encontramos também três nós alopátricos na filogenia, que separam: Dicotiledôneas de Monocotiledôneas, Eriocaulaceae de Poaceae e Xyridaceae de Cyperaceae.

Com isso pudemos revelar os nós com maiores valores de divergência geográfica e ambiental, o que pôde revelar também as mudanças biogeográficas nas suas distribuições. Por fim, concluímos que existe um padrão de diversidade filogenética e estrutural ao longo do gradiente de altitude na Serra do Cipó e também em consequência da grande variação de propriedades do solo. Assim, as espécies vegetais de campos rupestres devem apresentar seus principais traços conservados e serem influenciadas, em maior parte, por filtros ambientais.

Palavras-chave: Campos rupícolas. Diversidade Filogenética. Biogeografia. Alopatria de nós. Evolução. Diversidade vegetal.

RESUMO EM LÍNGUA ESTRANGEIRA

Since the beginning of ecology studies, scientists have been worried in exploring natural communities and how the vary across time and space, looking for patterns to describe. Mountains are often great systems to study these patterns of diversity and how environmental factors can shape them. Phylogenetic diversity, one of the ways of measuring biological diversity, incorporates the evolutionary history of species, and along with other methods of species distributions, can help in the investigation of biogeographic patterns in many scales. In the present study, we used four metrics of phylogenetics diversity and spatial structure (phylogenetic species richness, phylogenetics species variability, specific overrepresentation score and geographic node divergence) and their relationship to environmental filters, along an elevational gradient, to study the influence of niche conservatism and node allopatry. We have studied the vascular plant flora of rocky grasslands in the Cipó Mountains, located in the Espinhaço Range, Southeastern Brazil. We allocated 180 1m² plots in five areas along the altitude gradient (ranging from 800 to 1400 m) and collected all angiosperm species present in those. We also collected soil properties and declivity. The phylogenetic species variability decreased with altitude, whereas richness increased. Therefore, the clustering of species increased towards more elevated areas. Both metrics presented significate relationships with environmental variables such as pH, nitrogen, phosphorus and potassium, confirming that intensity of environmental filters have also increased with altitude. Regarding the other two metrics, we found three allopatric nodes in the phylogeny, which separates: Monocots from Eudicots, Eriocaulaceae from Poaceae, Xyridaceae from Cyperaceae. With that we could reveal the nodes with the higher degrees of environmental and geographic divergence, which could also lead to exploration of major biogeographical changes in their distributions. Finally, we concluded that there is a pattern of phylogenetic diversity and structure along the environmental gradient of the Cipó Mountains. Thus, plant species from rocky grasslands probably have their main traits conserved, and mostly, are shaped by environmental filters.

Key-words: Rocky grasslands. Phylogenetic Diversity. Biogeography. Node allopatry. Evolution. Plant diversity.

SUMÁRIO

1. Introdução Geral

Cientistas tentam entender como as comunidades naturais variam desde o início da Ecologia, principalmente no que diz respeito à sua variação e coexistência no espaço e no tempo (Palmer 1994). Alguns padrões de diversidade como relacão da riqueza de espécies com área, latitude, produtividade e isolamento em ilhas já foram identificados há muitos anos (McIntosh 1985, Huston 1994, Rosenzweig 1995). Até hoje, no entanto, ainda é difícil fazer previsões assertivas sobre esses padrões (Peters 1991, Ricklefs 2004). O mais comum é utilizar o número de espécies para estimativas de diversidade (Magurran 2004), mas esse índice de riqueza pode ser um tanto contraditório e simplista, pois quando o fazemos consideramos espécies de uma comunidade como sendo idênticas (Cianciaruso et al. 2009). Para evitar esse problema, além da riqueza, podemos medir também a diversidade funcional, que considera atributos funcionais de cada espécie nesta conta (Petchey e Gaston 2002), mas que apresenta um problema prático ao ter a necessidade de medir todos os traços de interesse (Pausas e Verdú 2010).

Uma outra boa opção para se estimar a biodiversidade é chamada de ‘diversidade filogenética’, que incorpora a história evolutiva de espécies de uma mesma comunidade (Magurran 2004). Quanto maior for a história evolutiva das espécies, ou seja, quanto menos aparentadas forem as espécies, maior é a diversidade filogenética (Magurran 2004). Neste trabalho, utilizamos dois índices de diversidade filogenética muito interessantes: a “Variabilidade Filogenética de Espécies” ("Phylogenetic Species Variability" ou PSV) e a “Riqueza Filogenética de Espécies” ("Phylogenetic Species Richness" ou PSR). O PSV quantifica, em média, o quão aparentadas são as espécies de uma comunidade, enquanto o PSR combina o número de espécies e o parentesco (Helmus et al. 2007). Ainda, se os traços dessas espécies forem conservados, a diversidade filogenética consegue prover informação sobre a história evolutiva e a similaridade funcional, levando a pistas sobre os padrões estruturais dessas comunidades e também sobre os fatores ambientais que os determinam (Marchese 2015).

Gradientes ambientais são ótimos para se estudar padrões de diversidade e como as comunidades estão estruturadas no espaço, uma vez que a composição de comunidades está relacionada a fatores ambientais (Helmus et al. 2007). Esses fatores podem, em diversas ocasiões, mudar paulatinamente e formar gradientes onde atuam com diferentes intensidades (Qian et al. 2014). A latitude como gradiente ambiental foi um dos primeiros padrões a serem estudados, existindo uma relação inversamente proporcional entre a diversidade de espécies e a latitude (Mittelbach et al. 2007). A Teoria do Conservadorismo de Nicho é uma das possiveis explicações para tal padrão, e postula que as linhagens de espécies tendem a se manter estáveis ao longo do tempo, mantendo, em geral, seus traços conservados (Wiens et al. 2010). No que se foi estudado até hoje, as espécies teriam se originado em ambientes tropicais e, à medida que se afastaram dos trópicos, o número de espécies que seriam capazes de suportar as diferentes condições diminuiria (Wiens et al. 2010). Uma vez que os traços sejam conservados, esperaríamos uma agregação filogenética, ou seja, espécies aparentadas coocorrendo no espaço (Webb et al. 2002). No entanto, pode não haver esse conservadorismo de nicho e os traços serem convergentes, o que levaria a uma dispersão filogenética (Webb et al. 2002). Um outro possível cenário não apresenta fatores ambientais como principal força estruturando as comunidades – havendo a predominância, por exemplo, da competição interespecífica – e, assim, as comunidades seriam dispersas filogeneticamente se os traços fossem conservados ou seriam aleatórias, caso os traços fossem convergentes (Webb et al, 2002).

Para estudos de biogeografia, podemos integrar a diversidade filogenética e a distrbuição de espécies, utilizando abordagens baseadas em sítios e em clados, ou ainda uma combinação de ambas. Abordagens baseadas em sítios utilizam filogenias para estudar o quão aparentadas são as espécies de uma comunidade, mas às vezes podem ser simplistas demais. Abordagens baseadas em clados conseguem estudar a distribuição de clados individualmente e responder questões sobre a alopatria como um modo de especiação (Borregaard et al. 2014). Utilizar uma combinação de ambas as abordagens pode ser muito vantojoso, e por isso utilizamos duas métricas de Borregaard et al. (2014) que nos permite estudar a alopatria de nós e padrões macroevolutivos de maneira mais efetiva. A primeira métrica é o "escore de sobre-representação específica" (do inglês *specific overrepresentation score*), que percorre os nós de uma árvore filogenética e compara o número de espécies de clados irmãos em cada comunidade com o que seria esperado pelo acaso. Esses escores podem ser resumidos para todas as comunidades de modo a produzir a segunda métrica, chamada de "divergência geográfica de nós" (do inglês *geographic node divergence*), que quantifica a divergência espacial entre dois clados irmãos de um dado nó e identifica quais nós são os principais responsáveis pelos padrões espaciais observados de diversidade filogenética e alopatria (Borregaard et al. 2014). O uso de tal abordagem pode ser uma estratégia poderosa para detectar de forma mais minuciosa padrões nas comunidades e distinguir diferentes processos biogeográficos por trás deles (Graham et al. 2016). Além disso, estudar alopatria de nós é interessante, pois a especiação alopátrica parece ser o modo de especiação mais comum em comunidades naturais (Barraclough and Vogler 2000).

Gradientes altitudinais são ótimos sistemas para testar as relações entre diversidade filogenética, fatores ambientais e alopatria de nós. Um gradiente de altitude é análogo a um gradiente de latitude em aspectos como as mudanças de temperatura, a qual representa um fator primário agindo nos padrões de diversidade (Mittelbach et al. 2007), possuindo ainda a vantagem de que tais mudanças ocorrem em escalas espaciais muito menores. Por esse motivo, ambientes montanhosos são propícios à esses estudos. A Cadeia do Espinhaço, no

Centro-Sul do Brasil, é uma cadeia de rochas muito antigas, a qual possui paisagens erodidas que se desenvolveram sob longa estabilidade tectônica (Silveira et al. 2016). Nossa área de estudo é a Serra do Cipó, que fica localizada na parte sul dessa Cadeia e tem suas paisagens dominadas por campos rupícolas, caracterizados por um mosaico de vegetações campestres, com predominância de ervas e arbustos, crescendo principalmente em afloramentos rochosos de arenito e quartzito (Silveira et al. 2016). Nessas paisagens, fragmentos de cerrado e florestas de galeria também ocorrem, e incêndios são muito comuns (Silveira et al. 2016). Nas regiões de campos rupícolas do Espinhaço há uma grande diversidade de espécies. Além disso, também encontramos um alto grau de endemismo e uma grande variedade de tipos vegetacionais ao longo da montanha – indo de cerrado nos locais mais baixos (abaixo de 900m) a campos rupícolas nos locais mais altos (acima de 900 m) (Silveira et al. 2016). Devido à longa estabilidade climática desses ambientes e também às rochas de idade muito antigas, muitas vezes datando do Pré-Cambriano (Alkmim 2012), os campos rupícolas podem ser considerados "paisagens antigas, tamponadas climaticamente e inférteis ("old, climatically buffered, infertile landscapes" ou OCBIL), um conceito que define ambientes muito antigos, com solos inférteis, e com altos níveis de diversidade e endemismo (Hopper 2009). Nessa paisagem, a diversidade de tipos vegetacionais é definida regionalmente por fatores como temperatura, precipitação, velocidade do vento e frequência de queimadas (Fernandes et al. 2016), e localmente por propriedades do solo, que mudam rapidamente ao longo desse gradiente altitudinal (Giulietti et al. 1987, Silveira et al. 2015, Fernandes et al. 2016).

Neste trabalho, o objetivo principal foi de investigar a diversidade filogenética e estrutural das comunidades vegetais no gradiente de altitude da Serra do Cipó. Por meio das métricas de Helmus et al. (2007) – '*phylogenetic species richness'* e *'phylogenetic species variability',* e de Borregaard et al. (2014) – '*geographic node divergence'* e *'specific overrepresentation score'*, nossa meta foi explorar como as espécies dessas montanhas são relacionadas evolutivamente e como se distribuem no espaço. Considerando que as linhagens de campos rupícolas e também de áreas montanhosas costumam possuir seus nichos conservados (Miazaki et al. 2015, Pugliesi & Rapini 2015, Machac et al. 2011, Qian et al. 2014, Zhang et al. 2016), e também que essas áreas passaram por intensos eventos biogeográficos e climáticos durante sua história geológica (Rapini et al. 2008), esperamos encontrar um padrão de estruturação dessas comunidades, bem como a diversidade filogenética diminuindo com a altitude (Rahbek 1995; McCain and Grytnes 2010; Smith et al. 2014). Quanto maior a altitude, mais rigoroso tende a ser o ambiente e, portanto, maior deve ser a intensidade dos filtros ambientais. Assim, espécies que ocorrem em uma dada comunidade podem ser restritas a alguns poucos clados (Silveira et al. 2015), e apenas alguns nós da árvore filogenética devem ser identificados com uma possível associação de divergências evolutivas com segregação espacial (Borregaard et al. 2014).

2. PLANT PHYLOGENETIC DIVERSITY OF ROCKY GRASSLANDS IN SOUTHEASTERN BRAZIL: LOCAL AND REGIONAL CONSTRAINTS

Abstract – Mountains are interesting systems for studying patterns of diversity distribution and the role of environmental filters and competition on community assembly. According to the phylogenetic niche conservatism theory, the co-occurrence of closely related species might indicate that environmental filters are more important than competition when structuring communities in time and space. We investigated the patterns of phylogenetic diversity and the influence of environmental filters in the Brazilian rocky grasslands and tested the influence of phylogenetic niche conservatism. We placed 180 1 m^2 plots in five sites along an altitudinal gradient at the Cipó Mountains (Espinhaço Range, southeastern Brazil) and surveyed vascular plant species and edaphic variables. We assessed the phylogenetic diversity of the communities calculating the phylogenetic species variability and phylogenetic species richness. Then, we related them with altitude and the edaphic variables through multiple regressions. Phylogenetic species variability decreased with altitude, whereas phylogenetic species richness increased. Thus, the number of species and the degree of phylogenetic clustering increased with altitude. Both phylogenetic diversity metrics were significantly related with edaphic variables, such as pH, nitrogen, phosphorous, and potassium, suggesting that the intensity of abiotic factors acting as environmental filters increased with altitude, constraining species in the community to a smaller number of clades.

Key words: cerrado, community assembly rules, elevational gradient, Espinhaço Range, mountain grasslands, rupestrian grasslands.

2.1 Introduction

It has long been recognized that biological communities are somehow structured along habitats (Lomolino 2001), which generally influences the species distribution. For example, species richness along latitudes and altitudes are probably the oldest known patterns of species distribution in Ecology and had already been noticed by Alexander von Humboldt, Alfred Wallace, and Charles Darwin back in the 1800s (Lomolino 2001). Although changes in species composition and distribution of biological communities have long been known, we still lack predictive power towards the evolutionary processes acting on these patterns (Ricklefs 2004). Measuring biological diversity has also been a widely used approach for investigating communities, and a simple way to do that is by counting the number of species (Magurran 2004). More recently, biological diversity has been assessed by estimating the phylogenetic diversity of a community, which incorporates the evolutionary history of the species and may be assessed using the current molecular and analytical tools for generating phylogenies (Webb et al. 2002).

Evolutionary history has been widely used in the fields of community ecology, macroecology, and conservation biology (Webb et al. 2002, Parra et al. 2010). Nowadays, due to many different methods to build megaphylogenies for a variety of taxonomic groups and to analyse phylogenetic data (Smith et al. 2009, Leibold et al. 2010, Beaulieu et al. 2012), it is easier to study the evolutionary relationships of species. In this sense, new metrics and indices have arisen in the past few decades (Tucker et al. 2016), such as Faith’s phylogenetic diversity (Faith 1992), mean pairwise distance (Clarke & Warwick 1998, Webb et al. 2002), and net relatedness index (Webb 2000). Helmus et al. (2007a) proposed two metrics to estimate phylogenetic diversity: phylogenetic species variability (PSV) and phylogenetic species richness (PSR). They are both intuitive, because they account only for the variance of a neutral trait shared by all species in the community, giving the evolutionary relatedness among species in an easy statistical approach (Helmus et al. 2007a).

Ecological communities are assemblages of co-occurring species and are mainly structured and ruled by evolutionary processes, which can happen at different scales (Parra et al. 2010). Density-dependent interactions, such as competition, and abiotic factors, such as environmental filtering, act more at local scales, whereas extinction, speciation, and trait evolution act more regionally and throughout longer periods (Cavender-Bares et al. 2009). When we consider that assemblages of co-occurring species are predicted by their interactions and by the environment, we assume the concept of niche, the idea that species have specific environment requirements and constraints leading to their survival and relationships with other species (Hutchinson 1957). Niches tend to be conserved over time, and phylogenetically related species tend to be ecologically similar, the so-called "phylogenetic niche conservatism" (Losos 2008). Niche conservatism postulates that ecological differentiation between related species occurs less frequently than it would be expected if ecological diversification had occurred without evolutionary constraints (Losos 2008).

Environmental gradients are good models for assessing changes in community composition and structure and the evolutionary processes acting on the patterns of species diversity. As the latitudinal gradient, an altitudinal gradient also has changes in temperature, which is a primary factor acting on patterns of biodiversity (Mittelbach et al. 2007). Altitudinal gradients allow us to study changes in diversity at a smaller scale (Qian et al. 2014). In this sense, mountain landscapes are suitable to this kind of study. In southeastern Brazil, the Espinhaço Range is one of the largest mountain chains and is among the most ancient landscapes on Earth (Shaefer et al. 2016, Silveira et al. 2016). The landscape is strongly eroded and has evolved under extreme weathering and prolonged tectonic stability (Silveira et al. 2016, Shaefer et al. 2016). The Espinhaço Range mountaintops are covered by a vegetation complex that holds a high diversity of species, a high level of endemism, and a great variation of vegetation types, including the so-called "campo rupestre", rupestrian grassland, or rocky grassland (Fernandes et al. 2016, Silveira et al. 2016). Some sedimentary rocks from the Espinhaço Range are dated from the Precambrian (Alkmim 2012) and, because of that, the rocky grassland has been considered an "old, climatically buffered, infertile landscape" (Silveira et al. 2016), a concept that describes ancient communities with high levels of species richness, climate stability, and infertile soils (Hopper 2009). Some predictions associated with these old landscapes are found in the rocky grassland: reduced dispersability, increased local endemism, high degree of rarity, accentuated persistence, and nutritional specialisation (Hopper 2009, Lambers et al. 2014, Silveira et al. 2016, Morellato & Silveira 2018).

The Cipó Mountains present the second highest level of endemism in the Espinhaço Range (Echternacht et al. 2011). The rate of endemism is phylogenetically structured, and vicariance must have played an important role in the evolution of rocky grassland lineages (Echternacht et al. 2011). They harbour at least 1,590 angiosperm species (Silveira et al. 2016). In that ancient landscape, the rocky grasslands are characterised by poor, weathered, and acid soils, with limited water availability, and, thus, can be considered harsh environments (Silveira et al. 2016). The co-occurrence of different vegetation types are defined at local scales by edaphic factors, such as nutrient content, soil depth, and rockiness (Oliveira et al. 2015, Stradic et al. 2015, 2018, Shaefer et al. 2016). At regional scales, however, they are defined by changes on altitude-related factors, such as temperature, precipitation, wind speed, and drainage (Giulietti 1987, Fernandes et al. 2016, Shefer et al. 2016). The higher the altitude, the harsher the environment and, therefore, the higher the intensity of abiotic factors acting as environmental filters, which can restrain the species of a community to a smaller number of clades (Fernandes 2016, Silveira et al. 2016, Abrahão et al. 2018).

Many studies have addressed the relationship between altitude and patterns of species diversity. Whereas some quantitative studies showed that diversity may decrease with increasing altitude (Terborh 1977), others found a pattern called the "mid-domain effect” (Rahbek 1995), resulted from a unimodal curve in species richness pattern (Kromer et al. 2005; Samson et al. 2006). Qian et al. (2014), analysing the phylogenetic diversity of plant communities along an altitudinal gradient, showed that communities were more phylogenetically clustered at high altitudes and more dispersed in low ones, differing from what is usually found in the literature (Bryant et al. 2008). We investigated the local patterns of phylogenetic diversity and the influence of edaphic factors as key environmental filters along an altitudinal gradient in the Cipó Mountains. Because of previous findings regarding patterns of altitudinal gradients in species diversity (Rahbek 1995, McCain and Grytnes 2010, Smith et al. 2014) we expected that phylogenetic diversity of vascular flora – as estimated by the phylogenetic species variability and richness (Helmus et al. 2007a) – would decrease with altitude due to the increasing intensity of environmental filters (Zhang et al. 2016).

2.2 Methods

We carried out this study at the Cipó Mountains, the local designation of the mountains belonging to southern portion of the Espinhaço Range (19°10′–20′S and 43°30′–40′W), Minas Gerais State, southeastern Brazil (Figure 1). The area comprises de Serra do Cipó National Park and its buffer zone, Morro da Pedreira Environmental Protection Area. Soils are usually very shallow, with low nutrient content and high aluminum toxicity, over quartzite and sandstone substrates (Negreiros 2013, Stradic et al. 2018). The landscape is complex and comprises several vegetation types, varying with the physiographic conditions and altitude (Giulietti et al. 1987, Silveira et al. 2016). The cerrado predominates at altitudes lower than

900 m, a transition zone occurs around 900 m, and the rocky grassland dominates in altitudes higher than 1000 m (Fernandes et al. 2016). Regional climate is classified as Cwa according to Köppen (1931), with cold, dry winters and warm, wet summers.

At the study area, we assigned five study sites distributed in an altitudinal range from 800 to 1,400 m as follows: (1) "Rio Cipó", 821 masl (meters above sea level), with predominance of cerrado; (2) "Cedro", 1101 masl, (3) "Pedra do Elefante", 1255 masl, and (4) "Quadrante 16", 1303 masl with predominance of rocky grassland; and (5) "Alto Palácio", 1420 masl, with predominance of high altitude grassland (see Rocha et al. 2016 for descriptions). The sites represent a gradient of altitude-related variables estimated by the local weather stations at each site, considering mainly temperature, precipitation, humidity, atmospheric pressure, wind speed, and solar radiation (Fernandes et al. 2016). In general, the temperature decreases, whereas insolation and relative humidity increase with altitude. Annual precipitation tends to be higher at intermediate altitudes (Fernandes et al. 2016). During the year of 2016, at each site, we established four 270 m transects; along each we systematically set up nine 1 m² plots, every 30 m (Figure 1), summing 36 plots per site and a total of 180 plots in the area. We recorded the geographical coordinates, measured altitude and slope of each plot, and sampled all vascular plant species. We also collected superficial soil samples in the four corners of the plots, mixing them up to have one homogeneous soil sample per plot. The soil samples were analysed at the Federal University of Lavras, for measures of pH, N, P, K, Mg^{2+}, Ca^{2+}, Al^{3+}, sum of bases, base saturation, aluminum saturation, cation exchange capacity, and the proportions of sand, silt, and clay (Arruda et al. 2014). In these areas, the mosaic of microhabitats (mainly in relation to soil conditions) is very important for community composition as well (Silveira et al. 2016). We identified the plant species using identification keys (Mamede 1987, Wanderley 2011, Silva-Luz et al. 2012, Borges and Pirani 2013, Rando et al. 2013, Pscheidt 2015), comparing the vouchers with the reference collections, and with the help of taxonomists. Vouchers for the reproductive samples collected were lodged at the Herbarium Rioclarense (HRCB) of the São Paulo State University.

We checked species names on Plantminer (Carvalho et al. 2010) to look for synonyms and, then, built the phylogenetic tree with PhyloMaker (Qian & Jin 2016). We calculated two metrics of phylogenetic diversity (Helmus et al. 2007): phylogenetic species variability (PSV) and phylogenetic species richness (PSR). We built maps to show the different values for PSV and PSR along the altitude. PSV is independent of the species number and quantifies how the phylogenetic relatedness decreases the variance of some non-specified neutral trait shared by all species in the samples (Helmus et al. 2007), representing the mean phylogenetic difference among the taxa in a community (Tucker et al. 2016). Speciation will occur along a phylogenetic tree, whereas this non-specified neutral trait goes along its branches, with evolution proceeding independently along lineages (Helmus et al. 2007). PSR considers this phylogenetic difference among taxa but includes the number of species, so it is simply the PSV multiplied by the number of species (Helmus et al. 2007). PSR represents richness accounting for how much of biodiversity is added to the community considering more phylogenetically distinct species (Helmus et al. 2007). These two metrics have the advantage of providing an integrated approach, with well-defined statistical properties (Helmus et al. 2007). In addition, they allow an easy evaluation of the specific contributions to the different aspects of phylogenetic structure and facilitate the integration of phylogenetic information and strategies to biodiversity conservation (Helmus et al. 2007).

We did Pearson's correlation analyses to select environmental variables that were not correlated to others ($R < |0.7|$). We selected altitude, slope, pH, N, P, K, Al^{3+}, sum of bases, base saturation, and the proportions of sand, silt, and clay. To account for the relationship between phylogenetic diversity (PSV or PSR) and altitude, we used simple regressions. To account for the relationship between phylogenetic diversity and the environmental variables, we used multiple regressions with either PSV or PSR as response variable and the selected environmental variables as explanatory ones. We used Akaike's Information Criterion (AIC) to select the best model and redid the analyses with those variables. We carried out all the analyses in R (R Development Core Team 2018).

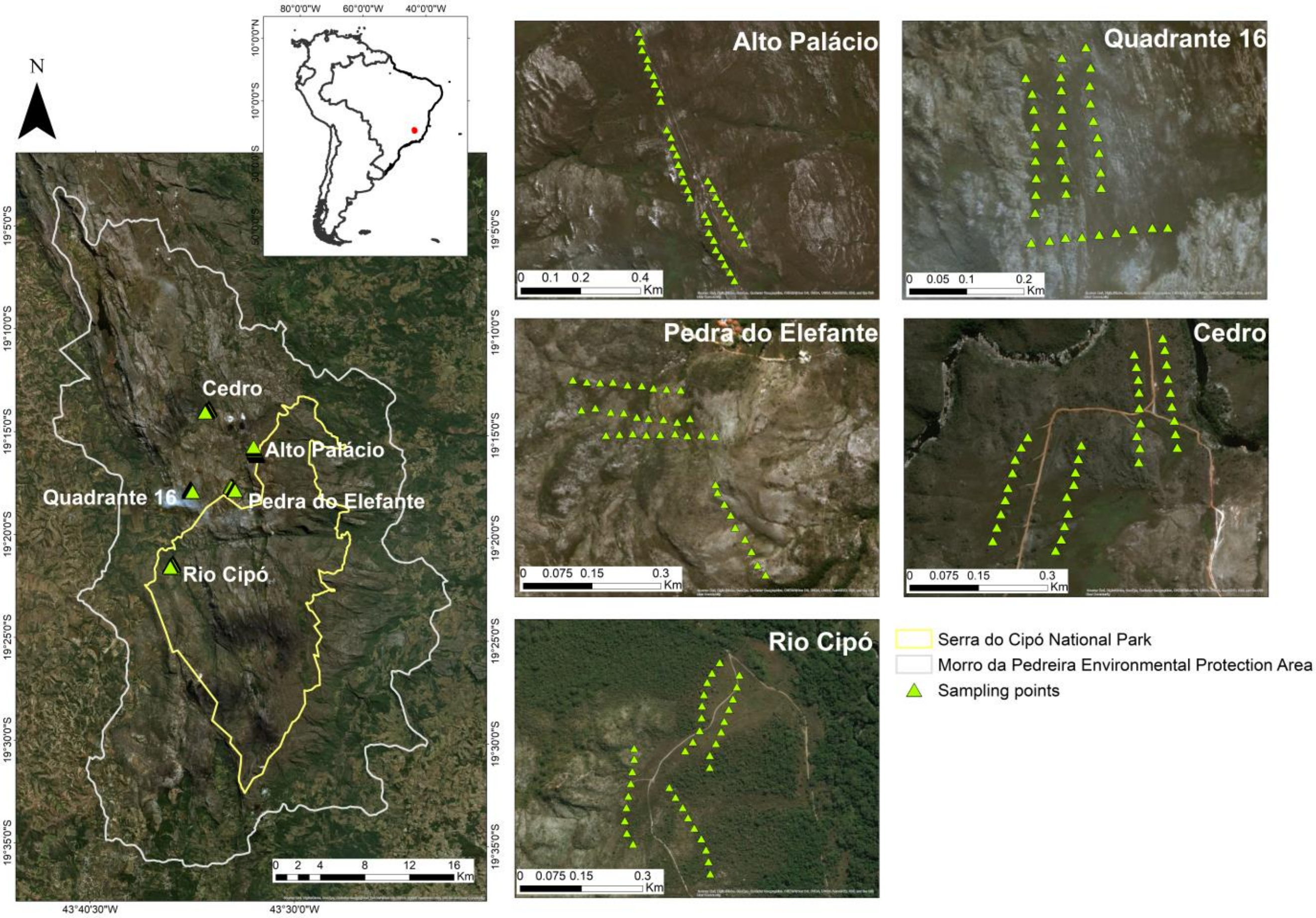

Figure 1. Location of the five study sites along the altitudinal gradient of the Cipó Mountains (Serra do Cipó National Park and the Morro da Pedreira Environmental Protection Area), Minas Gerais State, southeastern Brazil. (1) Rio Cipó - 821 m; (2) Cedro - 1101 m; (3) Pedra do Elefante - 1255 m; (4) Quadrante 16 - 1303 m; (5) Alto Palácio - 1420 m.

2.3 Results

We surveyed 438 plant species, comprising 62 angiosperm families (Appendix 2). The most abundant families were Poaceae (103 species), Asteraceae (41), Xyridaceae (35), Cyperaceae (31), Eriocaulaceae (23), Melastomataceae (21), Fabaceae (19), and Velloziaceae (15). Mean PSV was 0.70 in Rio Cipó (821 m), 0.57 in Cedro (1,101 m), 0.65 in Pedra do Elefante (1,255 m), 0.63 in Quadrante 16 (1,303 m) and 0.60 in Alto Palácio (1,420 masl). Mean PSR was 7.45 in Rio Cipó, 8.01 in Cedro, 12.11 in Pedra do Elefante, 11.03 in Quadrante 16 and 11.65 in Alto Palácio. Whereas PSV decreased with altitude ($P < 0.001$, $R^2_{adj} = 0.04$), PSR increased ($P < 0.001$, $R^2_{adj} = 0.17$) (Figures 2 and 3). In the best model ($P < 0.001$, $R^2_{adj} = 0.43$), PSV was positively related with phosphorus, potassium, and base saturation and negatively related with slope, pH, nitrogen, sand, and silt. In the best model ($P < 0.001$, $R^2_{adj} = 0.34$), PSR was positively related with altitude and potassium and negatively related with slope, nitrogen, and phosphorus.

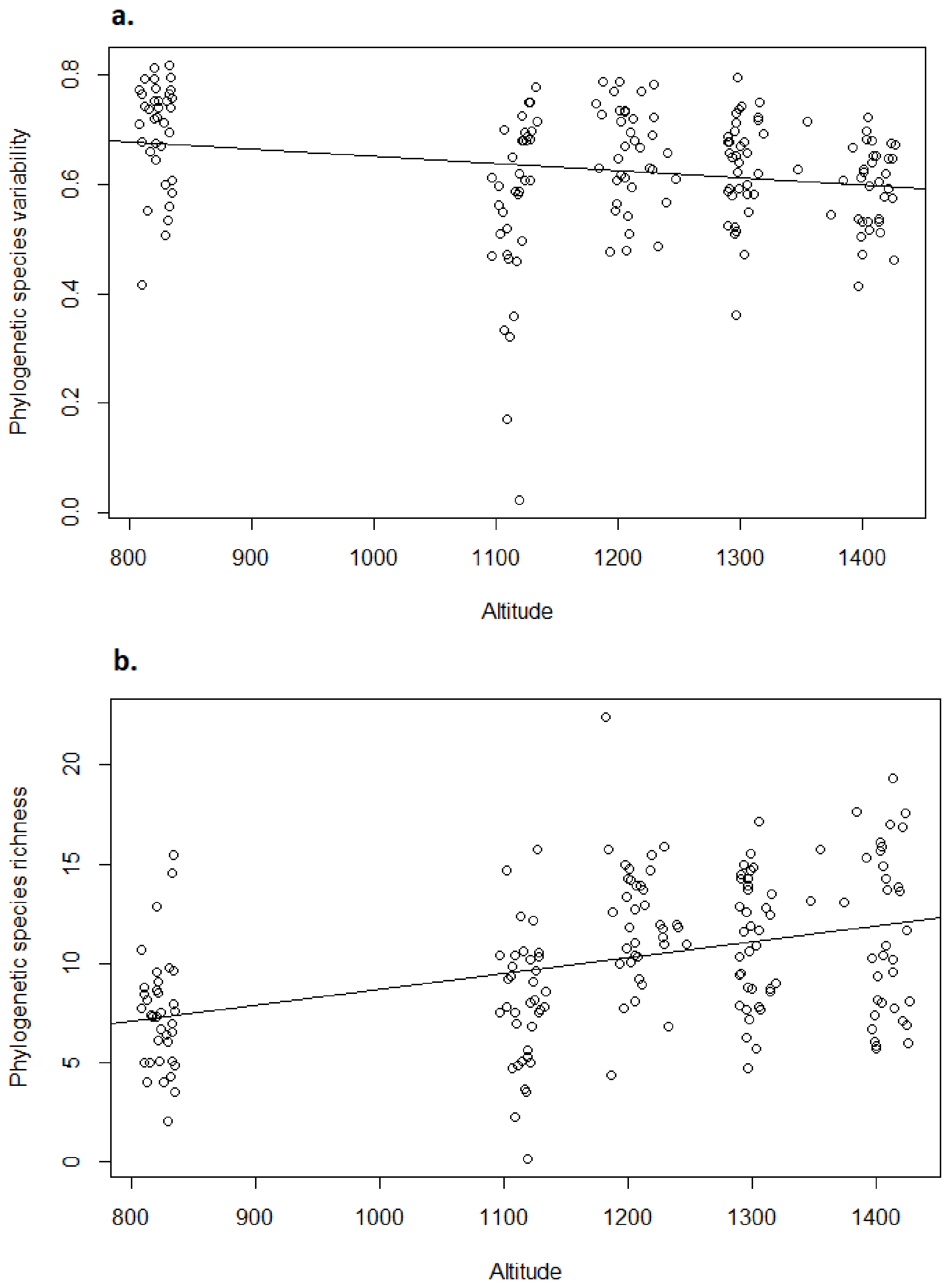

Figure 2. Phylogenetic species variability (a) and phylogenetic species richness (b) in relation to altitude at the Serra do Cipó rocky grasslands, Minas Gerais State, southeastern Brazil.

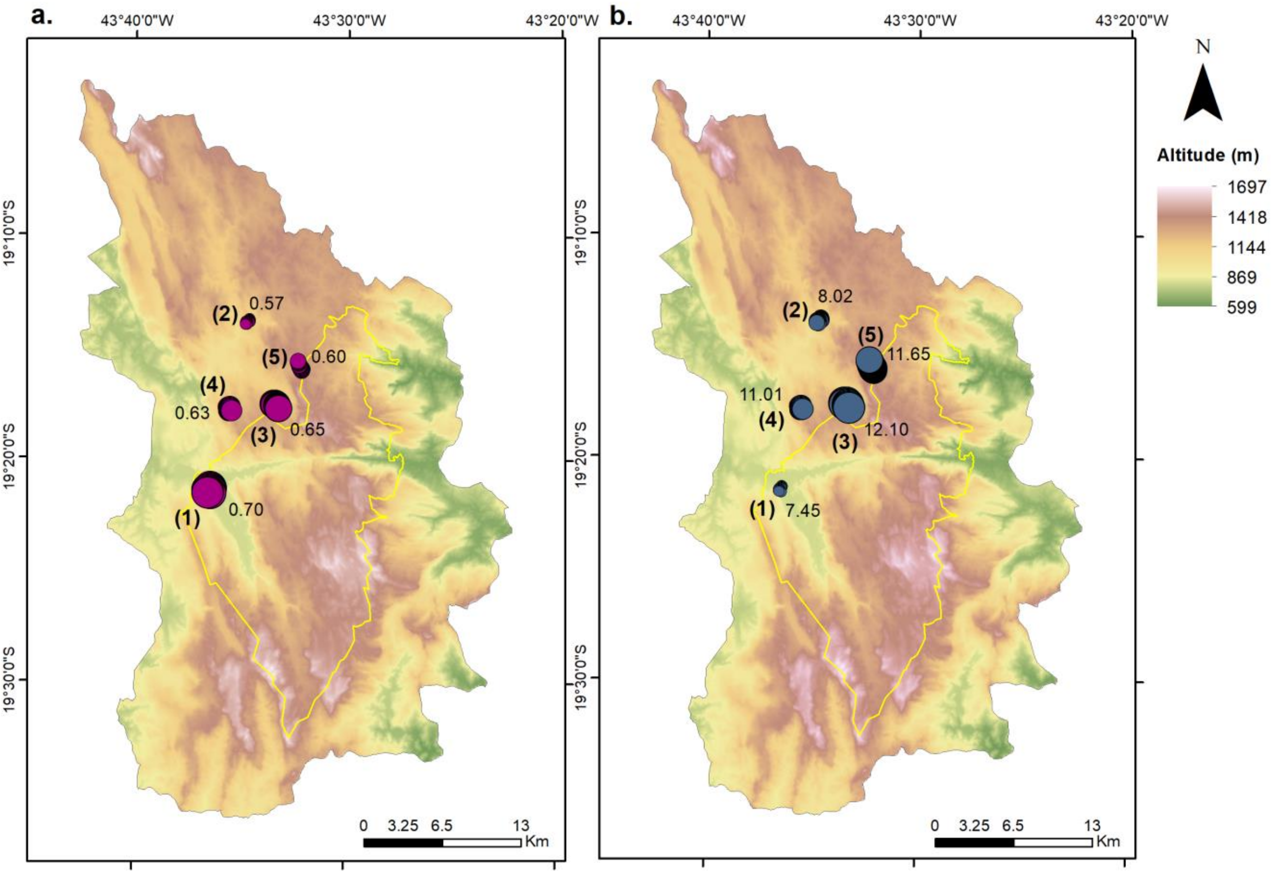

Figure 3. Altitudinal maps showing mean values of (a) phylogenetic species variability and (b) phylogenetic species richness at the Serra do Cipó, Minas Gerais State, southeastern Brazil. (1) Rio Cipó - 821 m; (2) Cedro - 1101 m; (3) Pedra do Elefante - 1255 m; (4) Quadrante 16 - 1303 m; (5) Alto Palácio - 1420 m.

2.4 Discussion

Our sample effort surveyed 438 species, representing well the diversity of plant species from the Cipó Mountains and the Espinhaço Range, comprising approximately 30% of the known Cipó flora (Giulietti et al. 1987, Pirani et al. 2003, Silveira et al. 2016). The total number of species we sampled was, however, 63.5% higher than the 278 species sampled in a previous systematic survey at the same area and study sites (Mota et al. 2018), because we sampled all life forms, including graminoid species, the dominant life forms across rocky grasslands, and not just larger herbs and woody plants. The richest families we sampled – Poaceae, Asteraceae, Xyridaceae, Cyperaceae, and Eriocaulaceae –, were somewhat different from the study that did not sample graminoids – Asteraceae, Melastomataceae, Eriocaulaceae, and Velloziaceae (Mota et al. 2018). Therefore, our all-inclusive survey demonstrated that the most species rich family on rocky grasslands are grasses or other herbaceous plants. Poaceae accounted for more than the double of species than the second richest family, Asteraceae. That is the expected result for a grassland-dominated landscape. Previous survey on stone and sandy grasslands also point out monocots as the dominant families (Le Stradic et al. 2015).

In the rocky grassland of the Cipó Mountains, PSV, which accounts for the relatedness among species and for pure phylogenetic signal (Helmus et al. 2007), decreased with altitude. On the other hand, PSR, which also considers the number of species, increased with it. Our suggestion here is the presence of phylogenetic niche conservatism, considering the decreasing pattern of phylogenetic species variability and assuming that traits are conserved for lineages in rocky grassland (Miazaki et al. 2015, Pugliesi and Rapini 2015). We argue that although more severe environments with strong environment filtering are expected to constrain lineages and the number of species that are able to colonize them, the observed increasing of phylogenetic species richness with altitude suggests that more species of these selected clades are occurring in these harsh environments.

The altitudinal gradient in Cipó Mountains is convenient for studying changes in community assembly, mainly because climate and soil have a direct effect on how the mosaics of micro-habitats are shaped and how the different vegetation physiognomies are distributed (Le Stradic et al. 2015, Silveira et al. 2016a). The Espinhaço Range also accounts for a wide latitudinal and altitudinal variation, providing habitat heterogeneity and isolation among vegetation islands (Giulietti et al. 1987, Silveira et al. 2016), influencing its high floristic richness. Still, we may consider that the altitudinal range in the Cipó Mountains is less pronounced than in other higher mountains of the world, such as the Andes or the Himalayas.

Phylogenetic diversity was linked to environmental constraints, such as nutrients (nitrogen, phosphorus, and potassium), which are fundamental for plant growth and development (Taiz & Zeiger 2002). Both PSV and PSR were negatively related with nitrogen, suggesting that plant development of these lineages was limited by that nutrient, therefore influencing directly in the number and variability of species that are able to grow. PSV was positively related with phosphorus, whereas PSR was negatively related, suggesting a dispersed pattern in which some species from different clades developed nutritional strategies for phosphorus acquisition (Oliveira et al. 2015). Both PSV and PSR were positively related with potassium, maybe because that nutrient is strongly associated with water uptake, root growth, and transpiration (Egilla et al. 2001; Wang et al. 2013). PSV was negatively related with silt and sand — the coarser the soil, the less fertile and more permeable it tends to be (Goodland and Pollard 1973; Schaefer et al. 2009; Valente 2009). PSV was also negatively related to pH, pointing out that communities on more acidic soils were phylogenetically more diverse. Acid soils can be related to the release of phosphorus making these areas less impoverished (Hinsinger 2001). Both PSV and PSR were negatively related with slope, probably because the environment is harsher in steep sites.

Some studies have already found evidence to support phylogenetic clustering and niche conservatism in rocky grasslands (Miazaki et al. 2015, Pugliesi & Rapini 2015) and in high locations (Machac et al. 2011, Qian et al. 2014, Zhang et al. 2016). Here, although we cannot confirm niche conservatism, we may argue in favor of it and harsh environmental filtering. Although altitudinal gradients are expected to have a decreasing or a mid-peak pattern in species richness (Rahbek 1995, McCain and Grytnes 2010, Smith et al. 2014), we found that incorporating phylogenetic information changes this scenario; in our case, to the opposite pattern. What is known about the evolution of the rocky grassland flora was corroborated by our results, which supported niche conservatism and older lineages evolving in situ (Miazaki et al. 2015). Gondwanan families, for example, play an important role in the composition of the Cipó flora and are thought to have diversified in situ there (Zappi et al. 2017). Moreover, the rocky grassland seems to be older than the cerrado in mountaintops (Simon et al. 2009, Antonelli et al. 2010). Considering the many climatic fluctuations that these two vegetation types went through (Gottsberger & Silberbauer-Gottsberger 2006), we may argue that the mountaintops could also behave floristically as islands, being currently isolated from other sources of dispersal and therefore presenting a more phylogenetically clustered pattern.

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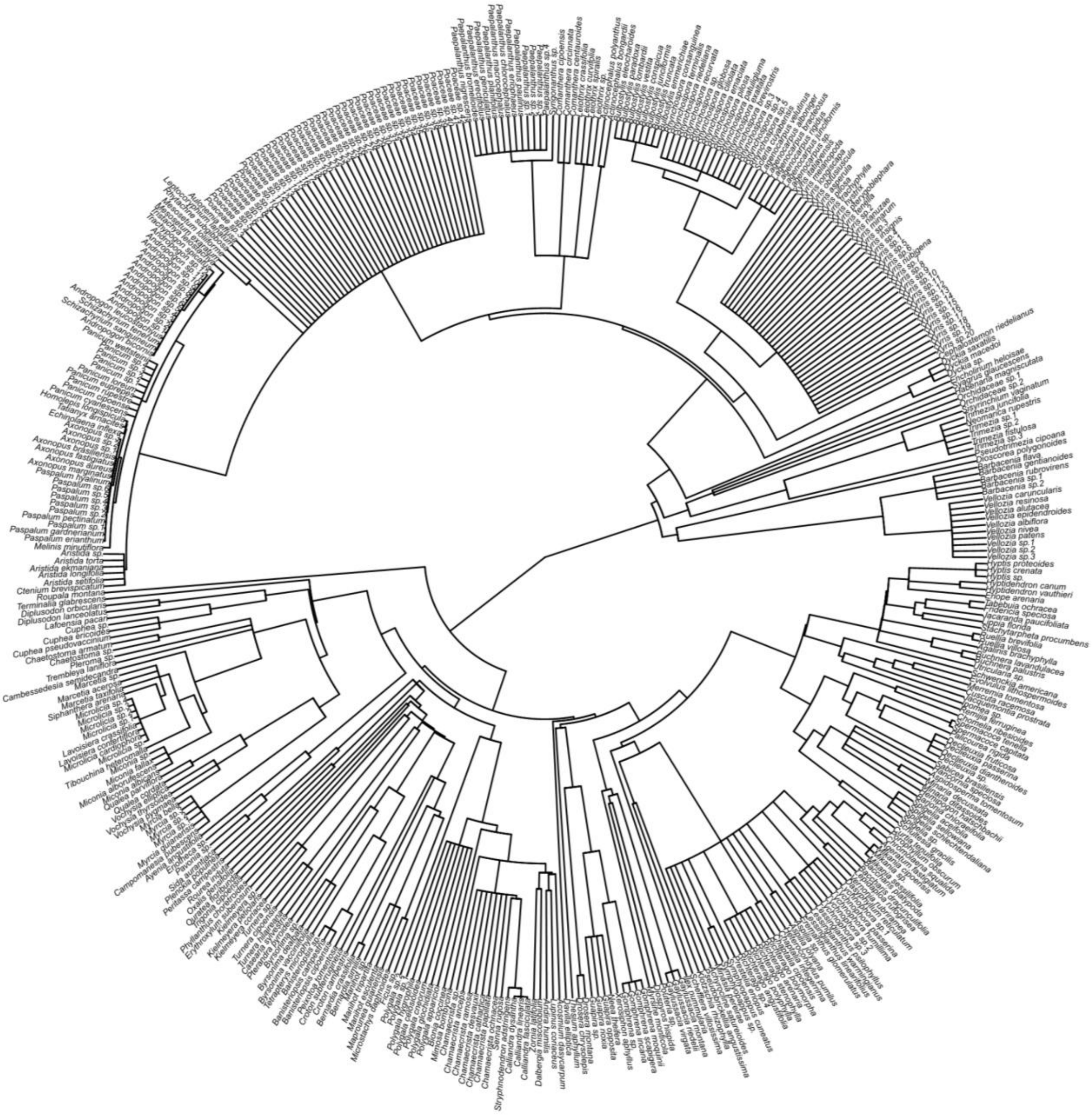
2.7 Appendix 1. Phylogenetic tree of plant species surveyed at Serra do Cipó, Minas Gerais State, southeastern Brazil.



2.8 Appendix 2. Species sampled at the Serra do Cipó altitudinal gradient, Minas Gerais State, southeastern Brazil, and their presence/absence records in each study site (RC = Rio Cipó, CE = Cedro, PE = Pedra do Elefante, Q16 = Quadrante 16, AP = Alto Palácio). Family names are abbreviated according to Weber (1982), except Calophyllaceae and Phyllanthaceae, which did not have corresponding abbreviations.

Species	***Family***	***RC***	***CE***	***PE***	***Q16***	***AP***
Ruellia brevifolia (Pohl) C.Ezcurra	ACA	0	0	1	0	0
Ruellia villosa Lindau	ACA	1	1	1	1	0
Gomphrena incana Mart.	AMA	0	1	1	1	0
Gomphrena moquinii Seub.	AMA	0	0	0	0	1
Gomphrena scapigera Mart.	AMA	0	0	1	1	0
Gomphrena sp.	AMA	0	0	0	0	1
Xerosiphon aphyllus (Pohl ex Moq.) Pedersen	AMA	0	0	0	1	1
Klotzschia rhizophylla Urb.	API	0	0	0	0	1
Aspidosperma tomentosum Mart.	APO	1	0	0	0	0
Barjonia chloraeifolia Decne.	APO	0	0	0	1	0
Hancornia speciosa Gomes	APO	0	1	0	0	0
Hemipogon hatschbachii (Fontella & Marquete) Rapini	APO	0	0	1	1	0
Minaria decussata (Mart.) T.U.P.Konno & Rapini	APO	0	0	1	1	0
Minaria ditassoides (Silveira) T.U.P.Konno & Rapini	APO	1	0	0	1	0
Ilex nummularia Reissek	AQF	0	0	1	0	0
Schefflera villosissima Fiaschi & Pirani	ARL	1	1	0	0	0
Syagrus glaucescens Glaz. ex Becc.	AST	1	0	0	0	0
Achyrocline satureioides (Lam.) DC.	AST	0	1	0	0	0
Ageratum fastigiatum (Gardner) R.M.King & H.Rob.	AST	0	1	0	0	0
Aspilia jolyana G.M.Barroso	AST	0	1	1	1	0
Aspilia sp.	AST	0	0	0	1	0
Baccharis dracunculifolia DC.	AST	1	0	1	0	0
Baccharis platypoda DC.	AST	0	0	0	0	1
Chaptalia cipoensis Roque	AST	0	0	0	0	1

Chaptalia integerrima (Vell.) Burkart	AST	0	0	0	0	1
Chromolaena squalida (DC.) R.M.King & H.Rob.	AST	1	0	0	0	0
Dasyphyllum reticulatum (DC.) Cabrera	AST	0	0	1	0	0
Eremanthus glomerulatus Less.	AST	1	1	0	0	0
Heterocondylus pumilus (Gardner) R.M.King & H.Rob.	AST	0	0	0	1	0
Lepidaploa rufogrisea (A. St.-Hil.) H.Rob.	AST	1	0	0	0	0
Lessingianthus linearifolius (Less.) H.Rob.	AST	1	0	1	1	0
Lessingianthus psilophyllus (DC.) H.Rob.	AST	0	1	1	1	1
Lessingianthus warmingianus (Baker) H.Rob.	AST	0	0	1	0	0
Lychnophora humillima Sch.Bip.	AST	0	0	0	0	1
Lychnophora passerina (Mart. ex DC.) Gardner	AST	0	1	0	0	0
Lychnophora sp.1	AST	0	0	1	0	0
Lychnophora sp.2	AST	0	0	1	0	0
Lychnophora sp.3	AST	0	0	0	1	0
Mikania cipoensis G.M.Barroso	AST	0	0	0	0	1
Mikania sessilifolia DC.	AST	0	1	1	1	1
Mikania sp.	AST	0	0	1	0	0
Minasia pereirae H.Rob.	AST	0	0	0	0	1
Porophyllum obscurum (Spreng.) DC.	AST	0	1	0	0	0
Prestelia eriopus Sch.Bip. ex Sch.Bip.	AST	0	0	0	1	0
Pseudobrickellia angustissima (Spreng. ex Baker) R.M.King	AST	1	0	0	0	0
Rhynchospora terminalis (Nees) Steud.	AST	1	1	1	1	1
Richterago angustifolia (Gardner) Roque	AST	0	0	0	0	1
Richterago arenaria (Baker) Roque	AST	0	0	1	1	1
Richterago polymorpha (Less.) Roque	AST	1	1	1	1	1
Richterago polyphylla (Baker ex Baker) Ferreyra	AST	0	1	1	1	0
Asteraceae sp.1	AST	0	0	1	0	0
Asteraceae sp.2	AST	0	0	0	0	1
Asteraceae sp.3	AST	0	1	0	0	0
Asteraceae sp.4	AST	1	0	0	1	0
Richterago stenophylla (Cabrera) Roque	AST	0	1	0	1	1
Symphyopappus cuneatus (DC.) Sch.Bip. ex Baker	AST	0	1	1	0	0
Symphyopappus sp.	AST	1	0	0	0	0

Vernonia rubriramea Mart. ex DC.	AST	1	0	0	0	0
Fridericia speciosa Mart.	BIG	1	0	0	0	0
Jacaranda paucifoliata Mart. ex DC.	BIG	1	0	0	0	0
Tabebuia ochracea A.H. Gentry	BIG	1	0	0	0	0
Dyckia macedoi L.B.Sm.	BML	1	0	0	0	1
Dyckia saxatilis Mez	BML	1	0	1	0	0
Dyckia sp.	BML	1	0	0	0	0
Encholirium heloisae (L.B.Sm.) Forzza & Wand.	BML	0	0	0	1	0
Kielmeyera petiolaris Mart. & Zucc.	CLP	0	0	1	0	0
Kielmeyera sp.	CLP	0	1	0	0	0
Peritassa campestris (Cambess.) A.C.Sm.	CEL	1	0	0	0	0
Plenckia populnea Reissek	CEL	1	0	0	0	0
Kielmeyera coriacea Mart.	CLU	1	0	0	0	0
Terminalia glabrescens Mart.	CMB	1	0	0	0	0
Rourea induta Planch.	CNN	1	0	0	0	0
Cuscuta racemosa Mart.	CNV	1	0	1	0	0
Evolvulus lithospermoides Mart.	CNV	0	1	0	0	0
Ipomea sp.	CNV	0	0	1	0	0
Jacquemontia prostrata Choisy	CNV	0	0	0	1	1
Merremia tomentosa Hallier	CNV	1	0	0	0	0
Bulbostylis conspicua (Boeckeler) H.Pfeiff.	CYP	0	0	1	0	1
Bulbostylis eleocharoides Kral & M.T.Strong	CYP	0	1	1	0	0
Bulbostylis emmerichiae T.Koyama	CYP	0	1	1	1	0
Bulbostylis junciformis (Kunth) C.B.Clarke	CYP	1	1	1	1	1
Bulbostylis lombardii Kral & M.T.Strong	CYP	0	0	0	1	1
Bulbostylis paradoxa (Spreng.) Lindm.	CYP	1	1	1	1	0
Bulbostylis truncata (Nees) M.T.Strong	CYP	0	1	1	1	0
Bulbostylis vestita (Kunth) C.B.Clarke	CYP	0	0	1	1	1
Lagenocarpus alboniger (A.St.-Hil.) C.B.Clarke	CYP	0	0	1	1	0
Lagenocarpus bracteosus C.B.Clarke	CYP	0	0	0	0	1
Lagenocarpus junciformis (Kunth) Kuntze	CYP	0	0	0	0	1
Lagenocarpus rigidus (Kunth) Nees	CYP	0	1	1	1	1
Lagenocarpus sp.	CYP	0	1	1	0	0

Lagenocarpus velutinus Nees	CYP	0	0	0	1	0
Rhynchospora brevirostris Griseb.	CYP	0	1	1	1	1
Rhynchospora ciliolata Boeckeler	CYP	0	0	0	1	1
Rhynchospora consanguinea (Kunth) Boeckeler	CYP	1	1	1	1	1
Rhynchospora emaciata (Nees) Boeckeler	CYP	0	1	1	1	1
Rhynchospora exaltata Kunth	CYP	1	0	0	0	0
Rhynchospora globosa (Kunth) Roem. & Schult.	CYP	0	1	0	0	0
Rhynchospora patuligluma C.B.Clarke ex Lindm.	CYP	0	0	0	0	1
Rhynchospora pilosa Boeckeler	CYP	0	1	1	0	1
Rhynchospora recurvata (Nees) Steud.	CYP	0	1	1	1	0
Rhynchospora riedeliana C.B.Clarke	CYP	0	1	1	1	1
Rhynchospora sp.	CYP	0	0	1	0	0
Cyperaceae sp.1	CYP	0	1	0	0	0
Cyperaceae sp.2	CYP	0	0	0	0	1
Rhynchospora sp.1	CYP	0	0	1	0	0
Rhynchospora sp.2	CYP	0	0	1	0	0
Rhynchospora sp.3	CYP	1	0	0	0	0
Scleria cuyabensis Pilg.	CYP	0	0	0	1	0
Davilla elliptica A.St.-Hil.	DLL	1	1	1	1	0
Dioscorea polygonoides Humb. & Bonpl. ex	DSC	1	0	0	0	0
Drosera chrysolepis Taub.	DRS	0	0	1	0	1
Drosera montana A.St.-Hil.	DRS	0	0	1	1	1
Diospyros hispida A.DC.	EBN	1	0	0	0	0
Gaylussacia montana (Pohl) Sleumer	ERI	0	0	1	1	0
Gaylussacia riedelii Meisn.	ERI	0	0	0	1	1
Gaylussacia virgata Mart. ex Meisn.	ERI	0	0	0	0	1
Actinocephalus bongardii (A.St.-Hil.) Sano	ERO	0	0	0	1	0
Actinocephalus polyanthus (Bong.) Sano	ERO	0	0	0	0	1
Comanthera centauroides (Bong.) L.R.Parra & Giul.	ERO	0	1	1	0	1
Comanthera cipoensis (Ruhland) L.R.Parra & Giul.	ERO	0	0	1	1	1
Comanthera circinnata (Bong.) L.R.Parra & Giul.	ERO	0	1	0	0	0
Leiothrix crassifolia (Bong.) Ruhland	ERO	0	0	1	1	1
Leiothrix curvifolia (Bong.) Ruhland	ERO	0	0	0	0	1
Leiothrix sp.	ERO	0	0	0	0	1

Leiothrix spiralis (Bong.) Ruhland	ERO	0	0	0	0	1
Paepalanthus bromelioides Silveira	ERO	0	0	1	0	0
Paepalanthus chlorocephalus Silveira	ERO	0	0	0	0	1
Paepalanthus erectifolius Silveira	ERO	0	1	0	1	0
Paepalanthus eriophaeus Ruhland	ERO	0	1	0	0	0
Paepalanthus geniculatus (Bong.) Kunth	ERO	0	1	1	1	1
Paepalanthus macrocephalus (Bong.) Körn.	ERO	0	1	0	0	0
Paepalanthus nigrescens Silveira	ERO	0	0	1	1	1
Paepalanthus paulinus Ruhland	ERO	0	0	1	0	0
Paepalanthus planifolius (Bong.) Körn.	ERO	0	0	0	0	1
Paepalanthus sp.1	ERO	0	0	1	0	0
Paepalanthus sp.2	ERO	0	0	0	0	1
Paepalanthus sp.3	ERO	0	1	0	0	0
Paepalanthus sp.4	ERO	0	0	1	0	0
Syngonanthus sp.	ERO	0	0	1	0	1
Erythroxylum suberosum A.St.-Hil.	ERX	0	1	1	0	0
Bernardia crassifolia Müll.Arg.	EUP	1	0	0	0	0
Bernardia similis Pax & K.Hoffm.	EUP	0	1	0	0	0
Croton campestris A.St.-Hil.	EUP	0	0	1	0	0
Croton subferrugineus Müll.Arg.	EUP	1	1	1	0	0
Manihot esculenta Crantz	EUP	1	0	0	0	0
Manihot sp.	EUP	1	0	0	0	0
Manihot tripartita (Spreng.) Müll.Arg.	EUP	1	0	0	0	0
Maprounea guianensis Aubl.	EUP	1	0	0	0	0
Microstachys daphnoides (Mart.) Müll.Arg.	EUP	1	0	0	0	0
Acosmium dasycarpum (Vogel) Yakovlev	FAB	1	0	0	0	0
Andira humilis Mart. ex Benth.	FAB	1	0	0	0	0
Bionia coccinea Mart. ex Benth.	FAB	1	0	1	0	0
Calliandra dysantha Benth.	FAB	1	0	0	0	0
Calliandra fasciculata Benth.	FAB	1	0	0	0	0
Calliandra linearis Benth.	FAB	0	1	1	1	0
Chamaecrista anceps (Benth.) H.S.Irwin & Barneby	FAB	0	1	0	0	0
Chamaecrista cathartica (Mart.) H.S.Irwin & Barneby	FAB	0	0	0	1	0

Chamaecrista desvauxii (Collad.) Killip	FAB	0	1	0	1	1
Chamaecrista ochnacea (Vogel) H.S.Irwin & Barneby	FAB	0	1	1	1	0
Chamaecrista papillata H.S.Irwin & Barneby	FAB	1	1	0	1	0
Chamaecrista ramosa (Vogel) H.S.Irwin & Barneby	FAB	1	0	1	0	0
Chamaecrista sp.	FAB	0	0	1	0	0
Dalbergia miscolobium Benth.	FAB	0	1	1	0	0
Lupinus coriaceus Benth.	FAB	0	0	0	0	1
Mimosa bombycina Barneby	FAB	1	0	0	0	0
Senna rugosa (G.Don) H.S.Irwin & Barneby	FAB	1	0	0	0	0
Stryphnodendron adstringens (Mart.) Coville	FAB	0	1	0	0	0
Zornia latifolia Sm.	FAB	0	0	0	1	1
Curtia tenuifolia (Aubl.) Knobl.	GEN	0	0	0	1	1
Schultesia gracilis Mart.	GEN	0	0	0	1	0
Neomarica rupestris (Ravenna) Chukr	IRI	0	1	1	1	0
Pseudotrimezia cipoana Ravenna	IRI	0	0	1	1	0
Sisyrinchium vaginatum Spreng.	IRI	1	0	1	1	0
Trimezia fistulosa R.C.Foster	IRI	0	0	1	0	0
Trimezia juncifolia (Klatt) Benth. & Hook.f.	IRI	1	1	1	1	1
Trimezia sp.1	IRI	0	1	0	0	0
Trimezia sp.2	IRI	0	0	0	0	1
Trimezia sp.3	IRI	0	0	1	1	1
Eriope arenaria Harley	LAM	0	1	1	1	0
Hyptidendron canum (Pohl ex Benth.) Harley	LAM	1	0	0	0	0
Hyptidendron vauthieri (Briq.) Harley	LAM	0	1	0	0	0
Hyptis crenata Pohl ex Benth.	LAM	1	0	1	0	0
Hyptis proteoides A.St.-Hil. ex Benth.	LAM	1	0	1	1	0
Hyptis sp.	LAM	0	1	0	0	0
Spigelia aceifolia Woodson	LOG	0	0	0	1	0
Spigelia schlechtendaliana Mart.	LOG	0	0	0	0	1
Spigelia sellowiana Cham. & Schltdl.	LOG	0	1	0	1	0
Spigelia sp.	LOG	0	0	0	1	1
Cuphea ericoides Cham. & Schltdl.	LYT	0	0	1	0	0
Cuphea pseudovaccinium A.St.-Hil.	LYT	0	1	1	0	1

Cuphea sp.	LYT	0	0	1	0	0
Diplusodon lanceolatus Pohl	LYT	0	1	0	0	0
Diplusodon orbicularis Koehne	LYT	0	1	1	1	0
Lafoensia pacari A. St.-Hil.	LYT	1	0	0	0	0
Banisteriopsis campestris (A.Juss.) Little	MLP	1	0	0	0	0
Banisteriopsis cipoensis B.Gates	MLP	1	1	0	0	0
Banisteriopsis sp.	MLP	1	1	0	0	0
Byrsonima dealbata Griseb.	MLP	1	1	0	1	0
Byrsonima sp.	MLP	1	0	0	0	0
Byrsonima vacciniifolia A.Juss.	MLP	1	0	1	0	0
Peixotoa tomentosa A. Juss.	MLP	0	1	0	0	0
Pterandra pyroidea A. Juss.	MLP	1	0	0	0	0
Tetrapterys microphylla Nied.	MLP	1	0	1	0	0
Ayenia angustifolia A.St.-Hil. & Naudin	MLV	1	0	0	0	0
Pavonia sp.	MLV	1	0	0	0	0
Sida aurantiaca A. St.-Hil.	MLV	1	0	0	0	0
Eriotheca sp.	MLV	1	0	0	0	0
Cambessedesia semidecandra A. St.-Hil. ex A.B.	MLS	0	0	0	1	1
Chaetostoma sp.	MLS	0	0	1	1	0
Lavoisiera confertiflora Naudin	MLS	0	1	1	0	1
Lavoisiera crassifolia DC.	MLS	0	0	0	1	1
Marcetia acerosa DC.	MLS	0	0	1	0	0
Marcetia sp.	MLS	0	0	0	0	1
Marcetia taxifolia (A. St.-Hil.) DC.	MLS	0	1	1	1	1
Miconia albicans (Sw.) Steud.	MLS	1	1	0	0	0
Miconia alborufescens Naudin	MLS	1	0	0	0	0
Miconia fallax DC.	MLS	1	0	0	0	0
Miconia sp.	MLS	1	0	0	0	0
Microlicia cardiophora Naudin	MLS	1	0	0	0	0
Microlicia sp.	MLS	1	0	1	0	0
Microlicia sp.1	MLS	0	0	1	0	0
Microlicia sp.2	MLS	0	0	1	0	0
Microlicia sp.3	MLS	0	0	1	0	0

Microlicia sp.4	MLS	0	0	1	0	0
Pleroma sp.	MLS	0	0	1	0	0
Siphanthera arenaria (DC.) Cogn.	MLS	0	0	1	1	1
Tibouchina heteromalla (D. Don) Cogn.	MLS	1	0	0	0	0
Trembleya laniflora (D. Don) Cogn.	MLS	0	0	1	0	0
Ficus sp.	MOR	1	0	0	0	0
Campomanesia pubescens (Mart. ex DC.) O.Berg	MRT	0	1	0	0	0
Myrcia bella Cambess.	MRT	1	0	0	0	1
Myrcia guianensis (Aubl.) DC.	MRT	1	1	1	0	0
Myrcia sp.1	MRT	1	0	0	0	0
Myrcia sp.2	MRT	1	0	0	0	0
Myrcia sp.3	MRT	1	0	0	0	0
Guapira noxia (Netto) Lundell	NYC	1	0	0	0	0
Guapira opposita (Vell.) Reitz	NYC	1	0	0	0	0
Guapira sp.	NYC	0	0	0	0	1
Neea theifera Oerst.	NYC	1	1	1	0	0
Ouratea floribunda Engl.	OCH	0	1	1	1	0
Habenaria magniscutata Catling	ORC	0	0	1	0	0
Habenaria sp.1	ORC	0	1	0	0	0
Habenaria sp.2	ORC	0	0	1	0	0
Habenaria sp.3	ORC	0	0	0	1	0
Habenaria sp.4	ORC	0	0	0	0	1
Agalinis brachyphylla (Cham. & Schltdl.) D'Arcy	ORO	0	1	0	0	1
Buchnera lavandulacea Cham. & Schltdl.	ORO	0	0	0	1	0
Buchnera palustris (Aubl.) Spreng.	ORO	0	1	0	0	0
Oxalis densifolia Mart. ex Zucc.	OXL	1	0	0	0	0
Phyllanthus choretroides Müll.Arg.	PLL	0	1	0	0	0
Andropogon bicornis L.	POA	1	1	0	0	0
Andropogon leucostachyus Kunth	POA	1	1	1	0	0
Andropogon sp.1	POA	1	0	0	0	0
Andropogon sp.10	POA	1	0	0	0	0
Andropogon sp.11	POA	1	0	0	0	0
Andropogon sp.12	POA	0	0	1	0	0

Andropogon sp.2	POA	0	1	0	0	0
Andropogon sp.3	POA	1	1	1	0	0
Andropogon sp.4	POA	0	0	0	1	0
Andropogon sp.5	POA	0	0	0	1	0
Andropogon sp.6	POA	0	0	1	0	0
Andropogon sp.7	POA	1	0	0	0	0
Andropogon sp.8	POA	1	0	0	1	0
Andropogon sp.9	POA	1	0	0	0	0
Anthaenantia sp.	POA	0	1	1	0	0
Aristida ekmaniana Henrard	POA	1	0	0	0	0
Aristida longifolia Trin.	POA	1	0	0	0	0
Aristida setifolia Kunth	POA	1	0	0	0	0
Aristida sp.	POA	0	1	0	0	0
Aristida torta (Nees) Kunth	POA	0	0	1	1	1
Aulonemia effusa (Hack.) McClure	POA	0	0	0	1	0
Axonopus aureus P.Beauv.	POA	1	0	0	0	0
Axonopus brasiliensis (Spreng.) Kuhlm.	POA	0	1	1	1	1
Axonopus fastigiatus (Nees) Kuhlm.	POA	1	0	1	0	1
Axonopus marginatus (Trin.) Chase ex Hitchc.	POA	0	1	0	0	0
Axonopus sp.1	POA	0	0	0	0	1
Axonopus sp.2	POA	0	1	0	0	0
Axonopus sp.3	POA	1	1	1	0	0
Ctenium brevispicatum J.G.Sm.	POA	0	1	1	1	0
Echinolaena inflexa (Poir.) Chase	POA	1	1	1	1	1
Homolepis longispicula (Döll) Chase	POA	1	1	1	1	1
Leptocoryphium lanatum (Kunth) Nees	POA	0	1	0	0	0
Melinis minutiflora P.Beauv.	POA	1	0	0	0	0
Mesosetum exaratum (Trin.) Chase	POA	0	1	1	1	1
Mesosetum loliiforme (Steud.) Hitchc.	POA	1	1	1	0	0
Panicum cipoense Renvoize & Send.	POA	0	0	0	1	1
Panicum cyanescens Nees ex Trin.	POA	0	1	1	1	1
Panicum euprepes Renvoize	POA	0	1	1	1	0
Panicum loreum Trin.	POA	0	0	0	0	1

Panicum rupestre Trin.	POA	0	1	0	0	1
Poaceae sp.1	POA	0	0	1	1	1
Poaceae sp.2	POA	1	1	0	0	0
Poaceae sp.3	POA	1	0	0	0	0
Poaceae sp.4	POA	1	0	0	0	0
Poaceae sp.5	POA	0	0	0	1	0
Poaceae sp.6	POA	1	0	0	0	0
Poaceae sp.7	POA	0	0	1	1	0
Poaceae sp.8	POA	0	1	0	0	0
Poaceae sp.9	POA	0	1	0	1	0
Poaceae sp.10	POA	0	0	1	0	0
Poaceae sp.11	POA	1	0	0	0	0
Poaceae sp.12	POA	0	0	1	0	0
Poaceae sp.13	POA	1	0	0	0	0
Poaceae sp.14	POA	1	0	0	0	0
Poaceae sp.15	POA	0	0	1	0	1
Poaceae sp.16	POA	0	0	1	0	0
Poaceae sp.17	POA	0	0	1	0	0
Poaceae sp.18	POA	0	0	1	0	0
Poaceae sp.19	POA	1	0	0	0	0
Poaceae sp.20	POA	1	0	0	0	0
Poaceae sp.21	POA	0	0	0	1	0
Poaceae sp.22	POA	0	0	0	1	0
Poaceae sp.23	POA	0	0	0	0	1
Poaceae sp.24	POA	1	0	0	0	0
Poaceae sp.25	POA	0	0	1	0	0
Poaceae sp.26	POA	0	0	0	0	1
Poaceae sp.27	POA	1	0	0	0	0
Poaceae sp.28	POA	1	0	1	0	0
Poaceae sp.29	POA	0	0	0	1	0
Poaceae sp.30	POA	0	1	0	0	0
Poaceae sp.31	POA	0	1	0	0	0
Poaceae sp.32	POA	0	1	0	0	0

Poaceae sp.33	POA	0	1	0	0	0
Poaceae sp.34	POA	1	0	0	0	0
Poaceae sp.35	POA	0	1	0	0	0
Poaceae sp.36	POA	0	0	1	0	0
Poaceae sp.37	POA	0	1	0	0	0
Poaceae sp.38	POA	0	0	0	1	0
Poaceae sp.39	POA	1	0	0	0	0
Poaceae sp.40	POA	0	0	1	0	0
Poaceae sp.41	POA	0	0	0	1	0
Poaceae sp.42	POA	0	0	1	0	0
Poaceae sp.43	POA	0	0	1	0	0
Poaceae sp.44	POA	0	0	0	0	1
Poaceae sp.45	POA	0	0	1	1	1
Poaceae sp.46	POA	0	0	0	0	1
Poaceae sp.47	POA	0	1	0	0	0
Poaceae sp.48	POA	0	0	0	1	0
Poaceae sp.49	POA	0	1	0	0	0
Poaceae sp.50	POA	0	0	0	1	1
Poaceae sp.51	POA	0	0	0	0	1
Panicum wettsteinii Hack.	POA	0	0	0	0	1
Paspalum erianthum Nees ex Trin.	POA	0	1	1	1	1
Paspalum gardnerianum Nees	POA	1	0	0	0	0
Paspalum hyalinum Nees ex Trin.	POA	1	1	1	1	1
Paspalum pectinatum Nees	POA	0	1	1	1	1
Paspalum sp.	POA	0	0	0	0	1
Rhytachne subgibbosa (Winkler ex Hack.) Clayton	POA	1	0	0	0	0
Schizachyrium sanguineum (Retz.) Alston	POA	1	0	0	1	1
Schizachyrium tenerum Nees	POA	0	1	1	1	1
Tatianyx arnacites (Trin.) Zuloaga & Soderstr.	POA	1	1	1	1	1
Trachypogon spicatus (L.f.) Kuntze	POA	1	1	1	1	1
Tristachya leiostachya Nees	POA	1	0	0	0	0
Polygala appariciori Brade	PGL	0	0	0	1	1
Polygala celosioides A.W. Benn.	PGL	0	0	0	0	1

Polygala cneorum A. St.-Hil. & Moq.	PGL	0	0	0	1	1
Polygala glochidiata Kunth	PGL	0	0	0	1	1
Polygala hygrophila Kunth	PGL	0	1	0	0	0
Polygala sp.1	PGL	0	0	0	1	0
Polygala sp.2	PGL	0	0	0	0	1
Myrsine monticola Mart.	PRM	1	1	1	1	0
Roupala montana Aubl.	PRT	1	1	0	1	0
Cephalostemon riedelianus Körn.	RPT	0	0	1	1	0
Chomelia ribesioides Benth. ex A.Gray	RUB	0	0	1	0	0
Declieuxia fruticosa (Willd. ex Roem.)	RUB	0	0	0	1	0
Declieuxia passerina Mart. & Zucc. ex	RUB	1	1	1	0	0
Declieuxia sp.	RUB	1	0	0	0	0
Palicourea rigida Kunth	RUB	0	1	1	0	0
Remijia ferruginea (A.St.-Hil.) DC.	RUB	0	0	1	0	0
Sabicea brasiliensis Wernham	RUB	1	0	1	0	0
Spermacoce capitata Ruiz & Pav.	RUB	1	0	1	0	1
Spermacoce tenella Kunth	RUB	1	0	0	0	0
Casearia sylvestris Sw.	SAL	1	0	0	0	0
Thesium aphyllum Mart. ex A. DC.	SAN	0	0	0	1	0
Pouteria sp.	SPT	1	0	0	0	0
Schwenckia americana L.	SOL	1	0	1	0	0
Trigonia cipoensis Fromm & E. Santos	TRG	0	1	1	0	0
Turnera cipoensis Arbo	TNR	1	1	0	0	0
Turnera hilaireana Urb.	TNR	0	0	1	0	1
Turnera sp.	TNR	0	1	1	1	0
Utricularia sp.	LNT	0	0	0	1	0
Barbacenia flava Mart. ex Schult. &	VLL	0	1	0	0	0
Barbacenia gentianoides Goethart & Henrard	VLL	0	0	0	1	1
Barbacenia rubrovirens Mart.	VLL	0	0	0	1	0
Barbacenia sp.1	VLL	1	0	0	0	0
Barbacenia sp.2	VLL	0	0	1	0	0
Vellozia albiflora Pohl	VLL	1	1	1	1	0
Vellozia alutacea Pohl	VLL	0	1	1	1	0

Vellozia caruncularis Mart. ex Seub.	VLL	0	0	1	0	0
Vellozia epidendroides Mart.	VLL	0	1	1	1	1
Vellozia nivea L.B.Sm. & Ayensu	VLL	0	1	1	1	0
Vellozia patens L.B.Sm. & Ayensu	VLL	0	0	0	0	1
Vellozia resinosa Mart.	VLL	0	0	0	0	1
Vellozia sp.1	VLL	1	0	0	0	0
Vellozia sp.2	VLL	0	0	1	0	0
Vellozia sp.3	VLL	0	0	1	1	0
Lippia florida Cham.	VRB	0	0	1	1	0
Stachytarpheta procumbens Moldenke	VRB	0	0	1	1	1
Qualea cordata Spreng.	VOC	1	0	0	0	0
Qualea parviflora Mart.	VOC	1	0	0	0	0
Vochysia elliptica Mart.	VOC	0	0	1	0	0
Vochysia pygmaea Bong.	VOC	0	0	1	1	0
Vochysia thyrsoidea Pohl	VOC	0	0	1	0	0
Xyris asperula Mart.	XYR	0	1	0	1	1
Xyris melanopoda L.B.Sm. & Downs	XYR	0	0	1	0	1
Xyris hystrix Seub.	XYR	0	1	0	0	0
Xyris itatiayensis (Malme) Wand. & Sajo	XYR	0	0	1	0	1
Xyris longiscapa L.A.Nilsson	XYR	0	1	1	0	1
Xyris minarum Seub.	XYR	0	1	1	0	0
Xyris nanuzae Wand.	XYR	0	0	1	0	0
Xyris nubigena Kunth	XYR	0	0	0	1	0
Xyris obtusiuscula L.A.Nilsson	XYR	0	1	1	1	1
Xyris pilosa Kunth	XYR	0	0	1	0	1
Xyris pterygoblephara Steud.	XYR	0	1	1	0	1
Xyris sp.1	XYR	0	1	1	0	0
Xyris sp.10	XYR	0	0	1	0	0
Xyris sp.11	XYR	0	0	0	1	1
Xyris sp.12	XYR	0	0	0	0	1
Xyris sp.13	XYR	0	0	1	0	0
Xyris sp.14	XYR	0	0	0	1	1
Xyris sp.15	XYR	0	0	0	1	0

Xyris sp.16	XYR	0	0	0	0	1
Xyris sp.17	XYR	0	0	0	1	0
Xyris sp.18	XYR	0	0	0	0	1
Xyris sp.19	XYR	0	0	0	1	0
Xyris sp.2	XYR	0	0	1	0	1
Xyris sp.20	XYR	0	0	0	0	1
Xyris sp.3	XYR	0	0	1	0	0
Xyris sp.4	XYR	0	0	1	0	0
Xyris sp.5	XYR	0	1	1	0	1
Xyris sp.6	XYR	0	0	0	1	0
Xyris sp.7	XYR	0	0	1	1	0
Xyris sp.8	XYR	0	0	0	0	1
Xyris sp.9	XYR	0	0	0	0	1
Xyris tenella Kunth	XYR	0	0	1	0	1
Xyris tortula Mart.	XYR	0	1	0	1	1
Xyris trachyphylla Mart.	XYR	0	1	1	1	0
Xyris insignis L.A. Nilsson	XYR	0	0	1	0	1

3. NODE-BASED ANALYSIS OF PLANT SPECIES DISTRIBUTION IN AN ANCIENT TROPICAL MOUNTAIN LANDSCAPE, SOUTHEASTERN BRAZIL

Abstract - The composition and structure of biological communities as we see today take us back to questions regarding the evolution and speciation events that led to those configurations. The integration of phylogenetic methods and species distribution can really help in the investigation of these biogeographical patterns and allow us to explore the relationships and gaps on evolutionary ecology. Here we used a node-based analysis of species distributions that uses the concepts of over and underrepresentation and takes into account the relationship between sister clades, in order to yield two very statistically tractable metrics – the geographic node divergence and specific overrepresentation score. We studied the vascular flora of the Cipó Mountains, located in the Espinhaço Range, southeastern Brazil. We collected and identified all plant species that were present in our sample design along an elevational gradient ranging from 800 to 1400 masl. We also collected environmental variables such as altitude, slope and soil properties. Through the light of niche conservatism hypothesis, we found evidence to support the idea that environmental filtering is in fact significantly important in shaping biological communities and in restraining clades in a phylogeny. We found three allopatric nodes, which revealed the split events between sister clades and the major biogeographical changes in their distribution. We hope our study can lead to many insights into the evolution and biogeographic history of the rocky grasslands flora and for other mountaintop vegetation systems in general.

Key words: allopatry, cerrado, elevational gradient, plant evolution, phylogeny, rocky grassland, vicariance

3.1 Introduction

The composition and structure of biological communities as we see today take us back to questions regarding the evolution and the processes that led to speciation (Losos 2008). What is the degree of evolutionary relatedness that species in a community share? Darwin assumed that related species tend to be functionally similar as well (Darwin 1859), and many phylogenetic comparative methods have since taken this assumption into account (Losos 2008). Phylogenies can be a great way of assessing information on the split events and on the processes involved in the diversification of species (Barraclough and Vogler 2000, Barraclough 2015). There are many phylogenetic approaches to test the relationship between phylogenetic relatedness and ecological similarity, among which the phylogenetic signal and niche conservatism (Wiens and Graham 2005). A phylogenetic signal can be either positive – when closely related species resemble each other more than what would be expected by chance – or negative – when they resemble each other less (Blomberg et al. 2003). The concept of phylogenetic niche conservatism postulates that there is usually a positive phylogenetic signal, since species tend to retain their ancestral traits (Losos 2008).

Integrating species distributions and phylogenetic relationships can be useful in investigating biogeographical patterns, for which three approaches are available: the node- and the clade-based approaches, and a third one that combines both (Borregaard et al. 2014). They are different in the sense that while site-based approaches use phylogenies to answer questions on how related are species from a community, clade-based ones are able to compare the distribution of clades individually (Borregaard et al. 2014). Site-based approaches, such as the net relatedness index (Webb et al. 2008), reduces the complexity of phylogenetic relationships into a single value and may be misleading, thus being considered too simplistic (Borregaard et al. 2014). Clade-based metrics have been used to answer questions about the importance of allopatry as a speciation mode (Barraclough and Vogler 2000). We used two metrics that combine the node- and the clade-based approaches (Borregaard et al. 2014). These metrics go through a phylogeny and explore each node by comparing the spatial distribution of the descendant clades to that of a null model (Borregaard et al. 2014). In this case, we can explore node allopatry and investigate macroevolutionary patterns within a phylogeny in a very effective way (Borregaard et al. 2014).

The concept that biological communities change along altitude in mountainous landscapes is not new: in the 19th century, many scientists, such as Darwin, Wallace, and Humboldt, pointed out that certain changes towards the summit of a mountain could be predicted (Lomolino 2001). Due to their rapid environmental changes over small distances, mountains have become good models for studying changes in community composition and structure (Brown 2001, McCain and Grytnes 2010). In Brazil, a highly rich vegetation type is the ‘rocky grassland’, which occurs mainly in the states of Minas Gerais and Bahia, prevailing, for instance, on mountaintops from the Espinhaço Range (Silveira et al. 2016, Zappi et al. 2017). The rocky grassland landscape is composed of a mosaic of vegetation types, all of them dominated by herbs and shrubs and strictly associated with quartzite, ironstones, and sandstones, with litholic soils that are usually shallow and acidic (Silveira et al. 2016). The rocky grassland occurs mainly on areas above 900 masl (Silveira et al. 2016) and are considered to be an 'old climatically buffered infertile landscape' (Hopper 2009), which explains its high levels of richness and endemism. The combination of environmental constraints and a great variation in floristic composition is suitable for studying evolutionary processes and phylogenetic spatial structure (Zappi et al. 2017).

We aimed to investigate the spatial distribution of plant phylogenetic structure in a rocky grassland landscape at the Cipó Mountains, southern portion of the Espinhaço Range, southeastern Brazil. Our main goal was to estimate the degree of node allopatry and identify the nodes responsible for the main spatial structure, considering that rocky grassland lineages tend to be very old (Zappi et al. 2017) and might have been through many biogeographical and climatic events, such as Pleistocene climatic fluctuations (Rapini et al. 2008). Thus, we investigated the degree of node allopatry within a phylogeny of plant species from the Cipó Mountains, by analysing patterns of over- and underrepresentation of sister clades (Borregaard et al. 2014). We postulated that, because of the severe, old and persistent environmental filtering that has been associated with the rocky grassland (Miazaki *et al.*, 2015), there should be a non-random phylogenetic structure, with sister clades – at least for some nodes – separated in space and related to different environmental variables.

3.2 Methods

The Cipó Mountains have an altitudinal range from 800 to 1,400 masl and quartzite and sandstones as rocky substrates, with shallow and poor soils (Negreiros 2013). The vegetation is diverse and comprises different types (Giulietti et al. 1987). At altitudes lower than 900 masl, there is a predominance of the cerrado and above 900 masl, of rocky grasslands. Based on data collected in five meteorological stations at the study area, climate is defined as Cwa (Köppen 1931).

We surveyed vascular plant species at the Cipó Mountains, located in the Espinhaço Range Range (19°10′–20′S and 43°30′–40′W), Minas Gerais state, southeastern Brazil (Figure 1). We assigned five study areas, located in different altitudes, ranging from 821 to 1420 masl (Figure 1). At each site, we established four transects with nine plots each (1 m^2), systematically placed every 30 m. We collected all vascular plant species and identified them with identification keys (Mamede 1987, Wanderley 2011, Silva-Luz et al. 2012, Borges and Pirani 2013, Rando et al. 2013, Pscheidt 2015), by comparing the vouchers with the reference collection lodged at the São Paulo University Herbarium (SPF), and with the aid of many taxonomists. We used Plantminer (Carvalho et al. 2010) to check our species list for synonyms. In each plot, we assessed geographical coordinates and altitude. We also collected superficial soil samples in each corner of a given plot, mixing them up to have homogeneous soil samples. We determined the following variables: pH, N, P, K, Mg^{2+}, Ca^{2+}, Al^{3+}, exchangeable aluminum, sum of bases, base saturation, cationic exchange capacity, aluminum saturation, and the proportions of sand, silt, and clay (Arruda et al. 2014). These

To assess phylogenetic structure and which nodes were responsible for the major geographical shifts in species distributions, we used two indices by Borregaard et al. (2014): the specific overrepresentation score (SOS) and the geographic node divergence (GND). SOS is a measure of clade overrepresentation and is calculated by going through each node in the phylogeny and comparing the species richness of sister clades to that of a null model, generating a matrix of SOS values for each combination of nodes and communities. GND is the summary of all SOS values across occupied sites, yielding a measure of phylogenetic spatial structure and species co-occurrence. We used a cut-off value of 0.5 to select the nodes with the highest degrees of allopatry.

We did Pearson's correlation analyses to select environmental variables that were not correlated to others ($R < |0.7|$). We selected altitude, slope, pH, N, P, K, Al^{3+}, sum of bases, base saturation, and the proportions of sand, silt, and clay. To account for the relationship between the most allopatric nodes and the environmental variables, we did a principal component analysis and regressed the SOS scores of a given node against the scores of the first two components. We carried out all analyses in R (R Development Core Team 2018) and built the maps in ArcGIS (ESRI 2017).

3.3 Results

Along the elevational gradient in the Cipó Mountains, we found 438 plant species, belonging to 62 angiosperm families (Appendix 1), for which we built a phylogenetic tree (Appendix 2). The most abundant families were Poaceae (103 species), Asteraceae (41), Xyridaceae (35), Cyperaceae (31), Eriocaulaceae (23), Melastomataceae (21), Fabaceae (19), and Velloziaceae (15).

Three nodes had the highest degrees of allopatry (Figure 2). One node (node A in Figure 2) separated monocots , with positive scores, from eudicots, with negative scores (Figure 3); the other node (node B in Figure 2), Eriocaulaceae, with positive scores, from Poaceae, with negative scores (Figure 3); and the other (node C in Figure 2), Xyridaceae, with positive scores, from Cyperaceae, with negative scores (Figure 3).

We found significant relationships between the three most allopatric nodes and the selected environmental variables. The first component of the ordination explained 37.7% of the variation and was positively related with altitude (Figure 4). The second component explained an additional 24.5% and was negatively related with soil fertility (Figure 4). Node A was positively related with both components ($P < 0.001$; $R^2_{adj} = 0.29$), as well as node B ($P < 0.001$; $R^2_{adj} = 0.23$). Node C had a significant relationship only with the second component ($P < 0.001$; $R^2_{adj} = 0.13$).

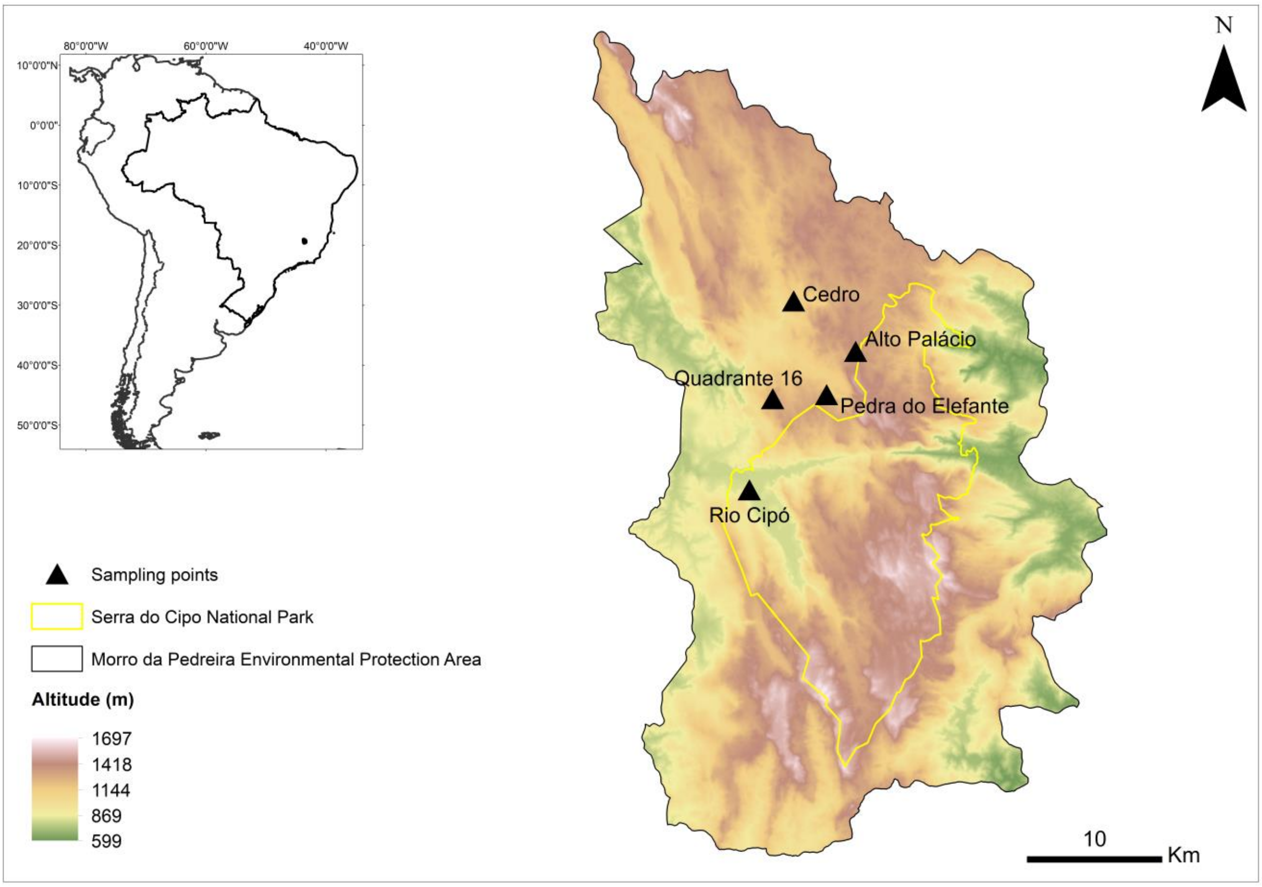


Figure 1. Location of the five study sites along the altitudinal gradient of the Cipó Mountains (Serra do Cipó National Park and the Morro da Pedreira Environmental Protection Area), Minas Gerais state, southeastern Brazil. Rio Cipó - 821 m; Cedro - 1101 m; Pedra do Elefante - 1255 m; Quadrante 16 - 1303 m; Alto Palácio - 1420 m.

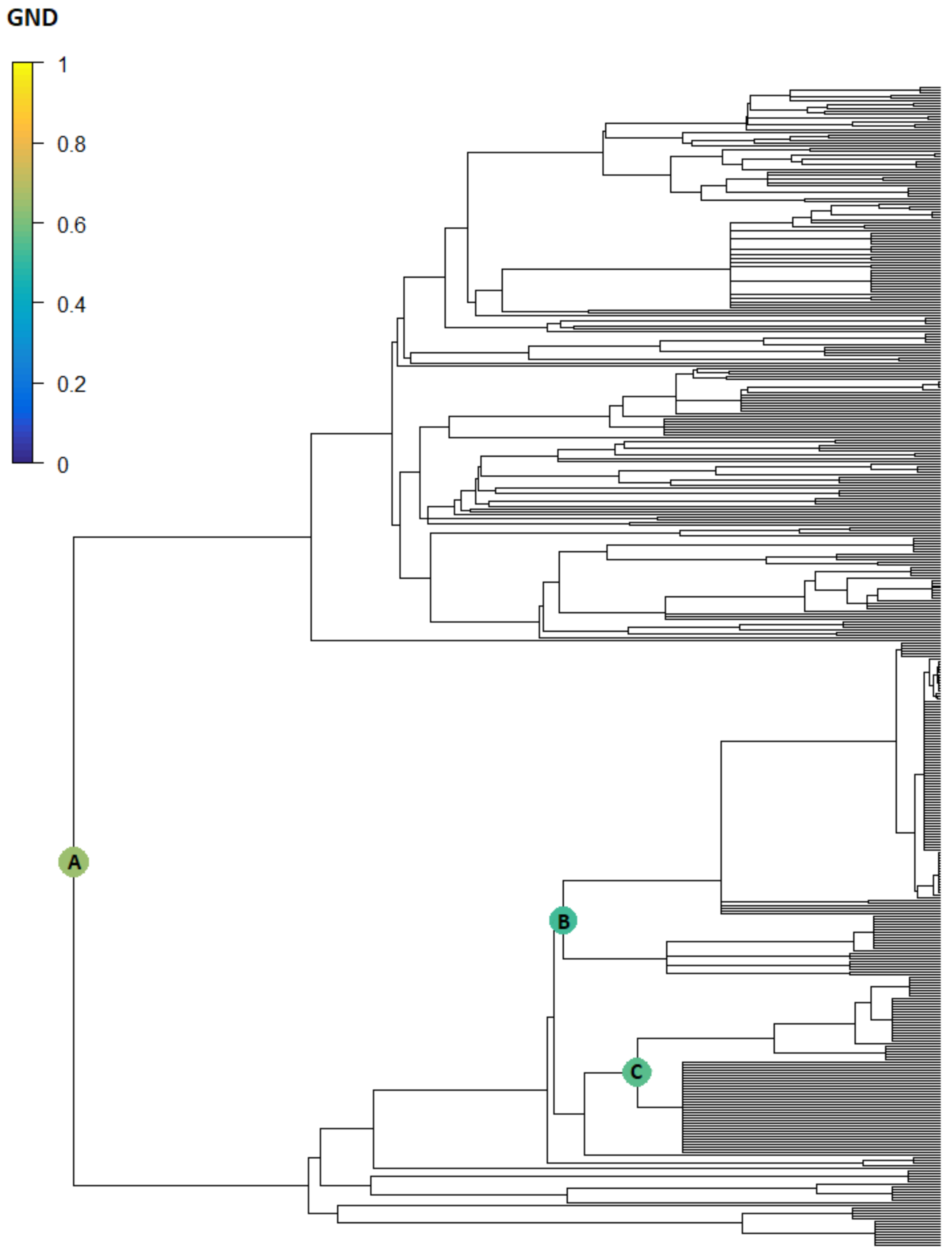


Figure 2. Geographic Node Divergence (GND) scores for plant communities at the Cipó Mountains, southeastern Brazil. A cut-off value of 0.5 was used in the analysis, selecting three nodes with the highest degrees of node allopatry. Node A separates Magnoliopsida from

Liliopsida, node B separates Poaceae from Eriocaulaceae, and node C separates Cyperaceae from Xyridaceae.

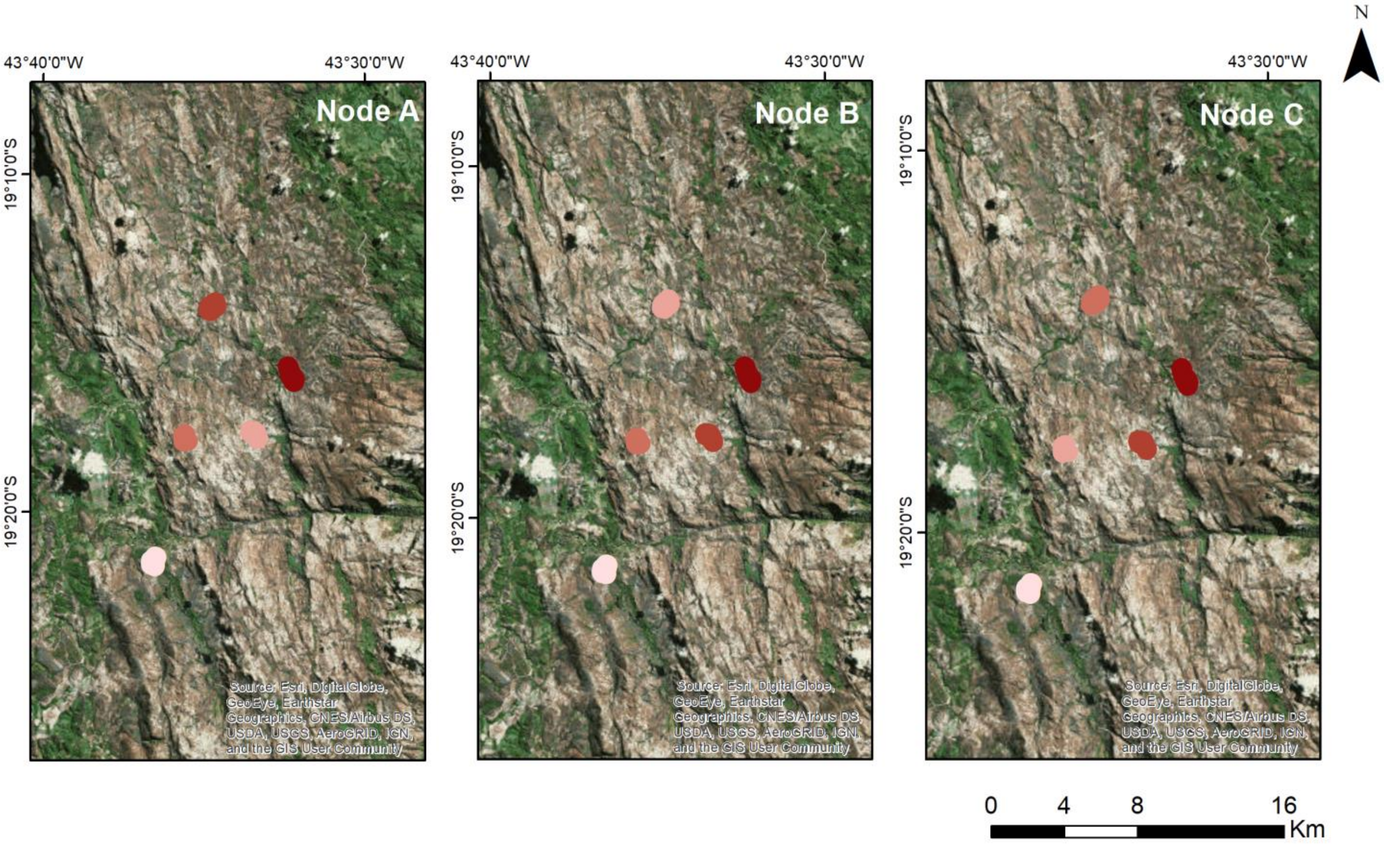


Figure 3. Distribution of specific overrepresentation scores of the three nodes with the highest degrees of node allopatry. Node A separates monocots, with positive scores (dark red), from eudicots, with negative scores (pale pink). Node B separates Eriocaulaceae, with positive scores (dark red), from Poaceae, with negative scores (pale pink). Node C separates Xyridaceae, with positive scores (dark red), from Cyperaceae, with negative scores (pale pink).

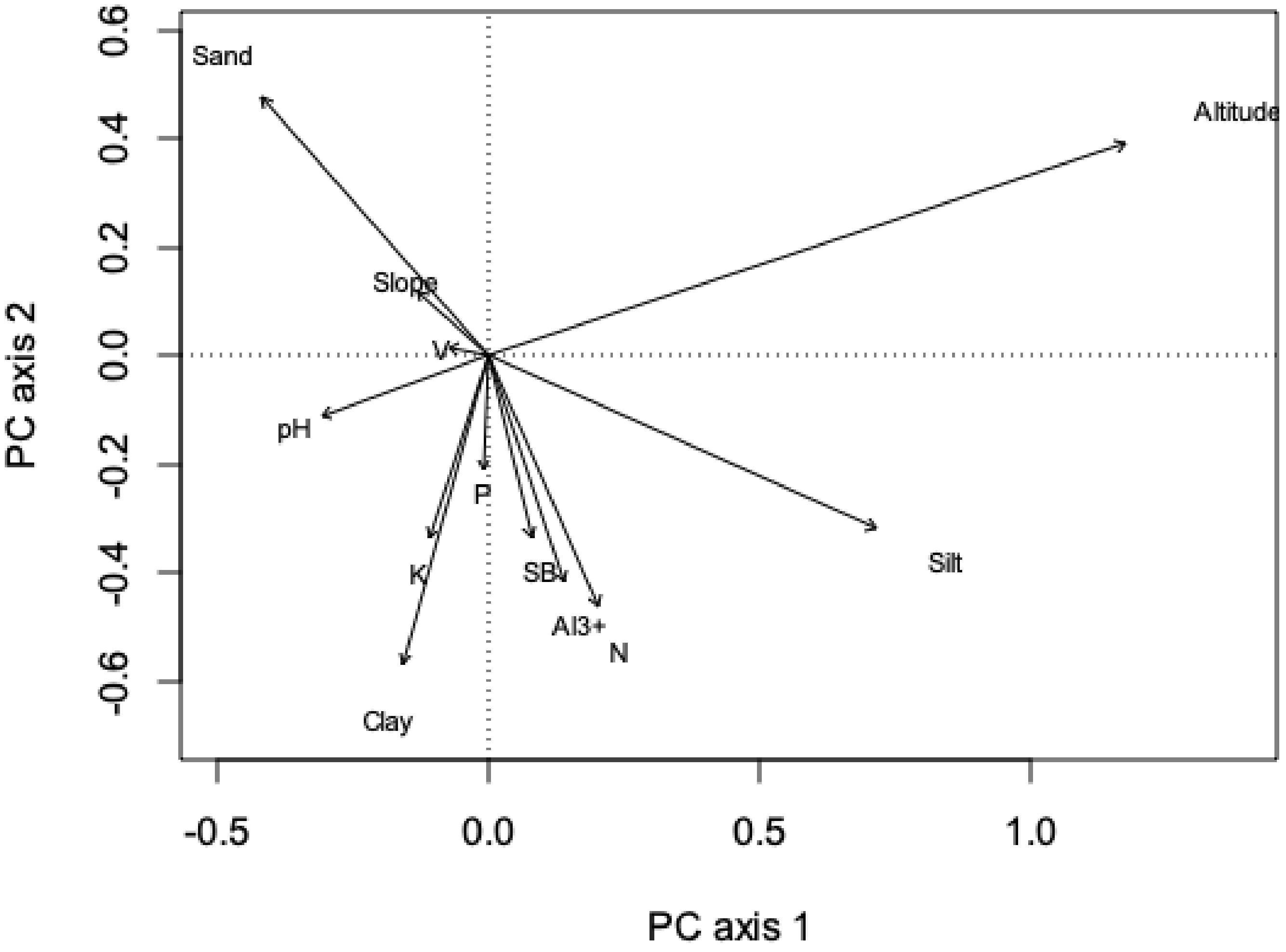


Figure 4. Principal component analysis on the 12 selected environmental variables (arrows). The first component explained 37.7% and was mostly related with altitude. The second component explained an additional 24.5% of the variation was mostly a fertility gradient, with more fertile presenting negative scores.

3.4 Discussion

The approach we used to infer the distributional divergence of sister clades (Borregaard et al. 2014) from the Cipó Mountains was highly informative. As both SOS (Specific Overrepresentation Score) and GND (Geographic Node Divergence) are comparable among nodes in a phylogeny and also between phylogenies, they are expected to be more statiscally tractable and useful than other indices often used in community phylogenetics (Parra et al. 2010, Borregaard et al. 2014). We supported niche conservatism theory, as we found significant phylogenetic spatial structure in the ancient landscape of the Cipó Mountains. Not only were the lineages structured in the geographic space, but also their distributions were intrinsically related to the environment. Interpretation of GND values, however, depends also on the scale and geographic extent of the study (Borregaard et al. 2014). At larger spatial scales, it can relate to major biogeographical events, such as movements across biomes or continents (Borregaard et al. 2014). At local scales, high GND can be related to changes in environmental preferences. Regional constraints are mostly linked to altitude-related factors, such as temperature, wind speed, precipitation, and humidity (Fernandes et al. 2016), whereas local constraints are mainly shaped by soil features (Fernandes et al. 2016, Mota et al. 2018). In the Cipó Mountains, we found that both regional and local constraints are shaping plant communities, because altitude, slope and soil features presented significant relationships with the three most allopatric nodes in the phylogeny.

Because GND is a correlative measure, it does not imply a fixed condition of geographical ranges, but, instead, high values just mean that sister clades are more segregated in space than they would be expected by chance (Borregaard et al. 2014). The first most allopatric node represented the divergence between eudicots (Magnoliopsida) and monocots (Liliopsida). This node represents the oldest speciation event in that phylogenetic tree. The split between monocots and eudicots dates from 140-150 Myr ago, during the late Jurassic-early Cretaceous (Chaw et al. 2004), and in the Cipó Mountains, these two clades were more segregated in space than expected, with their distribution being mostly related to altitude and sand. Monocots are mostly herbaceous species that prevail on open habitats (Zappi et al. 2017), thus we can argue that the distribution of monocots is prevailing in less fertile (Goodland and Pollard 1973; Schaefer et al. 2009; Valente 2009) open habitats located in high altitudes. Eudicots, on the other hand, have been found in other studies to be more clustered in lower areas with more closed environments (Zappi et al. 2017) in the Espinhaço Range, corroborating the association we found here.

The second most allopatric node represented the divergence between Eriocaulaceae and Poaceae, both monocot families, very abundant in the rocky grassland vegetation (Zappi et al. 2017). The specific overrepresentation scores associated with this node indicated that this spatial segregation had a significant relationship with both regional constraints (represented by altitude) and local constraints (soil features and slope). Eriocaulaceae, which presented higher values of SOS, tend to occupy higher areas with low levels of fertility. Indeed, it has been found on previous studies that Eriocaulaceae species mostly occupy highlands and rocky dry soils (Hensold 1991, Trovo et al. 2013). Meanwhile, Poaceae species were more related to higher levels of clay, nitrogen, potassium and other essential nutrients, typically present in more fertile, lowland environments.

The third most allopatric node showed the divergence between Cyperaceae and Xyridaceae. Their segregation was associated mainly with the soil fertility gradient, representing local constraints. Xyridaceae occupied less fertile environments, with high levels of sand and lower levels of primary nutrients, including P-impoverished areas (Oliveira et al. 2015). Xyridaceae presents many nutrient-acquisition strategies that Cyperaceae does not. For instance, Oliveira et al. (2015) reported 32 rocky grassland species that contain fine root specialization for phosphorus acquisition, and most of these species are Xyridaceae. Therefore, the evolution of the clade must have led Xyridaceae species to develop strategies to cope with the harsh environment, whereas Cyperaceae species were able to live in more fertile sites. Geographical shifts in the three most allopatric nodes, alongside with climatic and altitudinal shifts, show that adaptation to new environments are allowing clades to colonise other areas (Borregaard et al. 2014).

The rocky grassland might have been the oldest open vegetation in southeastern Brazil after the climate cooling that followed the Mid-Miocene optimum (Antonelli et al. 2010). There has been evidence for a high species turnover during the Cenozoic (Hughes et al. 2013), and most extant plant species are thought to have diversified after the late Miocene (11.3-5.3 Ma) (Hughes et al. 2013). Most families, though, are Gondwanan lineages that have probably evolved in situ in harsh environments at the Cipó Mountains (Zappi et al. 2017), including the families we found here as being the most allopatric ones. Some studies about endemism suggested that vicariance might have played an important role in these mountains (Echternacht et al. 2011), mainly due to the barrier to gene flow created by the very accentuated depressions on relief and insular properties leading to limited dispersability (Lousada et al. 2011, Leles et al. 2015).

Because the Cipó Mountains present a mosaic of vegetation types associated with soil features, local topography, and micro-environmental aspects (Silveira et al. 2015), we can assume that both soil features - acting locally – and climatic factors – acting regionally along altitude – can function as good predictors to biogeographical patterns of these lineages. We intended to take a further step into the node allopatry and spatial structure of vascular plant clades in this ancient mountaintop vegetation from southeastern Brazil, bringing to the spot the neglected rocky grassland. We found that the evolutionary history of Cipó lineages are strongly marked by environmental filters, such as edaphic factors, altitude and other micro-environmental aspects, and that few nodes in the phylogeny presented a high degree of allopatry, suggesting that these clades are the ones that differ the most both in their geographical and environmental preferences.

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3.7 Appendix 1. Sampled plant species and their presence/absence records in each study site (altitude). Family names are abbreviated according to Weber (1982), except Calophyllaceae and Phyllanthaceae, which did not have corresponding abbreviations.

Species	*Family*	*821 masl*	*1101 masl*	*1255 masl*	*1303 masl*	*1420 masl*
Ruellia brevifolia (Pohl) C.Ezcurra	ACA	0	0	1	0	0
Ruellia villosa Lindau	ACA	1	1	1	1	0
Gomphrena incana Mart.	AMA	0	1	1	1	0
Gomphrena moquinii Seub.	AMA	0	0	0	0	1
Gomphrena scapigera Mart.	AMA	0	0	1	1	0
Gomphrena sp.	AMA	0	0	0	0	1
Xerosiphon aphyllus (Pohl ex Moq.) Pedersen	AMA	0	0	0	1	1
Klotzschia rhizophylla Urb.	API	0	0	0	0	1
Aspidosperma tomentosum Mart.	APO	1	0	0	0	0
Barjonia chloraeifolia Decne.	APO	0	0	0	1	0
Hancornia speciosa Gomes	APO	0	1	0	0	0
Hemipogon hatschbachii (Fontella & Marquete) Rapini	APO	0	0	1	1	0
Minaria decussata (Mart.) T.U.P.Konno & Rapini	APO	0	0	1	1	0
Minaria ditassoides (Silveira) T.U.P.Konno & Rapini	APO	1	0	0	1	0
Ilex nummularia Reissek	AQF	0	0	1	0	0
Schefflera villosissima Fiaschi & Pirani	ARL	1	1	0	0	0
Syagrus glaucescens Glaz. ex Becc.	AST	1	0	0	0	0
Achyrocline satureioides (Lam.) DC.	AST	0	1	0	0	0
Ageratum fastigiatum (Gardner) R.M.King & H.Rob.	AST	0	1	0	0	0
Aspilia jolyana G.M.Barroso	AST	0	1	1	1	0
Aspilia sp.	AST	0	0	0	1	0
Baccharis dracunculifolia DC.	AST	1	0	1	0	0
Baccharis platypoda DC.	AST	0	0	0	0	1
Chaptalia cipoensis Roque	AST	0	0	0	0	1
Chaptalia integerrima (Vell.) Burkart	AST	0	0	0	0	1
Chromolaena squalida (DC.) R.M.King & H.Rob.	AST	1	0	0	0	0
Dasyphyllum reticulatum (DC.) Cabrera	AST	0	0	1	0	0
Eremanthus glomerulatus Less.	AST	1	1	0	0	0

Heterocondylus pumilus (Gardner) R.M.King & H.Rob.	AST	0	0	0	1	0
Lepidaploa rufogrisea (A. St.-Hil.) H.Rob.	AST	1	0	0	0	0
Lessingianthus linearifolius (Less.) H.Rob.	AST	1	0	1	1	0
Lessingianthus psilophyllus (DC.) H.Rob.	AST	0	1	1	1	1
Lessingianthus warmingianus (Baker) H.Rob.	AST	0	0	1	0	0
Lychnophora humillima Sch.Bip.	AST	0	0	0	0	1
Lychnophora passerina (Mart. ex DC.) Gardner	AST	0	1	0	0	0
Lychnophora sp.1	AST	0	0	1	0	0
Lychnophora sp.2	AST	0	0	1	0	0
Lychnophora sp.3	AST	0	0	0	1	0
Mikania cipoensis G.M.Barroso	AST	0	0	0	0	1
Mikania sessilifolia DC.	AST	0	1	1	1	1
Mikania sp.	AST	0	0	1	0	0
Minasia pereirae H.Rob.	AST	0	0	0	0	1
Porophyllum obscurum (Spreng.) DC.	AST	0	1	0	0	0
Prestelia eriopus Sch.Bip. ex Sch.Bip.	AST	0	0	0	1	0
Pseudobrickellia angustissima (Spreng. ex Baker) R.M.King	AST	1	0	0	0	0
Rhynchospora terminalis (Nees) Steud.	AST	1	1	1	1	1
Richterago angustifolia (Gardner) Roque	AST	0	0	0	0	1
Richterago arenaria (Baker) Roque	AST	0	0	1	1	1
Richterago polymorpha (Less.) Roque	AST	1	1	1	1	1
Richterago polyphylla (Baker ex Baker) Ferreyra	AST	0	1	1	1	0
Asteraceae sp.1	AST	0	0	1	0	0
Asteraceae sp.2	AST	0	0	0	0	1
Asteraceae sp.3	AST	0	1	0	0	0
Asteraceae sp.4	AST	1	0	0	1	0
Richterago stenophylla (Cabrera) Roque	AST	0	1	0	1	1
Symphyopappus cuneatus (DC.) Sch.Bip. ex Baker	AST	0	1	1	0	0
Symphyopappus sp.	AST	1	0	0	0	0
Vernonia rubriramea Mart. ex DC.	AST	1	0	0	0	0
Fridericia speciosa Mart.	BIG	1	0	0	0	0
Jacaranda paucifoliata Mart. ex DC.	BIG	1	0	0	0	0

Tabebuia ochracea A.H. Gentry	BIG	1	0	0	0	0
Dyckia macedoi L.B.Sm.	BML	1	0	0	0	1
Dyckia saxatilis Mez	BML	1	0	1	0	0
Dyckia sp.	BML	1	0	0	0	0
Encholirium heloisae (L.B.Sm.) Forzza & Wand.	BML	0	0	0	1	0
Kielmeyera petiolaris Mart. & Zucc.	CLP	0	0	1	0	0
Kielmeyera sp.	CLP	0	1	0	0	0
Peritassa campestris (Cambess.) A.C.Sm.	CEL	1	0	0	0	0
Plenckia populnea Reissek	CEL	1	0	0	0	0
Kielmeyera coriacea Mart.	CLU	1	0	0	0	0
Terminalia glabrescens Mart.	CMB	1	0	0	0	0
Rourea induta Planch.	CNN	1	0	0	0	0
Cuscuta racemosa Mart.	CNV	1	0	1	0	0
Evolvulus lithospermoides Mart.	CNV	0	1	0	0	0
Ipomea sp.	CNV	0	0	1	0	0
Jacquemontia prostrata Choisy	CNV	0	0	0	1	1
Merremia tomentosa Hallier	CNV	1	0	0	0	0
Bulbostylis conspicua (Boeckeler) H.Pfeiff.	CYP	0	0	1	0	1
Bulbostylis eleocharoides Kral & M.T.Strong	CYP	0	1	1	0	0
Bulbostylis emmerichiae T.Koyama	CYP	0	1	1	1	0
Bulbostylis junciformis (Kunth) C.B.Clarke	CYP	1	1	1	1	1
Bulbostylis lombardii Kral & M.T.Strong	CYP	0	0	0	1	1
Bulbostylis paradoxa (Spreng.) Lindm.	CYP	1	1	1	1	0
Bulbostylis truncata (Nees) M.T.Strong	CYP	0	1	1	1	0
Bulbostylis vestita (Kunth) C.B.Clarke	CYP	0	0	1	1	1
Lagenocarpus alboniger (A.St.-Hil.) C.B.Clarke	CYP	0	0	1	1	0
Lagenocarpus bracteosus C.B.Clarke	CYP	0	0	0	0	1
Lagenocarpus junciformis (Kunth) Kuntze	CYP	0	0	0	0	1
Lagenocarpus rigidus (Kunth) Nees	CYP	0	1	1	1	1
Lagenocarpus sp.	CYP	0	1	1	0	0
Lagenocarpus velutinus Nees	CYP	0	0	0	1	0
Rhynchospora brevirostris Griseb.	CYP	0	1	1	1	1
Rhynchospora ciliolata Boeckeler	CYP	0	0	0	1	1

Rhynchospora consanguinea (Kunth) Boeckeler	CYP	1	1	1	1	1
Rhynchospora emaciata (Nees) Boeckeler	CYP	0	1	1	1	1
Rhynchospora exaltata Kunth	CYP	1	0	0	0	0
Rhynchospora globosa (Kunth) Roem. & Schult.	CYP	0	1	0	0	0
Rhynchospora patuligluma C.B.Clarke ex Lindm.	CYP	0	0	0	0	1
Rhynchospora pilosa Boeckeler	CYP	0	1	1	0	1
Rhynchospora recurvata (Nees) Steud.	CYP	0	1	1	1	0
Rhynchospora riedeliana C.B.Clarke	CYP	0	1	1	1	1
Rhynchospora sp.	CYP	0	0	1	0	0
Cyperaceae sp.1	CYP	0	1	0	0	0
Cyperaceae sp.2	CYP	0	0	0	0	1
Rhynchospora sp.1	CYP	0	0	1	0	0
Rhynchospora sp.2	CYP	0	0	1	0	0
Rhynchospora sp.3	CYP	1	0	0	0	0
Scleria cuyabensis Pilg.	CYP	0	0	0	1	0
Davilla elliptica A.St.-Hil.	DLL	1	1	1	1	0
Dioscorea polygonoides Humb. & Bonpl. ex	DSC	1	0	0	0	0
Drosera chrysolepis Taub.	DRS	0	0	1	0	1
Drosera montana A.St.-Hil.	DRS	0	0	1	1	1
Diospyros hispida A.DC.	EBN	1	0	0	0	0
Gaylussacia montana (Pohl) Sleumer	ERI	0	0	1	1	0
Gaylussacia riedelii Meisn.	ERI	0	0	0	1	1
Gaylussacia virgata Mart. ex Meisn.	ERI	0	0	0	0	1
Actinocephalus bongardii (A.St.-Hil.) Sano	ERO	0	0	0	1	0
Actinocephalus polyanthus (Bong.) Sano	ERO	0	0	0	0	1
Comanthera centauroides (Bong.) L.R.Parra & Giul.	ERO	0	1	1	0	1
Comanthera cipoensis (Ruhland) L.R.Parra & Giul.	ERO	0	0	1	1	1
Comanthera circinnata (Bong.) L.R.Parra & Giul.	ERO	0	1	0	0	0
Leiothrix crassifolia (Bong.) Ruhland	ERO	0	0	1	1	1
Leiothrix curvifolia (Bong.) Ruhland	ERO	0	0	0	0	1
Leiothrix sp.	ERO	0	0	0	0	1
Leiothrix spiralis (Bong.) Ruhland	ERO	0	0	0	0	1
Paepalanthus bromelioides Silveira	ERO	0	0	1	0	0
Paepalanthus chlorocephalus Silveira	ERO	0	0	0	0	1

Paepalanthus erectifolius Silveira	ERO	0	1	0	1	0
Paepalanthus eriophaeus Ruhland	ERO	0	1	0	0	0
Paepalanthus geniculatus (Bong.) Kunth	ERO	0	1	1	1	1
Paepalanthus macrocephalus (Bong.) Körn.	ERO	0	1	0	0	0
Paepalanthus nigrescens Silveira	ERO	0	0	1	1	1
Paepalanthus paulinus Ruhland	ERO	0	0	1	0	0
Paepalanthus planifolius (Bong.) Körn.	ERO	0	0	0	0	1
Paepalanthus sp.1	ERO	0	0	1	0	0
Paepalanthus sp.2	ERO	0	0	0	0	1
Paepalanthus sp.3	ERO	0	1	0	0	0
Paepalanthus sp.4	ERO	0	0	1	0	0
Syngonanthus sp.	ERO	0	0	1	0	1
Erythroxylum suberosum A.St.-Hil.	ERX	0	1	1	0	0
Bernardia crassifolia Müll.Arg.	EUP	1	0	0	0	0
Bernardia similis Pax & K.Hoffm.	EUP	0	1	0	0	0
Croton campestris A.St.-Hil.	EUP	0	0	1	0	0
Croton subferrugineus Müll.Arg.	EUP	1	1	1	0	0
Manihot esculenta Crantz	EUP	1	0	0	0	0
Manihot sp.	EUP	1	0	0	0	0
Manihot tripartita (Spreng.) Müll.Arg.	EUP	1	0	0	0	0
Maprounea guianensis Aubl.	EUP	1	0	0	0	0
Microstachys daphnoides (Mart.) Müll.Arg.	EUP	1	0	0	0	0
Acosmium dasycarpum (Vogel) Yakovlev	FAB	1	0	0	0	0
Andira humilis Mart. ex Benth.	FAB	1	0	0	0	0
Bionia coccinea Mart. ex Benth.	FAB	1	0	1	0	0
Calliandra dysantha Benth.	FAB	1	0	0	0	0
Calliandra fasciculata Benth.	FAB	1	0	0	0	0
Calliandra linearis Benth.	FAB	0	1	1	1	0
Chamaecrista anceps (Benth.) H.S.Irwin & Barneby	FAB	0	1	0	0	0
Chamaecrista cathartica (Mart.) H.S.Irwin & Barneby	FAB	0	0	0	1	0
Chamaecrista desvauxii (Collad.) Killip	FAB	0	1	0	1	1
Chamaecrista ochnacea (Vogel) H.S.Irwin & Barneby	FAB	0	1	1	1	0
Chamaecrista papillata H.S.Irwin & Barneby	FAB	1	1	0	1	0
Chamaecrista ramosa (Vogel) H.S.Irwin & Barneby	FAB	1	0	1	0	0

Chamaecrista sp.	FAB	0	0	1	0	0
Dalbergia miscolobium Benth.	FAB	0	1	1	0	0
Lupinus coriaceus Benth.	FAB	0	0	0	0	1
Mimosa bombycina Barneby	FAB	1	0	0	0	0
Senna rugosa (G.Don) H.S.Irwin & Barneby	FAB	1	0	0	0	0
Stryphnodendron adstringens (Mart.) Coville	FAB	0	1	0	0	0
Zornia latifolia Sm.	FAB	0	0	0	1	1
Curtia tenuifolia (Aubl.) Knobl.	GEN	0	0	0	1	1
Schultesia gracilis Mart.	GEN	0	0	0	1	0
Neomarica rupestris (Ravenna) Chukr	IRI	0	1	1	1	0
Pseudotrimezia cipoana Ravenna	IRI	0	0	1	1	0
Sisyrinchium vaginatum Spreng.	IRI	1	0	1	1	0
Trimezia fistulosa R.C.Foster	IRI	0	0	1	0	0
Trimezia juncifolia (Klatt) Benth. & Hook.f.	IRI	1	1	1	1	1
Trimezia sp.1	IRI	0	1	0	0	0
Trimezia sp.2	IRI	0	0	0	0	1
Trimezia sp.3	IRI	0	0	1	1	1
Eriope arenaria Harley	LAM	0	1	1	1	0
Hyptidendron canum (Pohl ex Benth.) Harley	LAM	1	0	0	0	0
Hyptidendron vauthieri (Briq.) Harley	LAM	0	1	0	0	0
Hyptis crenata Pohl ex Benth.	LAM	1	0	1	0	0
Hyptis proteoides A.St.-Hil. ex Benth.	LAM	1	0	1	1	0
Hyptis sp.	LAM	0	1	0	0	0
Spigelia aceifolia Woodson	LOG	0	0	0	1	0
Spigelia schlechtendaliana Mart.	LOG	0	0	0	0	1
Spigelia sellowiana Cham. & Schltdl.	LOG	0	1	0	1	0
Spigelia sp.	LOG	0	0	0	1	1
Cuphea ericoides Cham. & Schltdl.	LYT	0	0	1	0	0
Cuphea pseudovaccinium A.St.-Hil.	LYT	0	1	1	0	1
Cuphea sp.	LYT	0	0	1	0	0
Diplusodon lanceolatus Pohl	LYT	0	1	0	0	0
Diplusodon orbicularis Koehne	LYT	0	1	1	1	0
Lafoensia pacari A. St.-Hil.	LYT	1	0	0	0	0

Banisteriopsis campestris (A.Juss.) Little	MLP	1	0	0	0	0
Banisteriopsis cipoensis B.Gates	MLP	1	1	0	0	0
Banisteriopsis sp.	MLP	1	1	0	0	0
Byrsonima dealbata Griseb.	MLP	1	1	0	1	0
Byrsonima sp.	MLP	1	0	0	0	0
Byrsonima vacciniifolia A.Juss.	MLP	1	0	1	0	0
Peixotoa tomentosa A. Juss.	MLP	0	1	0	0	0
Pterandra pyroidea A. Juss.	MLP	1	0	0	0	0
Tetrapterys microphylla Nied.	MLP	1	0	1	0	0
Ayenia angustifolia A.St.-Hil. & Naudin	MLV	1	0	0	0	0
Pavonia sp.	MLV	1	0	0	0	0
Sida aurantiaca A. St.-Hil.	MLV	1	0	0	0	0
Eriotheca sp.	MLV	1	0	0	0	0
Cambessedesia semidecandra A. St.-Hil. ex A.B.	MLS	0	0	0	1	1
Chaetostoma sp.	MLS	0	0	1	1	0
Lavoisiera confertiflora Naudin	MLS	0	1	1	0	1
Lavoisiera crassifolia DC.	MLS	0	0	0	1	1
Marcetia acerosa DC.	MLS	0	0	1	0	0
Marcetia sp.	MLS	0	0	0	0	1
Marcetia taxifolia (A. St.-Hil.) DC.	MLS	0	1	1	1	1
Miconia albicans (Sw.) Steud.	MLS	1	1	0	0	0
Miconia alborufescens Naudin	MLS	1	0	0	0	0
Miconia fallax DC.	MLS	1	0	0	0	0
Miconia sp.	MLS	1	0	0	0	0
Microlicia cardiophora Naudin	MLS	1	0	0	0	0
Microlicia sp.	MLS	1	0	1	0	0
Microlicia sp.1	MLS	0	0	1	0	0
Microlicia sp.2	MLS	0	0	1	0	0
Microlicia sp.3	MLS	0	0	1	0	0
Microlicia sp.4	MLS	0	0	1	0	0
Pleroma sp.	MLS	0	0	1	0	0
Siphanthera arenaria (DC.) Cogn.	MLS	0	0	1	1	1
Tibouchina heteromalla (D. Don) Cogn.	MLS	1	0	0	0	0

Trembleya laniflora (D. Don) Cogn.	MLS	0	0	1	0	0
Ficus sp.	MOR	1	0	0	0	0
Campomanesia pubescens (Mart. ex DC.) O.Berg	MRT	0	1	0	0	0
Myrcia bella Cambess.	MRT	1	0	0	0	1
Myrcia guianensis (Aubl.) DC.	MRT	1	1	1	0	0
Myrcia sp.1	MRT	1	0	0	0	0
Myrcia sp.2	MRT	1	0	0	0	0
Myrcia sp.3	MRT	1	0	0	0	0
Guapira noxia (Netto) Lundell	NYC	1	0	0	0	0
Guapira opposita (Vell.) Reitz	NYC	1	0	0	0	0
Guapira sp.	NYC	0	0	0	0	1
Neea theifera Oerst.	NYC	1	1	1	0	0
Ouratea floribunda Engl.	OCH	0	1	1	1	0
Habenaria magniscutata Catling	ORC	0	0	1	0	0
Habenaria sp.1	ORC	0	1	0	0	0
Habenaria sp.2	ORC	0	0	1	0	0
Habenaria sp.3	ORC	0	0	0	1	0
Habenaria sp.4	ORC	0	0	0	0	1
Agalinis brachyphylla (Cham. & Schltdl.) D'Arcy	ORO	0	1	0	0	1
Buchnera lavandulacea Cham. & Schltdl.	ORO	0	0	0	1	0
Buchnera palustris (Aubl.) Spreng.	ORO	0	1	0	0	0
Oxalis densifolia Mart. ex Zucc.	OXL	1	0	0	0	0
Phyllanthus choretroides Müll.Arg.	PLL	0	1	0	0	0
Andropogon bicornis L.	POA	1	1	0	0	0
Andropogon leucostachyus Kunth	POA	1	1	1	0	0
Andropogon sp.1	POA	1	0	0	0	0
Andropogon sp.10	POA	1	0	0	0	0
Andropogon sp.11	POA	1	0	0	0	0
Andropogon sp.12	POA	0	0	1	0	0
Andropogon sp.2	POA	0	1	0	0	0
Andropogon sp.3	POA	1	1	1	0	0
Andropogon sp.4	POA	0	0	0	1	0
Andropogon sp.5	POA	0	0	0	1	0

Andropogon sp.6	POA	0	0	1	0	0
Andropogon sp.7	POA	1	0	0	0	0
Andropogon sp.8	POA	1	0	0	1	0
Andropogon sp.9	POA	1	0	0	0	0
Anthaenantia sp.	POA	0	1	1	0	0
Aristida ekmaniana Henrard	POA	1	0	0	0	0
Aristida longifolia Trin.	POA	1	0	0	0	0
Aristida setifolia Kunth	POA	1	0	0	0	0
Aristida sp.	POA	0	1	0	0	0
Aristida torta (Nees) Kunth	POA	0	0	1	1	1
Aulonemia effusa (Hack.) McClure	POA	0	0	0	1	0
Axonopus aureus P.Beauv.	POA	1	0	0	0	0
Axonopus brasiliensis (Spreng.) Kuhlm.	POA	0	1	1	1	1
Axonopus fastigiatus (Nees) Kuhlm.	POA	1	0	1	0	1
Axonopus marginatus (Trin.) Chase ex Hitchc.	POA	0	1	0	0	0
Axonopus sp.1	POA	0	0	0	0	1
Axonopus sp.2	POA	0	1	0	0	0
Axonopus sp.3	POA	1	1	1	0	0
Ctenium brevispicatum J.G.Sm.	POA	0	1	1	1	0
Echinolaena inflexa (Poir.) Chase	POA	1	1	1	1	1
Homolepis longispicula (Döll) Chase	POA	1	1	1	1	1
Leptocoryphium lanatum (Kunth) Nees	POA	0	1	0	0	0
Melinis minutiflora P.Beauv.	POA	1	0	0	0	0
Mesosetum exaratum (Trin.) Chase	POA	0	1	1	1	1
Mesosetum loliiforme (Steud.) Hitchc.	POA	1	1	1	0	0
Panicum cipoense Renvoize & Send.	POA	0	0	0	1	1
Panicum cyanescens Nees ex Trin.	POA	0	1	1	1	1
Panicum euprepes Renvoize	POA	0	1	1	1	0
Panicum loreum Trin.	POA	0	0	0	0	1
Panicum rupestre Trin.	POA	0	1	0	0	1
Poaceae sp.1	POA	0	0	1	1	1
Poaceae sp.2	POA	1	1	0	0	0
Poaceae sp.3	POA	1	0	0	0	0

Poaceae sp.4	POA	1	0	0	0	0
Poaceae sp.5	POA	0	0	0	1	0
Poaceae sp.6	POA	1	0	0	0	0
Poaceae sp.7	POA	0	0	1	1	0
Poaceae sp.8	POA	0	1	0	0	0
Poaceae sp.9	POA	0	1	0	1	0
Poaceae sp.10	POA	0	0	1	0	0
Poaceae sp.11	POA	1	0	0	0	0
Poaceae sp.12	POA	0	0	1	0	0
Poaceae sp.13	POA	1	0	0	0	0
Poaceae sp.14	POA	1	0	0	0	0
Poaceae sp.15	POA	0	0	1	0	1
Poaceae sp.16	POA	0	0	1	0	0
Poaceae sp.17	POA	0	0	1	0	0
Poaceae sp.18	POA	0	0	1	0	0
Poaceae sp.19	POA	1	0	0	0	0
Poaceae sp.20	POA	1	0	0	0	0
Poaceae sp.21	POA	0	0	0	1	0
Poaceae sp.22	POA	0	0	0	1	0
Poaceae sp.23	POA	0	0	0	0	1
Poaceae sp.24	POA	1	0	0	0	0
Poaceae sp.25	POA	0	0	1	0	0
Poaceae sp.26	POA	0	0	0	0	1
Poaceae sp.27	POA	1	0	0	0	0
Poaceae sp.28	POA	1	0	1	0	0
Poaceae sp.29	POA	0	0	0	1	0
Poaceae sp.30	POA	0	1	0	0	0
Poaceae sp.31	POA	0	1	0	0	0
Poaceae sp.32	POA	0	1	0	0	0
Poaceae sp.33	POA	0	1	0	0	0
Poaceae sp.34	POA	1	0	0	0	0
Poaceae sp.35	POA	0	1	0	0	0
Poaceae sp.36	POA	0	0	1	0	0

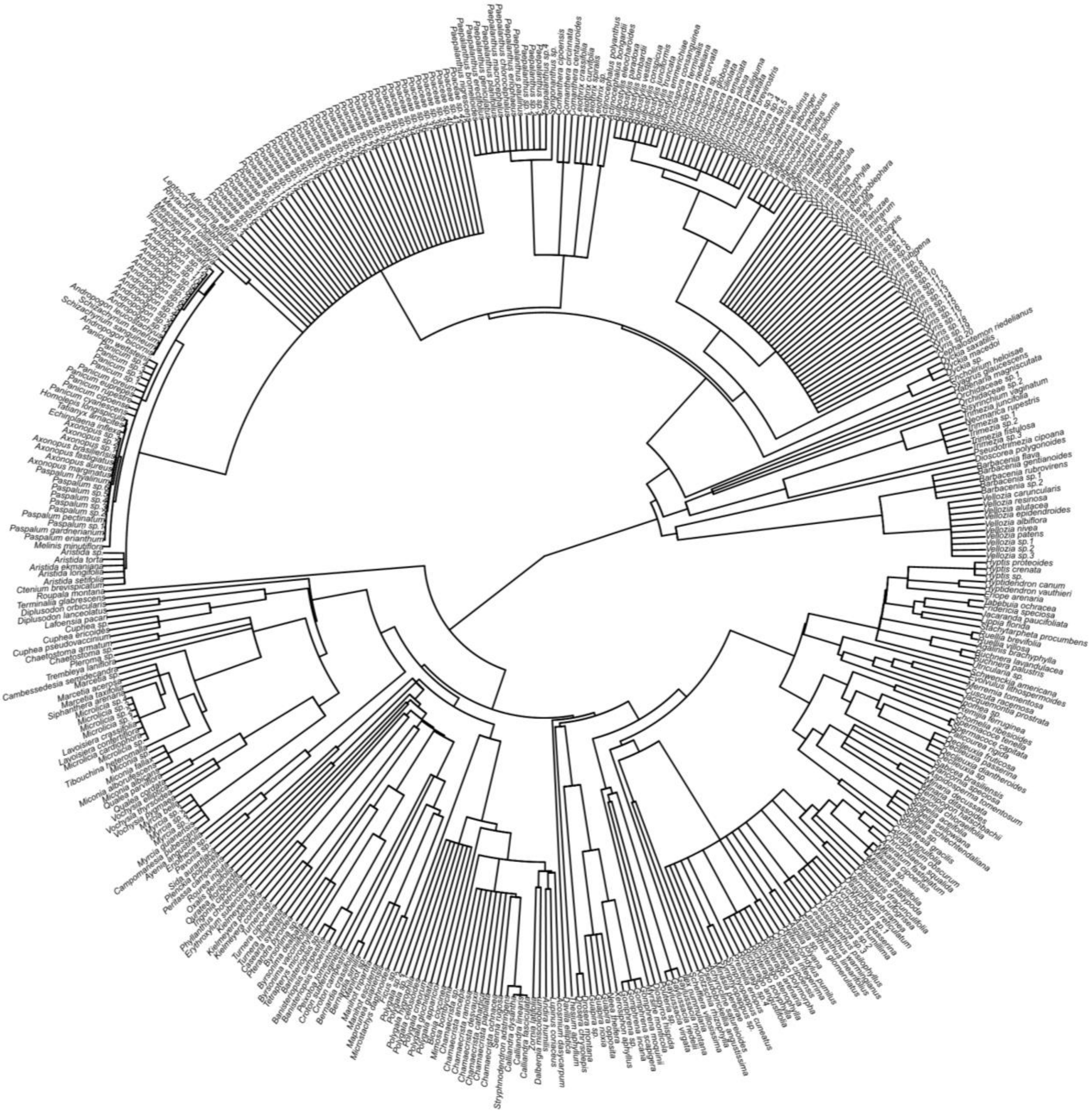
Poaceae sp.37	POA	0	1	0	0	0
Poaceae sp.38	POA	0	0	0	1	0
Poaceae sp.39	POA	1	0	0	0	0
Poaceae sp.40	POA	0	0	1	0	0
Poaceae sp.41	POA	0	0	0	1	0
Poaceae sp.42	POA	0	0	1	0	0
Poaceae sp.43	POA	0	0	1	0	0
Poaceae sp.44	POA	0	0	0	0	1
Poaceae sp.45	POA	0	0	1	1	1
Poaceae sp.46	POA	0	0	0	0	1
Poaceae sp.47	POA	0	1	0	0	0
Poaceae sp.48	POA	0	0	0	1	0
Poaceae sp.49	POA	0	1	0	0	0
Poaceae sp.50	POA	0	0	0	1	1
Poaceae sp.51	POA	0	0	0	0	1
Panicum wettsteinii Hack.	POA	0	0	0	0	1
Paspalum erianthum Nees ex Trin.	POA	0	1	1	1	1
Paspalum gardnerianum Nees	POA	1	0	0	0	0
Paspalum hyalinum Nees ex Trin.	POA	1	1	1	1	1
Paspalum pectinatum Nees	POA	0	1	1	1	1
Paspalum sp.	POA	0	0	0	0	1
Rhytachne subgibbosa (Winkler ex Hack.) Clayton	POA	1	0	0	0	0
Schizachyrium sanguineum (Retz.) Alston	POA	1	0	0	1	1
Schizachyrium tenerum Nees	POA	0	1	1	1	1
Tatianyx arnacites (Trin.) Zuloaga & Soderstr.	POA	1	1	1	1	1
Trachypogon spicatus (L.f.) Kuntze	POA	1	1	1	1	1
Tristachya leiostachya Nees	POA	1	0	0	0	0
Polygala appariciois Brade	PGL	0	0	0	1	1
Polygala celosioides A.W. Benn.	PGL	0	0	0	0	1
Polygala cneorum A. St.-Hil. & Moq.	PGL	0	0	0	1	1
Polygala glochidiata Kunth	PGL	0	0	0	1	1
Polygala hygrophila Kunth	PGL	0	1	0	0	0
Polygala sp.1	PGL	0	0	0	1	0
Polygala sp.2	PGL	0	0	0	0	1

Myrsine monticola Mart.	PRM	1	1	1	1	0
Roupala montana Aubl.	PRT	1	1	0	1	0
Cephalostemon riedelianus Körn.	RPT	0	0	1	1	0
Chomelia ribesioides Benth. ex A.Gray	RUB	0	0	1	0	0
Declieuxia fruticosa (Willd. ex Roem.)	RUB	0	0	0	1	0
Declieuxia passerina Mart. & Zucc. ex	RUB	1	1	1	0	0
Declieuxia sp.	RUB	1	0	0	0	0
Palicourea rigida Kunth	RUB	0	1	1	0	0
Remijia ferruginea (A.St.-Hil.) DC.	RUB	0	0	1	0	0
Sabicea brasiliensis Wernham	RUB	1	0	1	0	0
Spermacoce capitata Ruiz & Pav.	RUB	1	0	1	0	1
Spermacoce tenella Kunth	RUB	1	0	0	0	0
Casearia sylvestris Sw.	SAL	1	0	0	0	0
Thesium aphyllum Mart. ex A. DC.	SAN	0	0	0	1	0
Pouteria sp.	SPT	1	0	0	0	0
Schwenckia americana L.	SOL	1	0	1	0	0
Trigonia cipoensis Fromm & E. Santos	TRG	0	1	1	0	0
Turnera cipoensis Arbo	TNR	1	1	0	0	0
Turnera hilaireana Urb.	TNR	0	0	1	0	1
Turnera sp.	TNR	0	1	1	1	0
Utricularia sp.	LNT	0	0	0	1	0
Barbacenia flava Mart. ex Schult. &	VLL	0	1	0	0	0
Barbacenia gentianoides Goethart & Henrard	VLL	0	0	0	1	1
Barbacenia rubrovirens Mart.	VLL	0	0	0	1	0
Barbacenia sp.1	VLL	1	0	0	0	0
Barbacenia sp.2	VLL	0	0	1	0	0
Vellozia albiflora Pohl	VLL	1	1	1	1	0
Vellozia alutacea Pohl	VLL	0	1	1	1	0
Vellozia caruncularis Mart. ex Seub.	VLL	0	0	1	0	0
Vellozia epidendroides Mart.	VLL	0	1	1	1	1
Vellozia nivea L.B.Sm. & Ayensu	VLL	0	1	1	1	0
Vellozia patens L.B.Sm. & Ayensu	VLL	0	0	0	0	1
Vellozia resinosa Mart.	VLL	0	0	0	0	1

Vellozia sp.1	VLL	1	0	0	0	0
Vellozia sp.2	VLL	0	0	1	0	0
Vellozia sp.3	VLL	0	0	1	1	0
Lippia florida Cham.	VRB	0	0	1	1	0
Stachytarpheta procumbens Moldenke	VRB	0	0	1	1	1
Qualea cordata Spreng.	VOC	1	0	0	0	0
Qualea parviflora Mart.	VOC	1	0	0	0	0
Vochysia elliptica Mart.	VOC	0	0	1	0	0
Vochysia pygmaea Bong.	VOC	0	0	1	1	0
Vochysia thyrsoidea Pohl	VOC	0	0	1	0	0
Xyris asperula Mart.	XYR	0	1	0	1	1
Xyris melanopoda L.B.Sm. & Downs	XYR	0	0	1	0	1
Xyris hystrix Seub.	XYR	0	1	0	0	0
Xyris itatiayensis (Malme) Wand. & Sajo	XYR	0	0	1	0	1
Xyris longiscapa L.A.Nilsson	XYR	0	1	1	0	1
Xyris minarum Seub.	XYR	0	1	1	0	0
Xyris nanuzae Wand.	XYR	0	0	1	0	0
Xyris nubigena Kunth	XYR	0	0	0	1	0
Xyris obtusiuscula L.A.Nilsson	XYR	0	1	1	1	1
Xyris pilosa Kunth	XYR	0	0	1	0	1
Xyris pterygoblephara Steud.	XYR	0	1	1	0	1
Xyris sp.1	XYR	0	1	1	0	0
Xyris sp.10	XYR	0	0	1	0	0
Xyris sp.11	XYR	0	0	0	1	1
Xyris sp.12	XYR	0	0	0	0	1
Xyris sp.13	XYR	0	0	1	0	0
Xyris sp.14	XYR	0	0	0	1	1
Xyris sp.15	XYR	0	0	0	1	0
Xyris sp.16	XYR	0	0	0	0	1
Xyris sp.17	XYR	0	0	0	1	0
Xyris sp.18	XYR	0	0	0	0	1
Xyris sp.19	XYR	0	0	0	1	0
Xyris sp.2	XYR	0	0	1	0	1

Xyris sp.20	XYR	0	0	0	0	1
Xyris sp.3	XYR	0	0	1	0	0
Xyris sp.4	XYR	0	0	1	0	0
Xyris sp.5	XYR	0	1	1	0	1
Xyris sp.6	XYR	0	0	0	1	0
Xyris sp.7	XYR	0	0	1	1	0
Xyris sp.8	XYR	0	0	0	0	1
Xyris sp.9	XYR	0	0	0	0	1
Xyris tenella Kunth	XYR	0	0	1	0	1
Xyris tortula Mart.	XYR	0	1	0	1	1
Xyris trachyphylla Mart.	XYR	0	1	1	1	0
Xyris insignis L.A. Nilsson	XYR	0	0	1	0	1

3.8 Appendix 2. Phylogenetic tree of the sampled plant species.



4. Considerações Finais

Neste estudo, concluímos que as comunidades vegetais da Serra do Cipó apresentam um padrão de diversidade filogenética ao longo da montanha e que são influenciadas principalmente por filtros ambientais, como altitude, declividade e propriedades do solo. Para a diversidade filogenética, concluímos que a variabilidade filogenética de espécies diminui com a altitude, enquanto a riqueza filogenética de espécies aumenta. Ambas estão mais relacionadas com fatores ambientais locais, como o solo. Também pudemos corroborar a teoria do conservadorismo de nicho, uma vez que em áreas mais altas da montanha obtivemos comunidades mais agregadas (com valores de variabilidade menores) e, ainda assim, mais ricas em espécies (valores de riqueza maiores), mostrando que a maior diversidade se concentra entre alguns poucos clados. Também pudemos concluir que três nós da árvore filogenética apresentam altos valores de alopatria, indicando que esses nós representam uma divergência evolutiva, espacial e geográfica entre seus clados descendentes. Com essas quatro métricas, pudemos avaliar a diversidade filogenética e espacial nos campos rupícolas da Serra do Cipó de uma maneira efetiva e estatisticamente tratável. Contribuímos com o fornecimento de pistas sobre a evolução desses clados em áreas montanhosas, sendo possível expandir esses resultados para outras cadeias de montanhas e outros ambientes funcionalmente similares. Além disso, procuramos também contribuir com a conservação desses ambientes incrivelmente diversos e mostrar que essa diversidade não se resume a um alto número de espécies, mas que existe uma longa história evolutiva construída e instituída nessas linhagens, muitas delas sendo tão antigas quanto o próprio continente americano. Por fim, propomos também que outros trabalhos de evolução e filogenia sejam conduzidos em áreas de campos rupícolas, como a Serra do Cipó, uma vez que existem grupos taxonômicos que ainda necessitam de estudos mais profundos sobre sua história evolutiva para que possam ser incorporados em estudos de diversidade filogenética.

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