

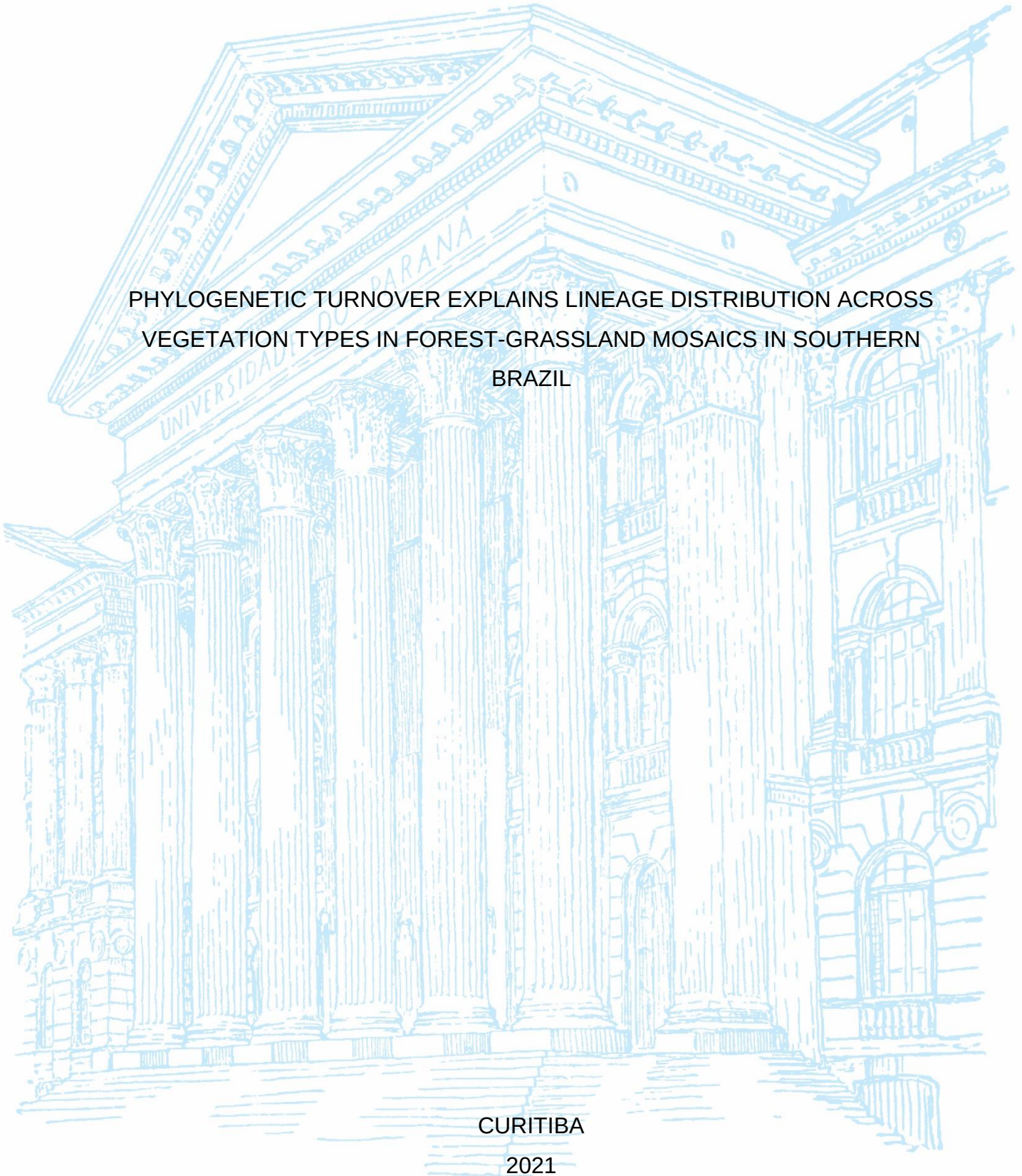
UNIVERSIDADE FEDERAL DO PARANÁ

ADLER DVORAK BARBOZA

PHYLOGENETIC TURNOVER EXPLAINS LINEAGE DISTRIBUTION ACROSS
VEGETATION TYPES IN FOREST-GRASSLAND MOSAICS IN SOUTHERN
BRAZIL

CURITIBA

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Monografia em formato de artigo de periódico apresentada ao curso de Ciências Biológicas, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Bacharel em Ciências Biológicas.

Orientador: Prof. Dr. Marcos Bergmann Carlucci

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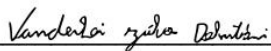
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**PHYLOGENETIC TURNOVER EXPLAINS LINEAGE DISTRIBUTION
ACROSS VEGETATION TYPES IN FOREST-GRASSLAND MOSAICS IN
SOUTHERN BRAZIL**

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RESUMO

Questões: Analisamos a composição e estrutura filogenética de diferentes fitofisionomias em mosaicos campo-floresta. Avaliamos (1) quanta informação filogenética há em comunidades vegetais em campos e florestas em mosaicos; e (2) quais diferenças na composição de linhagens entre campos e florestas.

Localização: Parque Estadual do Guartelá, em Tibagi e Parque Estadual de Vila Velha, em Ponta Grossa, Paraná, Brasil.

Métodos: Utilizamos dados fitossociológicos de diferentes tipos de vegetação (campos sujos, úmidos e rochosos, florestas e ecótonos de floresta-campo). Avaliamos a diversidade filogenética em cada tipo de vegetação e entre os diferentes tipos. Particionamos as diferenças de composição filogenética entre substituição de linhagens e aninhamento entre diferentes tipos de vegetação e

comparamos os valores observados com modelos nulos. Além disso, avaliamos a representatividade de linhagens nas fitofisionomias.

Resultados: Em ampla escala, os campos apresentam menor diversidade filogenética que as florestas. Encontramos baixos níveis de diversidade filogenética alfa nos tipos de campos e um agrupamento filogenético em campos úmidos. Floresta e campos diferiram em estrutura filogenética quando comparados entre si. A substituição de linhagens é alta entre as fitofisionomias, implicando que condições ambientais próprias de cada fisionomia moldam as comunidades dos mosaicos. Há padrões de associação de linhagens com os tipos de vegetação, como samambaias associadas aos ecótonos de floresta e campo.

Conclusões: A diversidade e composição filogenética da vegetação em mosaicos campo-floresta estão altamente relacionadas aos diferentes tipos de fitofisionomias, indicando a associação de processos ecológicos e evolutivos na organização das comunidades.

Palavras-chave: biogeografia histórica, campos sulinos, composição filogenética, estrutura filogenética, Floresta com Araucária.

ABSTRACT

Questions: We assessed phylogenetic composition and structure of plant communities across different vegetation types in forest-grassland mosaics. We asked (1) how much phylogenetic information grasslands and forests harbor in mosaics; and (2) what are the phylogenetic dissimilarities among grasslands and forests at broad and fine scales.

Location: Guartelá state park, Tibagi, Paraná, Brazil and Vila Velha state park, Ponta Grossa, Paraná, Brazil.

Methods: We used plant community data sampled in different vegetation physiognomies of grasslands and forests (i.e., dry, wet, and rocky grasslands, forests, and grassland-forest ecotones). We computed phylogenetic diversity for each vegetation type and among them. We partitioned phylogenetic composition differences into turnover and nestedness of lineages among the different vegetation types. Then, we compared all observed values with null expectations

from the regional lineage pool. Furthermore, we assessed the representation of plant clades and vegetation physiognomies.

Results: At a broader scale, grasslands show less phylogenetic diversity than forests. We found low levels of phylogenetic alpha diversity in the grassland types and a phylogenetic clustering in wet grasslands. Forests and grasslands differed in phylogenetic structure when compared to each other. Lineage turnover is high among vegetation physiognomies. This pattern implies that environmental conditions that are unique to each vegetation shape the mosaic assemblages. We found patterns of lineage association with vegetation types, such as ferns associated with grassland-forest ecotones.

Conclusions: The phylogenetic composition and structure of the vegetation in grassland-forest mosaics are highly related to the different vegetation physiognomies. That indicates ecological and evolutive processes are associated with the shaping of the mosaic communities.

Keywords: *Araucaria* Forest, *Campos*, historical biogeography, phylogenetic composition, phylogenetic structure.

INTRODUCTION

It is important to address other biodiversity dimensions than species richness to increase understanding on ecological processes (Lyashevskaya and Farnsworth, 2012). Evolutionary ideas have been present in ecological researches for about 100 years (Swenson, 2019), but it was only recently that robust frameworks to test phylogenetic hypotheses have been proposed in community ecology. The foundation of a study field called “phylogenetic community ecology” expanded the boundaries of community ecology and fostered possibilities for integration with other research fields (Webb *et al.*, 2002). Forest-grassland mosaics are intriguing to investigate phylogenetic ecology patterns because their vegetation types arose in the deep past and their modern cooccurrence results from climate changes from dry and hot conditions to wet and cold in the last few millennia (Behling, 2002). Common in tropical and subtropical ecosystems (Oliveras and Malhi, 2016), current forest-grassland

mosaics are associated with the last glaciation event, which allowed forests to expand beyond their mountain valley refugia (Carnaval and Moritz, 2008). The encroachment of woody plants on grasslands has been promoted by reduction in frequency of fire events and cattle grazing, mainly because of management shifts (Behling, 1997, 2002; Behling and Pillar, 2007). Studies of the current scenarios of woody encroachment enable the comprehension and the awareness of grassland conservation under climate change influence (Pio *et al.*, 2014; González-Orozco *et al.*, 2016; Li, Miller and Harrison, 2019; Park *et al.*, 2020).

One of the ways to apply phylogenetic data in ecological studies is the measure of phylogenetic diversity, which reflects the evolutionary history of a set of taxa in an environment (Gerhold *et al.*, 2015, 2018). The first phylogenetic metric incorporated in community ecology was proposed to assess conservation priority areas (Faith, 1992). Nowadays, phylogenetic diversity has been integrated into the studies of community assembly (Webb *et al.*, 2002; Verdú *et al.*, 2009; Mayfield and Levine, 2010; Pillar and Duarte, 2010), macroevolutionary processes (Gerhold *et al.*, 2015), species distribution (Cavender-Bares, Keen and Miles, 2006; Swenson *et al.*, 2006; Duarte *et al.*, 2014; Debastiani *et al.*, 2015), and biogeographic history (Graham and Fine, 2008; Leibold, Economo and Peres-Neto, 2010; Gerhold *et al.*, 2018). Similar to taxonomic diversity, the study of the phylogenetic organization of communities can occur under the views of alpha and beta diversity indexes (Graham and Fine, 2008; Gómez *et al.*, 2010; Swenson, 2011, 2019; Leprieur *et al.*, 2012). The phylogenetic relatedness of communities can reflect if dissimilarities are deep or shallow in the evolutionary history (Graham and Fine, 2008) and if there are patterns in the distribution of lineages across ecological assemblages (Duarte, 2011; Duarte, Prieto and Pillar, 2012). More specifically, the phylogenetic beta diversity may be the result of environmental filters and historical biogeographic acting upon communities profiles (Leibold, Economo and Peres-Neto, 2010; Baraloto *et al.*, 2021).

Transitional zones are different biomes merged and represent complex study places that harbor extensive biodiversity (Gosz, 1993). Biological diversity in transitional zones is explained by distinct environments structuring ecological gradients, which encompasses the establishment of a high species number and the rising of new lineages (Smith *et al.*, 1997, 2001; Haidar *et al.*, 2013; Dantas *et al.*, 2016). At finer scales, the ecotones represent the boundary between

contrasting plant communities with unique environmental conditions, which may drive different processes of assembly of both vegetations (Müller *et al.*, 2012; Fletcher, Wood and Haberle, 2014; Oliveras and Malhi, 2016; Souza *et al.*, 2020). In Brazil, the transitional zones between rainforests and savannas biomes are known for their high taxonomic, functional, and phylogenetic diversity (Dantas, Batalha and Pausas, 2013; Haidar *et al.*, 2013; Silva-Pereira *et al.*, 2020; Souza *et al.*, 2020). Silva-Pereira *et al.* (2020) showed that vegetation in the Amazon-Cerrado transition is phylogenetically overdispersed, a similar result to that found in the Cerrado-Atlantic forest local-scale ecotones in southeastern Brazil (Souza and Eisenlohr, 2020). Nevertheless, there are transition zones missing studies that delved into exploring the phylogenetic structure of vegetation. One of them is the region in southern Brazil known as *Campos Gerais* (but see Marcilio-Silva *et al.*, 2015; Moraes *et al.*, 2016), located in Paraná State. Campos Gerais landscapes are formed by natural grasslands contrasting with intermingled *Araucaria* mixed forest patches and *Cerrado* relicts under a subtropical climate (Carmo, Moro and Nogueira, 2007; Moro and Carmo, 2007). Studies about the phylogenetic diversity of forest-grassland mosaics in southern Brazil, but concentrated in the Atlantic forest-Pampas boundaries, highlight the association of ancient plant clades with forest interiors and more recently-diversified clades with forest edges and small forest patches in grasslands (Duarte, 2011; Debastiani *et al.*, 2015).

The formation of forest-grassland mosaics in southern Brazil is associated with paleoclimate variation and species habitat tracking (Behling *et al.*, 2004; Carnaval and Moritz, 2008). Over the past glacial and interglacial events, grasslands and forests changed their occurrence areas. The glacial events allowed the expansion of grasslands ranges and forced forest lineages to be restricted to tropical climatic stable refugia (Carnaval *et al.*, 2009), whereas in the interglacial periods, forests spread and forced grasslands to shrink and retreat to mountain tops (Fregonezi *et al.*, 2013; Peçanha *et al.*, 2017). Ancient lineages like the conifer *Araucaria angustifolia* held back to humid environments along riversides in the last glacial maximum (Behling, 1997) and now act as nurse plants on the woody encroachment in grassy biomes (Duarte *et al.*, 2006; Carlucci *et al.*, 2011; Marcilio-Silva *et al.*, 2015).

Assessing present-day ecological patterns and using phylogeny and information from historical biogeography of a region and its biota, we can better understand the underlying processes that shaped current patterns of phylogenetic diversity in grasslands and forest plant communities. We proposed two hypotheses to understand underlying historical processes that may have driven phylogenetic diversity of forests and grasslands in the Campos Gerais region: 1) During the last glaciation event, forests were kept in refugia, while grasslands expanded their range, which reflects habitat tracking of plant species to more suitable environments (Fregonezi *et al.*, 2013). Interglacial periods changed this dynamic. Forest lineages expanded from their refugia (Behling, 1997; Carnaval *et al.*, 2009), while temperature increase and fire suppression changed the range and species composition of grasslands (Behling, 2002). Given the current interglacial event, we expect to find lower values of phylogenetic structure in grasslands than in forests. The niche difference of plants in both vegetations could reflect on their phylogenetic dissimilarity in phylogenetic beta diversity measures through lineages turnover. 2) Herbaceous plants respond more to edaphic and microhabitat conditions than woody species (Smith and Beaulieu, 2009; Moraes *et al.*, 2016; Zhou *et al.*, 2021). At finer scales, the phylogenetic dissimilarities among vegetations with plants of the same life form tends to be lower than among physiognomies with different life forms. Dissonant vegetation types like the hygrophilous grassland reflects a strong filter (inundation), which selects specific lineages. This condition could lead to a phylogenetic diversity of the sites lower than the other vegetation physiognomies and keep a discrepancy of lineages across them. Therefore, the phylogenetic turnover could explain the phylogenetic dissimilarities among the vegetation physiognomies.

METHODS

STUDY SITE

The study was carried out in the Campos Gerais, which is a region in the Paraná State characterized by soils derived from rocks of the Devonian Escarpment geological formation. According to Köppen's classification, the climate varies from temperate with mild summers (Cfb) to subtropical with hot

summers (Cfa). More specifically, we focused on forest-grassland mosaics within two state parks. The Vila Velha State Park – PEVV (25°15'02" S, 49°59'59" W, 900 m a.s.l.) is located in the municipality of Ponta Grossa, comprises an area of 3803 ha, and is known by its sandstone formations. The Guartelá State Park – PEG (24°36'55" S, 50°15'37" W, 1030 m a.s.l.) is smaller (790 ha) and is located along the Iapó river canyon in the municipality of Tibagi (Fig. 1).

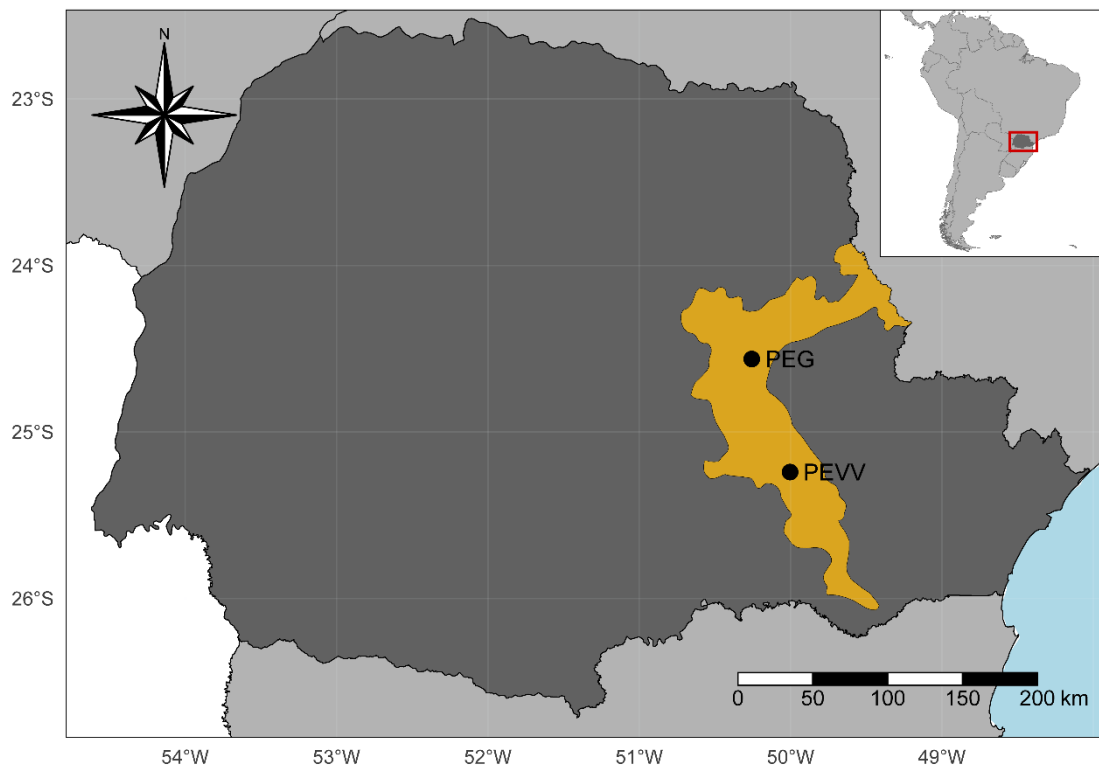


Figure 1. Study areas (points) in the *Campos Gerais* region (yellow), located in the Paraná State, southern Brazil. PEG: Guartelá state park, PEVV: Vila Velha state park.

The flora of the region comprises patches of grasslands and forests, which form a mosaic in the landscape (Ritter, Ribeiro and Moro, 2010). The grasslands present vegetational zonation due to soil depth, drainage, and topography (Moro and Carmo, 2007). These zonations are divided into *campos sujos* (grassland with small shrubs), *campos rochosos* (grasslands with rock outcrops), *campos úmidos* (hygrophilous grasslands), and *cerrado* relicts (savannas with sparse and small perennial trees) in both parks (Moro and Carmo, 2007; Ritter, Ribeiro and Moro, 2010). The forests are described as *Araucaria* Mixed Forests, a vegetation type of the Atlantic Forest (Oliveira-Filho and Fontes, 2000). Forests are present along riversides and at high elevations. The most

remarkable species in the forests is *Araucaria angustifolia*. (Carmo, Moro and Nogueira, 2007).

In *campo sujo* and *campo rochoso*, Poaceae is the most abundant family, and Asteraceae also shows a high species richness. In *campo úmido*, due to its moist soils, *Senecio bonariensis*, *Lobelia*, *Ludwigia*, and some Cyperaceae species are the most abundant herbs (Moro and Carmo, 2007). The *cerrado* patches in the Campos Gerais represent the most austral distribution of some species, especially in Ponta Grossa and surrounding areas, which shows few typical species from the core of the phytogeographical zone, i.e. Central Brazil (Ritter, Ribeiro and Moro, 2010). In forest interiors, Lauraceae and Aquifoliaceae, beyond *Araucaria angustifolia*, share the most of the canopy. Myrtaceae, Sapindaceae, and Euphorbiaceae are mostly present in the understory layer (Carmo, Moro and Nogueira, 2007). In forest edges and its ecotonal zone with grasslands, *Clethra scabra*, *Vernonanthura discolor*, *Moquiniastrum polymorphum*, *Myrsine umbellata*, and *Myrsine coriacea* are among the most common tree species (Carmo, Moro and Nogueira, 2007).

DATA COLLECTION

Data was obtained from vegetation surveys made in 2012 and 2013. These surveys were part of a research project focusing on the biodiversity of grasslands and their ecotones in southern Brazil, called SISBIOTA Campos Sulinos (Marcilio-Silva *et al.*, 2015; Moraes *et al.*, 2016), which was funded by CNPq (Brazil's National Council of Scientific and Technological Development) and state funding agencies. In the Paraná state, the project involved researchers from Universidade Federal do Paraná and Universidade Estadual de Ponta Grossa.

To record plant species in grasslands, the researchers designed three 70 x 70 m local plots, one in each grassland type (i.e., *campo rochoso*, *campo sujo*, and *campo úmido*). Inside these plots, they established nine 1x1 m subplots arranged 17 m apart from each other, disposed along three rows and three columns in a grid. The survey included all herbs (both angiosperms and ferns), grass, shrub, and tree species inside each subplot and an estimation of their cover (see Appendix 1 for the species list).

The collectors designed the sampling of forests to incorporate both their interior and the ecotonal edge with grasslands. Therefore, they established two adjacent 70 x 70 m local plots in forest patches, one in the interior and the other in the ecotone. Each study site had two of these designs. In each local plot, they divided the area into 49 subplots of 10 x 10 m and randomly sampled 15 of them. For these subplots, they recorded all woody species with a diameter at breast height higher than 5 cm. To record saplings – woody plants with height between 30 and 130 cm –, one 2.5 x 2.5 m quadrat was defined in each subplot.

REGIONAL PHYLOGENETIC TREE

We compiled vegetation checklists from Campos Gerais (Appendix 2) and adjusted species taxonomic information (i.e., families, subfamilies, tribes) based on APG IV (The Angiosperm Phylogeny Group, 2016) and PPG I (The Pteridophyte Phylogeny Group, 2016). We standardized binomial names according to Flora do Brasil 2020 (Jardim Botânico do Rio de Janeiro, 2020).

The final species list was used to build a phylogenetic tree for the Campos Gerais region. Our phylogenetic tree was based on the supertree of vascular plants by Qian and Jin (2016), which built their supertree based on a compilation of Smith & Brown (2018) seed plant tree with lycophytes and ferns subtrees from Zanne *et al.* (2014). We placed species (or genera) present in the compiled species list but absent in the phylogeny in the node of closest relatives as polytomies. This method generated a tree with 42.93% of terminal relationships ending as polytomies. The generation of the regional phylogenetic tree was done in RStudio (R Core Team, 2020) using *V.PhyloMaker* package (Jin and Qian, 2019).

PHYLOGENETIC DIVERSITY

Using our regional phylogenetic tree, we computed indices of community phylogenetic diversity for all subplots in different vegetational groupings: vegetation subtypes scale (i.e., *campos rochosos*, *campos sujos*, *campos úmidos*, forests, and ecotones) and major vegetation types scale (i.e., grassland as a whole and forests). We computed the indices in the software R (R Core Team, 2020).

Phylogenetic alpha diversity

We used three metrics of phylogenetic alpha diversity, which are usually complementary to each other, namely Faith's PD (Faith, 1992), mean pairwise distance (MPD; Webb *et al.*, 2002), and mean nearest taxon distance (MNTD; Webb *et al.*, 2002). PD consists of the sum of all branches' lengths of cooccurring species and quantifies total phylogenetic diversity in an assemblage. The other measures of phylogenetic alpha diversity use a phylogenetic distance matrix, a matrix with species names on the rows and columns and values in the cells defining the phylogenetic branch length separating each pair of species. Using a matrix generated from the regional phylogenetic tree, we calculated the MPD and the MNTD. The MPD metric is an average of the phylogenetic distances between cooccurring species and can detect phylogenetic patterns in the basal branches of the phylogeny. To obtain the phylogenetic diversity present on the tips of the phylogeny, we used the MNTD metric.

Phylogenetic beta diversity

To evaluate phylogenetic beta diversity, we used the phylogenetic Sorenson's index (PhyloSor; (Bryant *et al.*, 2008). Based on Baselga (2010) and Leprieur *et al.* (2012), we partitioned beta diversity into phylogenetic turnover (i.e., two communities present different lineages between them) and phylogenetic nestedness (i.e., phylogenetic branches of one community are a subset of the branches of another community). We performed these calculations using the R script provided by Leprieur *et al.* (2012).

Another metric to assess phylogenetic beta diversity is called phylogenetic fuzzy weighting (PFW) (Pillar and Duarte, 2010; Duarte *et al.*, 2016). PFW provides the distribution of clades across communities associated with fuzzy sets defined by phylogenetic similarities among species. The metrics requires an ultrametric and dated phylogenetic tree to compute the similarities between species. The similarity matrix ($\mathbf{S_F}$) is standardized by the marginal total values within columns, creating a matrix of fuzzy sets per species ($\mathbf{Q'}$). The multiplication of this matrix with a matrix describing a range of communities by the proportional abundances of species ($\mathbf{W}$) results in the phylogenetic-weighted species abundances per site ($\mathbf{P}$) (Duarte *et al.*, 2014, 2016).

To interpret PFW, we used a principal coordinates analysis (PCoA) on the dissimilarity's matrix of phylogenetic-weighted species abundances per site (**dP**), the so-called Principal Coordinates of Phylogenetic Structure (PCPS). PCPS enables exploring clade distribution across communities and the association of eigenvalues to spatial and environmental factors (Duarte *et al.*, 2014; Carlucci *et al.*, 2017; Bergamin *et al.*, 2021). We used PCPS to associate clades with vegetational groupings.

Null models

We quantified standardized effect sizes (SES) for all diversity metrics above described (except for PCPS) in order to investigate phylogenetic structure patterns in the communities. For this, we randomized phylogenetic data to generate 999 null communities through the “taxa labels” null model. This model maintains the topology of the phylogeny and the distribution of branch lengths in communities but swaps the species names on the tips of phylogeny. For each null community generated, we computed the metrics of phylogenetic diversity. Using the null phylogenetic diversity values, we computed standardized effect sizes following Swenson (2014) for SES.PD and Webb *et al.* (2002) for SES.MPD and SES.MNTD. The SES.MPD and SES.MNTD significant lower values indicates a community with phylogenetic clustering (i.e., whether p-values are less or equal to 0.025, the lineages are more related than expected by chance), whereas significant higher values are a reflect of phylogenetic overdispersion (i.e., whether p-values are greater or equal to 0.975, the lineages are less related than expected by chance; Webb *et al.*, 2002). The standardized effect size for phylogenetic beta diversity (i.e., PhyloSor, PhyloSor turnover, and PhyloSor nestedness) follow Leprieur *et al.* (2012) metrics. The standardized PhyloSor may show phylogenetic beta diversities lower than expected by the compositional beta diversities (i.e., $SES.PhyloSor < -1.96$), higher than expected (i.e., $SES.PhyloSor > 1.96$) or similar values to the expected (i.e., $-1.96 < SES.PhyloSor < 1.96$) (Leprieur *et al.*, 2012).

STATISTICAL ANALYSES

First, we checked for variance homogeneity and data normality. After, as our data did not show normal distribution, we tested our hypotheses using an

analysis of variance with permutation (PERMANOVA) for comparisons among each vegetational grouping (Pillar and Orlóci, 1996; Anderson, Ellingsen and McArdle, 2006). We submitted the data with significant variances to *a posteriori* pairwise comparison tests in the *pairwiseAdonis* package in R (Martinez Arbizu, 2020).

RESULTS

Our regional phylogenetic tree included 2195 species (Appendix 3). The species data set from the SISBIOTA *Campos Sulinos* project comprised 267 plant species belonging to 150 genera and 58 families. The species list consisted of five ferns, one conifer, 12 magnoliids, 37 monocots, and 207 eudicots. The most representative family was Asteraceae, with 15 genera and 39 species. All ferns represented five different families. Among the magnoliids, Lauraceae was the family with higher richness (5 genera and 12 species). Grasses were the predominant monocots in the survey areas. In PEG 172 species were recorded, which belong to 108 genera and 47 families. PEVV presented 167 species, representing 111 genera and 47 families (Appendix 1).

The survey areas classified as grasslands comprised 178 species belonging to 105 genera and 47 families, in which Asteraceae had the higher richness (38 species). While all forests encompassed 123 species in general, representing 82 genera and 41 families. With 19 species recorded, Myrtaceae was the most representative family in forest plots.

PHYLOGENETIC ALPHA DIVERSITY

Phylogenetic alpha diversity differed between grasslands and forests. The vegetations differed mainly in terms of PD (Fig. 2a; *pseudo-F*=167.41 *p-value*<0.01) and followed by MNTD (Fig. 2e; *pseudo-F*=4.083 *p-value*<0.05), but not MPD (Fig. 2c; *pseudo-F*=0.659 *p-value*>0.05). Using the standardized metrics, we found that grasslands and forests differed in terms of SES.MPD (Fig. 2d; *pseudo-F*=5.8281 *p-value*=0.016). The values did not differ for SES.PD (Fig. 2b; *pseudo-F*=0.269 *p-value*>0.05) and for SES.MNTD (Fig. 2f; *pseudo-F*=0.994 *p-value*>0.05).

In all standardized metrics, grasslands showed plots with both significant lower and higher values than expected by random (Fig. 2).

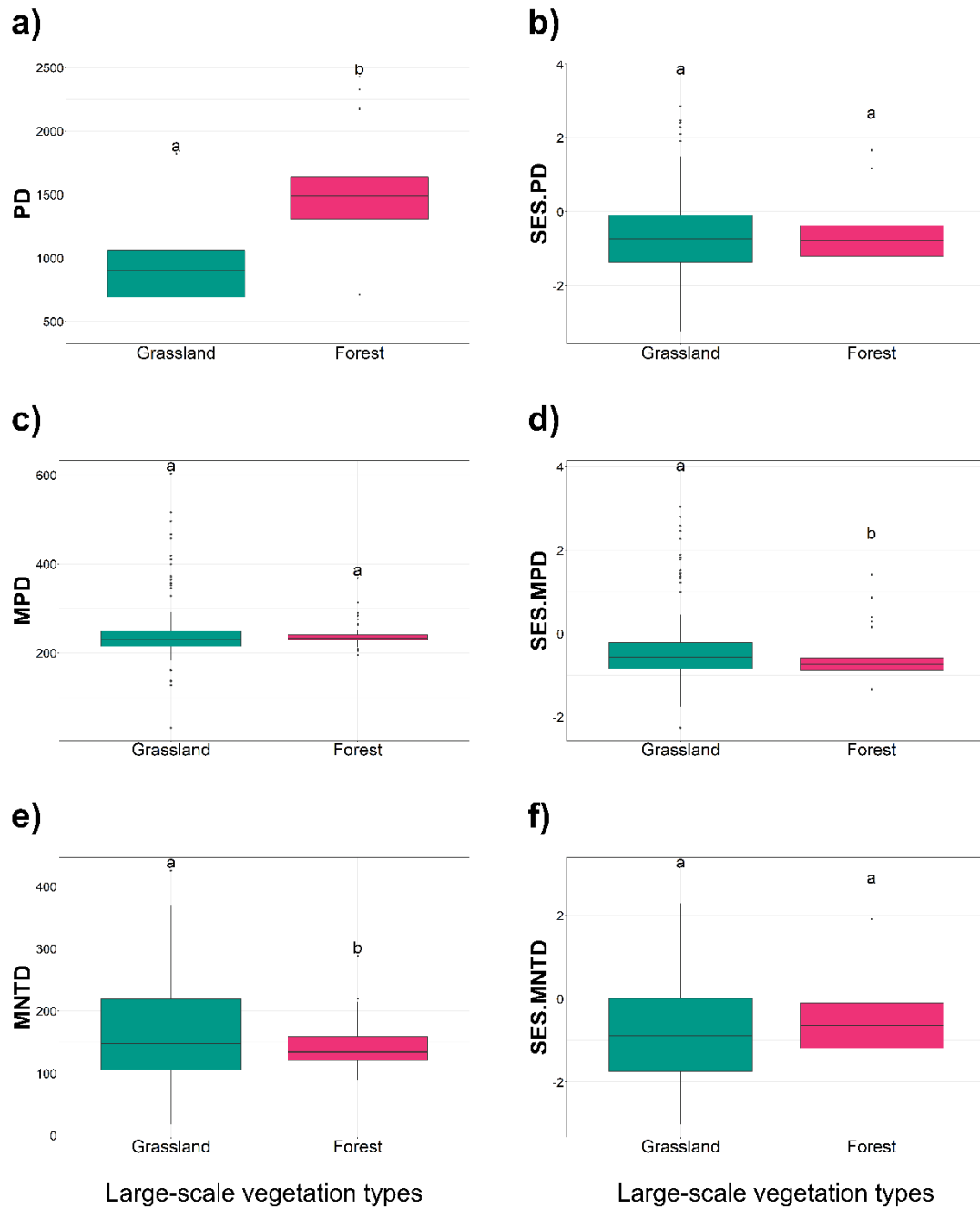


Figure 2. Variation in the phylogenetic alpha diversity metrics between grasslands and forests cooccurring in mosaics. Phylogenetic diversity indexes (a; c; e) and their standardized measures (b; d; f). PD: Faith's phylogenetic diversity index; SES.PD: standardized effect size of PD; MPD: mean pairwise distance; SES.MPD: standardized effect size of MPD; MNTD: mean nearest taxon distance; SES.MNTD: standardized effect size of MNTD.

Considering the vegetation physiognomies, forests harbored distinctive higher values of PD (Fig. 3a; $pseudo-F=45.489$ $p-value < 0.01$). But when compared it to null models, only *campo úmido* was different from the rest (Fig. 3b; $pseudo-F=3.7259$ $p-value < 0.01$). Statistically, few communities presented significant lower values of PD than expected by chance ($p-value < 0.025$). The

analysis of MPD did not differ among groups (Fig. 3c; $pseudo-F=0.670$ $p-value>0.05$). When analyzing the phylogenetic structure by SES.MPD, there was no distinction among the vegetation physiognomies (Fig. 3d; $pseudo-F=1.8496$ $p-value>0.05$). Only few communities of *campo úmido*, forest and ecotone presented significant lower values of SES.MPD ($p-value<0.025$), an indicative of phylogenetic clustering. The results of the MNTD metrics revealed lower values for *campo úmido* and differences between forest and ecotone (Fig. 3e; $pseudo-F=6.256$ $p-value<0.01$). Some communities presented significant lower values than expected by chance in the SES.MNTD analysis ($p-value<0.025$), and only one ecotone community showed a significant higher value ($p-value>0.975$). Overall, *campo úmido* differed from the other vegetation physiognomies in SES.MNTD values (Fig. 3f; $pseudo-F=6.711$ $p-value<0.01$).

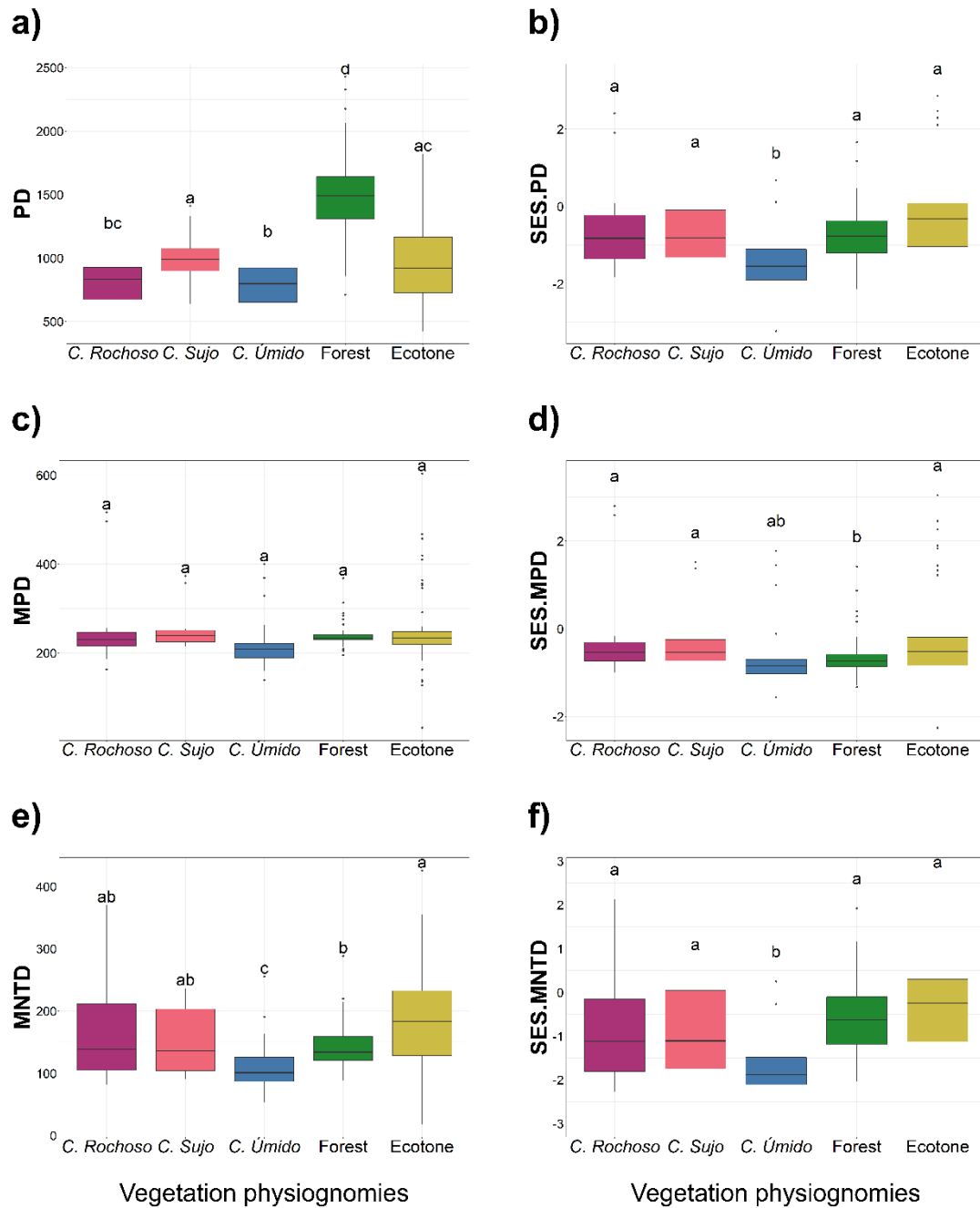


Figure 3. Variation in the phylogenetic alpha diversity metrics among the vegetation physiognomies present in the study areas. Phylogenetic diversity indexes (a; c; e) and their standardized measures (b; d; f).

PHYLOGENETIC BETA DIVERSITY

The phylogenetic beta diversity between grassland and forest showed a mid-low value of PhyloSor (i.e., 0.4584), which is essentially described by lineages turnover (i.e, $\text{PhyloSor}_{\text{turn}} = 0.4253$; $\text{PhyloSor}_{\text{nest}} = 0.0331$). These results did not differ from null expectation ($\text{SES.PhyloSor} = 0.1085$; $\text{SES.PhyloSor}_{\text{turn}} = 1.1982$; $\text{SES.PhyloSor}_{\text{nest}} = -1.5975$).

When comparing the phylogenetic composition of vegetation types, *campo úmido* and forest presented the higher dissimilarity (i.e., 0.8261; Table 1). The lowest dissimilarity values were in the pairwise comparisons involving *campo rochoso* and the other *campos* types (i.e., 0.3039 with *campo sujo* and 0.3358 with *campo úmido*). The value of PhyloSor for the forest-ecotone comparison was also low (i.e., 0.3783). When partitioning PhyloSor results, the turnover of lineages among the vegetation physiognomies mainly explained the differences observed in the total (Table 1). The phylogenetic dissimilarities between *campo rochoso*-ecotone and between *campo rochoso*-*campo sujo* was partially due to the loss of lineages, which is shown in nestedness values.

Only two pairwise dissimilarities were significantly lower than expected by null models: *campo rochoso*-*campo sujo* and *campo rochoso*-*campo úmido* (Table 1). Other nonrandom values include the relation between forest and the three *campos* types and between *campo úmido* and ecotone, which were higher than expected given taxonomic beta diversity. We found high values of lineage turnover than expected in two forests pairwise comparisons (i.e., forest-*campo úmido* and forest-*campo rochoso*) and just one significantly lower (i.e., *campo rochoso*-*campo sujo*). Solely, the nestedness in *campo sujo* and *campo úmido* lineages was higher than predicted by null models (Table 1).

Table 1. Decomposition of PhyloSor dissimilarity's index of the vegetation types into turnover of lineages and phylogenetic nestedness. Significant SES values are underlined. PhyloSor: Sorenson's phylogenetic dissimilarity index; PhyloSor_{turn}: "true" lineages turnover value in PhyloSor analysis; PhyloSor_{nest}: value of the nestedness of lineages in PhyloSor analysis; SES: standardized effect size.

Vegetation types	PhyloSor	PhyloSor _{turn}	PhyloSor _{nest}	SES.PhyloSor	SES.PhyloSor _{turn}	SES.PhyloSor _{nest}
<i>C. Rochoso-C. Sujo</i>	0.3039	0.1909	0.1130	<u>-3.2682</u>	<u>-2.9422</u>	0.3338
<i>C. Rochoso-C. Úmido</i>	0.3358	0.3277	0.0080	<u>-2.7664</u>	-1.1448	-1.7339
<i>C. Rochoso-Forest</i>	0.7534	0.5221	0.2313	<u>2.7060</u>	<u>2.1809</u>	-0.7036
<i>C. Rochoso-Ecotone</i>	0.5857	0.3197	0.2660	0.2245	-0.6697	1.0901
<i>C. Sujo-C. Úmido</i>	0.4700	0.3922	0.0778	-0.4799	-1.4257	<u>2.0227</u>
<i>C. Sujo-Forest</i>	0.6932	0.5136	0.1797	<u>2.5051</u>	1.4828	0.3285
<i>C. Sujo-Ecotone</i>	0.5259	0.3542	0.1717	-0.2087	-1.2888	1.7341
<i>C. Úmido-Forest</i>	0.8261	0.6689	0.1572	<u>5.6837</u>	<u>4.4688</u>	-0.7544
<i>C. Úmido-Ecotone</i>	0.6805	0.4840	0.1965	<u>3.2056</u>	1.2426	1.7694
Forest-Ecotone	0.3783	0.2977	0.0806	-1.0352	-0.9740	0.2097

When generating a principal coordinates analysis on the dissimilarity's matrix of phylogenetic-weighted species abundances, we found trends in lineages distribution across vegetation types (Fig. 4, Appendix 4). The first three PCPS explained, respectively, 36.5%, 15.5%, and 8.4% of phylogenetic beta diversity. The first PCPS eigenvector exposed the segregation amid ferns and spermatophyte lineages in the plots, with ferns being mainly represented in ecotone communities. Albeit, ecotone communities were well spread along the first PCPS (Fig. 4, Appendix 4, and Appendix 5). The second eigenvector described a gradient between monocots and eudicots. Commelinid monocots were well represented in *campo úmido*. Forest tended to accumulate more Core Eudicots lineages (Fig. 4). Overall, there was a minimal fluctuation of the phylogenetic composition of forest plots to the three principal PCPS eigenvectors (Appendix 3, also visible in Fig. 4 and Appendix 5).

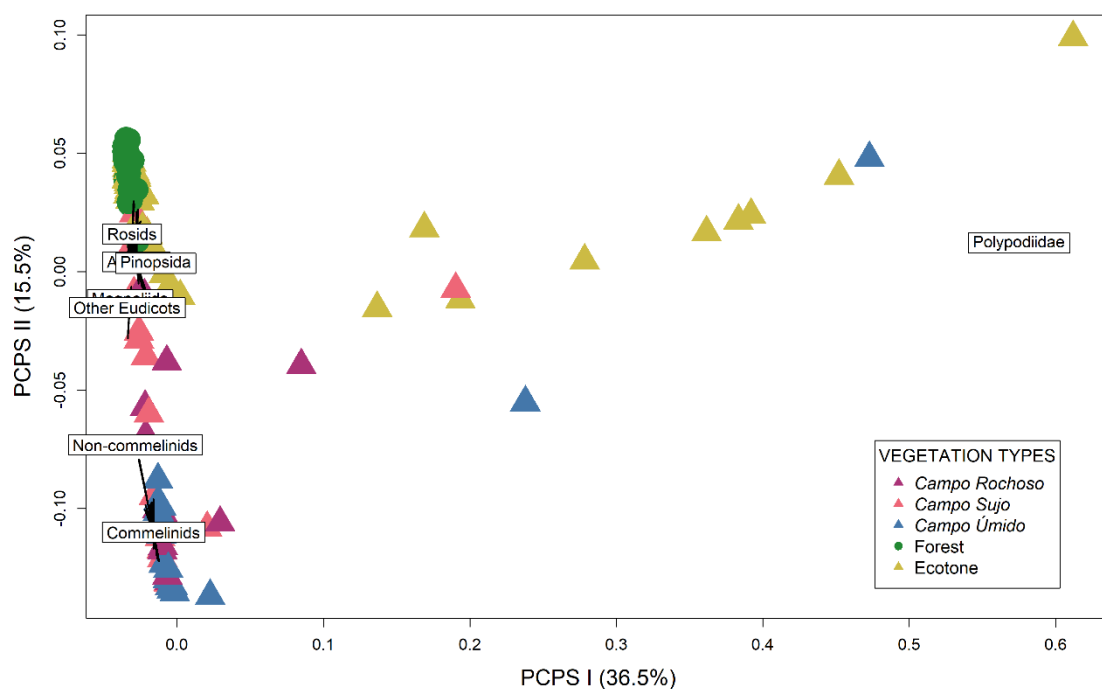


Figure 4. Scatter plot of the two main eigenvectors generated by Principal Coordinates of Phylogenetic Structure (PCPS) describing phylogenetic composition of plants among the vegetation types present in the study areas. Triangle points represent plots classified as “grassland” in the dichotomic mosaic scale. Forest plots are represented as circles.

DISCUSSION

The phylogenetic diversity of the grasslands did not differ from forests in all metrics utilized. Partially agreeing with our hypothesis, forest showed higher phylogenetic alpha diversity value than grasslands and lower variation in phylogenetic structure when compared to null models. These differences are due to the fact that herbaceous and woody plants respond to different abiotic variables (Zhou *et al.*, 2018, 2021). For example, grassland plants usually grow on nutrient-deficient soils with scarce water availability, whereas forest trees establish on soils with high organic matter and moisture (Oliveras and Malhi, 2016).

Overall, a high lineage turnover explains the dissimilarities in phylogenetic composition between forests and grasslands. Lineages turnover are interpreted as result of environmental filters upon vegetation assembly (Graham and Fine, 2008; Daru *et al.*, 2017), here associated with the differences in responses of herbaceous and woody plants to environmental variables. Lineage distribution patterns showed that core eudicots were better represented in the forest while grasslands presented the extant tracheophytes lineages. The vegetation physiognomies of our study ranged from shallow soils of rocky grasslands to the wet and acidic soil of *campo úmido*. This variation on environmental conditions at larger scales favors the establishment of multiple taxa, which changes the phylogenetic structure and composition of large sampled assemblages (Swenson *et al.*, 2006; Zhou *et al.*, 2018, 2021). The variation of phylogenetic structure is exemplified through the phylogenetically clustered or dispersed communities in grasslands.

As expected, the hygrophilous grasslands (i.e., *campo úmido*) present lower phylogenetic diversity than the other vegetation groups. Its hydromorphic soils filter species with specific traits (Moro and Carmo, 2007; Moraes *et al.*, 2016). Studies point to taxonomic and functional clusters on *campo úmido* more than on the other grasslands types (Dalazoana, Silva and Moro, 2008; Setubal and Boldrini, 2012; Moraes *et al.*, 2016). Our analysis corroborates the findings of these studies by showing a phylogenetic clustering on terminal branches in this vegetation. This clustering is most due to monocot clades being highly associated with grassland types, whereas predominant woody clades are present in forests and their ecotones. This pattern is consistent with environmental filtering and with

phylogenetic niche conservatism, once relative clades could present similar niche requirements (Crisp and Cook, 2012).

Nevertheless, the phylogenetic dissimilarity between *campo sujo* and *campo rochoso* reflects not only environmental filtering but also dispersion limitation of species and historical causes. The similar contributions of lineages turnover and nestedness to their phylogenetic beta values could be related to different process of community assembly (Graham and Fine, 2008; Jin *et al.*, 2020). The principal abiotic differences between those *campos* are related to soil, with *campo rochoso* presenting more shallow and sandy soils than *campo sujo* (Moro and Carmo, 2007). The nestedness of lineages is generally associated with small scales plots (Jin *et al.*, 2020), being a response of species dispersion limitations. We consider the division of *campo sujo* and *campo rochoso* vegetation physiognomies not relatively strong, since they are not phylogenetically distinguishable.

The phylogenetic dissimilarities between forests and their ecotonal edges are being investigated (Souza *et al.*, 2020). Our findings contribute by highlighting the phylogenetic turnover as a reason for this discrepancy. The species occupying grassland-forest ecotonal patches are sun-tolerant, with rapid growth and thick barks to resist fires (Oliveras and Malhi, 2016). They act as nurse plants, facilitating the establishment of forest shade-tolerant species and contributing to forest expansion over grasslands (Duarte *et al.*, 2006; Marcilio-Silva *et al.*, 2015; Carboni *et al.*, 2016; Oliveras and Malhi, 2016). There is a tendency of nursing interaction occurring among distantly related species (Valiente-Banuet and Verdú, 2007, 2013; Verdú *et al.*, 2009; Marcilio-Silva *et al.*, 2015), which could explain the lineages turnover between forests and ecotones.

Overall, the patterns of phylogenetic diversity we observed reflect phylogenetic niche conservatism and historical biogeography events. The dynamics of grassland-forest mosaics result from multiple factors acting at different scales (Oliveras and Malhi, 2016). The shaping of these landscapes has a relation with paleoclimate fluctuations (Behling, 1997, 2002; Behling *et al.*, 2004). In South America, glacial events of Pleistocene led forests to form refugia (Carnaval and Moritz, 2008; Carnaval *et al.*, 2009) while allowing grasslands to predominate in subtropical regions (Lorenz-Lemke *et al.*, 2010; Fregonezi *et al.*, 2013; Peçanha *et al.*, 2017). During interglacial periods, the opposite occurred:

forests expanded their range while grasslands escaped to colder regions (Lorenz-Lemke *et al.*, 2010). These contraction/expansion dynamics unleashed vicariance and dispersion events of populations, leaving recent phylogenetic imprints in the flora (Fregonezi *et al.*, 2013; Peçanha *et al.*, 2017). The high value of phylogenetic diversity in forests could be related to these dynamics, since the arrival of tropical lineages in the subtropical forest domains possibly enriched the phylogenetic diversity (Carnaval *et al.*, 2009). Even the permanence of ancient lineages is associated with these events, as they remain in “museums” areas (i.e., regions with the permanence of old clades harboring ancient traits; Chown and Gaston, 2000; Daru *et al.*, 2017; Gerhold *et al.*, 2018). For example, *Araucaria* and Lauraceae habited near rivers in glacial events and are currently associated with forest interiors in mild, altomontane ecosystems (Behling, 1997; Carlucci *et al.*, 2017). This pattern is also present in our analysis of phylogenetic composition, which highlights these ancient lineages cooccurring with modern core eudicots lineages in forests plots.

The resolution of hypothetical evolutionary trees can directly impact calculations of phylogenetic diversity (Swenson, 2009; Debastiani, Bastazini and Pillar, 2021). Our regional phylogeny contained many species that are not present in Qian and Jin (2016) supertree, which were added as polytomies to closest related nodes. Polytomies tend to overestimate terminal phylogenetic alpha diversity (Debastiani, Bastazini and Pillar, 2021). The random resolution of the polytomies many times and the quantification of the effect of phylogenetic uncertainty on phylogenetic diversity metrics is necessary in future studies.

Our study succeeded in assessing the phylogenetic diversity of the vegetation types of forest-grassland mosaics in southern Brazil. We found phylogenetic clusters in hygrophilous grasslands and their associations with commelinids monocots. Phylogenetic turnover showed to be the reason for differences in lineage composition among vegetation types, which reflects imprints of environmental filtering and historical processes in shaping the forest-grassland mosaics. After analysing the phylogenetic alpha and beta diversity of the vegetation in forest-grassland mosaics, we hope to contribute to the debate on ecological and historical factors that shape these heterogeneous vegetation landscapes.

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SUPPLEMENTARY MATERIALS

Appendix 1. List of plant species recorded for both study areas (i.e., *Guartelá* state park and *Vila Velha* state park) in *SISBIOTA Campos Sulinos* project. The binomial names and taxonomy information are fixed based on Flora do Brasil 2020, APG IV and PPG I.

Group/Family/Specie	PEG	PEVV
FERNS		
Blechnaceae		
<i>Parablechnum cordatum</i> (Desv.) Gasper & Salino		X
Cyatheaceae		
<i>Cyathea</i> sp.		X
Dennstaedtiaceae		
<i>Pteridium</i> sp.	X	X
Polypodiaceae		
<i>Pleopeltis lepidopteris</i> (Langsd. & Fisch.) de la Sota		X
Pteridaceae		
<i>Lytoneuron crenulans</i> (Fée) Yesilyurt	X	
CONIFER		
Araucariaceae		
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	X	X
MAGNOLIIDS		
Annonaceae		
<i>Annona emarginata</i> (Schltdl.) H.Rainer		X
<i>Guatteria australis</i> A.St.-Hil.		X
<i>Guatteria</i> sp.	X	
Lauraceae		
<i>Aiouea saligna</i> Meisn.		X
<i>Cinnamomum sellowianum</i> (Nees & Mart.) Kosterm.	X	X
<i>Nectandra grandiflora</i> Nees & Mart	X	X
<i>Nectandra lanceolata</i> Nees	X	
<i>Nectandra megapotamica</i> (Spreng.) Mez	X	X
<i>Ocotea corymbosa</i> (Meisn.) Mez	X	

<i>Ocotea diospyrifolia</i> (Meisn.) Mez	X	
<i>Ocotea indecora</i> (Schott) Mez	X	
<i>Ocotea porosa</i> (Nees & Mart.) Barroso	X	X
<i>Ocotea pulchella</i> (Nees & Mart.) Mez	X	
<i>Ocotea tristis</i> (Nees & Mart.) Mez	X	
<i>Persea alba</i> Nees & Mart.	X	
Monimiaceae		
<i>Mollinedia clavigera</i> Tul.	X	X
Piperaceae		
<i>Piper crassinervium</i> Kunth		X
MONOCOTYLEDONS		
Arecaceae		
<i>Allagoptera campestris</i> (Mart.) Kuntze	X	
<i>Geonoma schottiana</i> Mart.	X	
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	X	X
Cyperaceae		
<i>Bulbostylis capillaris</i> (L.) C.B. Clarke		X
<i>Bulbostylis junciformis</i> (Kunth) C.B. Clarke	X	
<i>Bulbostylis</i> sp.		X
<i>Cyperus ascocapensis</i> Bauters		X
<i>Eleocharis nudipes</i> (Kunth) Palla		X
<i>Lagenocarpus rigidus</i> Nees	X	
<i>Rhynchospora consanguinea</i> (Kunth) Boeckeler		X
<i>Rhynchospora emaciata</i> (Nees) Boeckeler		X
<i>Rhynchospora velutina</i> (Kunth) Boeckeler		X
Eriocaulaceae		
<i>Paepalanthus albobaginat</i> Silveira	X	
Iridaceae		
<i>Sisyrinchium densiflorum</i> Ravenna		X
<i>Sisyrinchium micranthum</i> Cav.		X
<i>Sisyrinchium vaginatum</i> Spreng.	X	X
Mayacaceae		
<i>Mayaca fluviatilis</i> Aubl.		X
Poaceae		
<i>Andropogon leucostachyus</i> Kunth		X
<i>Andropogon selloanus</i> (Hack.) Hack.	X	X
<i>Andropogon ternatus</i> (Spreng.) Nees	X	
<i>Andropogon virgatus</i> Desv.		X
<i>Arundinella hispida</i> (Humb. & Bonpl. ex Willd.) Kuntze		X
<i>Axonopus siccus</i> (Nees) Kuhl.	X	X
<i>Dichanthelium sabulorum</i> (Lam.) Gould & C.A. Clark		X
<i>Eragrostis</i> sp.		X
<i>Merostachys</i> sp.	X	
<i>Ocellochloa stolonifera</i> (Poir.) Zuloaga & Morrone		X
<i>Panicum glabripes</i> Döll	X	

<i>Paspalum cordatum</i> Hack.		X
<i>Paspalum ellipticum</i> Döll	X	
<i>Paspalum eucomum</i> Nees ex Trin.	X	
<i>Paspalum polyphyllum</i> Nees	X	
<i>Paspalum</i> sp.		X
<i>Saccharum angustifolium</i> (Nees) Trin.		X
<i>Schizachyrium tenerum</i> Nees	X	
<i>Steinchisma laxum</i> (Sw.) Zuloaga		X
<i>Trichantheum cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone		X
EUDICOTYLEDONS		
Acanthaceae		
<i>Justicia brasiliana</i> Roth.		X
Anacardiaceae		
<i>Lithraea molleoides</i> (Vell.) Engl.	X	X
Apiaceae		
<i>Eryngium canaliculatum</i> Cham. & Schltld.		X
Apocynaceae		
<i>Mandevilla pohliana</i> (Stadelm.) A.H.Gentry	X	
<i>Oxypetalum sublanatum</i> Malme		X
Aquifoliaceae		
<i>Ilex brevicuspis</i> Reissek	X	
<i>Ilex chamaedryfolia</i> Reissek	X	
<i>Ilex integerrima</i> (Vell.) Reissek	X	
<i>Ilex paraguariensis</i> A.St.-Hil.		X
<i>Ilex theezans</i> Mart. ex Reissek		X
Araliaceae		
<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	X	
Asteraceae		
<i>Ageratum conyzoides</i> L.		X
<i>Baccharis coridifolia</i> DC.		X
<i>Baccharis crispa</i> Spreng.	X	X
<i>Baccharis dracunculifolia</i> DC.	X	X
<i>Baccharis erioclada</i> DC.		X
<i>Baccharis genistelloides</i> (Lam). Pers.		X
<i>Baccharis helichrysoides</i> DC.	X	
<i>Baccharis pauciflosculosa</i> DC.		X
<i>Baccharis reticularia</i> DC.		X
<i>Baccharis</i> sp.1	X	X
<i>Baccharis</i> sp.2		X
<i>Baccharis</i> sp.3		X
<i>Baccharis uncinella</i> DC.		X
<i>Baccharis weirii</i> Baker	X	
<i>Calea cuneifolia</i> DC.	X	
<i>Calea parvifolia</i> (DC.) Baker	X	X
<i>Calea serrata</i> Less.	X	

<i>Calea triantha</i> (Vell.) Pruski	X	
<i>Campovassouria cruciata</i> (Vell.) R.M.King & H.Rob.		X
<i>Chromolaena laevigata</i> (Lam.) R.M.King & H.Rob.		X
<i>Chromolaena palmaris</i> (Baker) R.M.King & H.Rob.	X	
<i>Chromolaena</i> sp.		X
<i>Chrysolaena dusenii</i> (Malme) Dematt.	X	
<i>Chrysolaena platensis</i> (Spreng.) H.Rob.	X	
<i>Dimerostemma</i> sp.		X
<i>Grazielia intermedia</i> (DC.) R.M.King & H.Rob.		X
<i>Lessingianthus glaziovianus</i> (Baker) H.Rob.	X	
<i>Mikania anethifolia</i> (DC.) Matzenb.	X	
<i>Mikania cynanchifolia</i> Hook. & Arn. ex B.L.Rob.		X
<i>Mikania oblongifolia</i> DC.		X
<i>Moquiniastrium argyreum</i> (Dusén ex Malme) G. Sancho	X	
<i>Moquiniastrium polymorphum</i> (Less.) G. Sancho		X
<i>Piptocarpha axillaris</i> (Less.) Baker		X
<i>Praxelis sanctopaulensis</i> (B.L.Rob.) R.M.King & H.Rob.	X	X
<i>Senecio oleosus</i> Vell.		X
<i>Symphyopappus cuneatus</i> (DC.) Sch.Bip. ex Baker	X	X
<i>Vernonanthura crassa</i> (Vell.) H.Rob.	X	X
<i>Vernonanthura discolor</i> (Spreng.) H.Rob.	X	X
<i>Vernonanthura oligolepis</i> (Sch.Bip. ex Baker) H.Rob.	X	
<i>Vernonanthura</i> sp.	X	
Bignoniaceae		
<i>Jacaranda caroba</i> (Vell.) DC.	X	
<i>Jacaranda micrantha</i> Cham.		X
Cactaceae		
<i>Cereus hildmannianus</i> K.Schum.	X	
Celastraceae		
<i>Monteverdia evonymoides</i> (Reissek) Biral	X	X
<i>Monteverdia gonoclada</i> (Mart.) Biral	X	X
<i>Plenckia populnea</i> Reissek	X	
Clethraceae		
<i>Clethra scabra</i> Pers.	X	X
Cordiaceae		
<i>Cordia ecalyculata</i> Vell.		X
Ericaceae		
<i>Gaylussacia pseudogaultheria</i> Cham. & Schldtl.		X
Erythroxylaceae		
<i>Erythroxylum deciduum</i> A.St.-Hil.		X
Euphorbiaceae		
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	X	X
<i>Croton antisyphiliticus</i> Mart.		X
<i>Croton floribundus</i> Spreng.	X	
<i>Croton heterodoxus</i> Baill.		X
<i>Croton serpyllifolius</i> Baill.	X	

<i>Gymnanthes klotzschiana</i> Müll.Arg.	X	X
<i>Sapium glandulosum</i> (L.) Morong		X
<i>Sebastiania brasiliensis</i> Spreng.		X
Fabaceae		
<i>Anadenanthera colubrina</i> (Vell.) Brenan	X	
<i>Bauhinia forficata</i> Link	X	
<i>Bauhinia</i> sp.	X	
<i>Chamaecrista desvauxii</i> (Collad.) Killip	X	
<i>Chamaecrista punctata</i> (Vogel) H.S.Irwin & Barneby	X	X
<i>Chamaecrista ramosa</i> (Vogel) H.S.Irwin & Barneby	X	
<i>Collaea speciosa</i> (Loisel.) DC.		X
<i>Copaifera langsdorffii</i> Desf.	X	
<i>Dalbergia brasiliensis</i> Vogel	X	X
<i>Eriosema glabrum</i> Mart. ex Benth.		X
<i>Eriosema heterophyllum</i> Benth.	X	
<i>Leptolobium dasycarpum</i> Vogel	X	
<i>Leptolobium elegans</i> Vogel	X	
<i>Leucochloron incuriale</i> (Vell.) Barneby & J.W.Grimes	X	
<i>Machaerium stipitatum</i> Vogel		X
<i>Mimosa dolens</i> Vell.		X
<i>Mimosa dolens</i> var. <i>acerba</i> (Benth.) Barneby	X	
<i>Ormosia arborea</i> (Vell.) Harms	X	
<i>Periandra mediterranea</i> (Vell.) Taub.	X	
<i>Senegalia polyphylla</i> (DC.) Britton & Rose		X
<i>Stryphnodendron adstringens</i> (Mart.) Coville	X	
Lamiaceae		
<i>Aegiphila integrifolia</i> (Jacq.) Moldenke		X
<i>Aegiphila</i> sp.	X	
<i>Aegiphila verticillata</i> Vell.		X
<i>Hypenia macrantha</i> (A.St.-Hil. ex Benth.) Harley	X	
<i>Hyptis caespitosa</i> A.St.-Hil. ex Benth.	X	
<i>Hyptis meridionalis</i> Harley & J.F.B.Pastore	X	
<i>Hyptis</i> sp.	X	
<i>Vitex megapotamica</i> (Spreng.) Moldenke	X	X
Loganiaceae		
<i>Strychnos brasiliensis</i> (Spreng.) Mart.	X	
Malpighiaceae		
<i>Banisteriopsis campestris</i> (A.Juss.) Little	X	
<i>Byrsonima brachybotrya</i> Nied.	X	
Malvaceae		
<i>Guazuma ulmifolia</i> Lam.		X
<i>Luehea divaricata</i> Mart.		X
<i>Peltaea polymorpha</i> (A.St.-Hil.) Krapov. & Cristóbal	X	
<i>Peltaea speciosa</i> (Kunth) Standl.		X
Melastomataceae		
<i>Acisanthera alsinaefolia</i> (Mart. & Schrank ex DC.) Triana		X

<i>Chaetogastra debilis</i> Cham.	X	
<i>Chaetogastra herincquiana</i> (Cogn.) P.J.F.Guim. & Michelang.	X	
<i>Leandra aurea</i> (Cham.) Cogn.	X	X
<i>Leandra australis</i> (Cham.) Cogn.	X	X
<i>Leandra erostrata</i> (DC.) Cogn.	X	
<i>Leandra polystachya</i> (Naudin) Cogn.		X
<i>Leandra salicina</i> (DC.) Cogn.		X
<i>Leandra sp.</i>	X	X
<i>Miconia albicans</i> (Sw.) Triana	X	
<i>Miconia cinerascens</i> Miq.	X	X
<i>Miconia petropolitana</i> Cogn.		X
<i>Miconia sellowiana</i> Naudin	X	X
<i>Miconia tristis</i> Spring	X	X
<i>Pleroma martiale</i> (Cham.) Triana	X	X
<i>Tibouchina sp.</i>	X	X
Meliaceae		
<i>Cabralea canjerana</i> (Vell.) Mart.	X	X
<i>Cedrela fissilis</i> Vell.	X	X
<i>Trichilia clauseni</i> C.DC.		X
Moraceae		
<i>Ficus sp.1</i>		X
<i>Ficus sp.2</i>		X
<i>Ficus sp.3</i>	X	
<i>Sorocea bonplandii</i> (Baill.) W.C.Burger et al.	X	X
Myrtaceae		
<i>Blepharocalyx salicifolius</i> (Kunth) O.Berg	X	
<i>Campomanesia adamantium</i> (Cambess.) O.Berg	X	X
<i>Campomanesia pubescens</i> (Mart. ex DC.) O.Berg	X	
<i>Campomanesia xanthocarpa</i> (Mart.) O.Berg		X
<i>Eugenia bimarginata</i> DC.	X	
<i>Eugenia longipedunculata</i> Nied.	X	X
<i>Eugenia neoverrucosa</i> Sobral	X	X
<i>Eugenia pyriformis</i> Cambess.	X	
<i>Eugenia sp.</i>		X
<i>Eugenia uniflora</i> L.	X	X
<i>Myrceugenia myrcioides</i> (Cambess.) O.Berg		X
<i>Myrceugenia oxysepala</i> (Burret) D.Legrand & Kausel	X	
<i>Myrcia glomerata</i> (Cambess.) G.P.Burton & E.Lucas	X	X
<i>Myrcia hatschbachii</i> D.Legrand	X	
<i>Myrcia multiflora</i> (Lam.) DC.	X	X
<i>Myrcia neolucida</i> A.R.Lourenço & E.Lucas		X
<i>Myrcia retorta</i> Cambess.	X	
<i>Myrcia splendens</i> (Sw.) DC.	X	X
<i>Myrcia subcordata</i> DC.	X	
<i>Myrcia tomentosa</i> (Aubl.) DC.		X
<i>Myrcia venulosa</i> DC.	X	

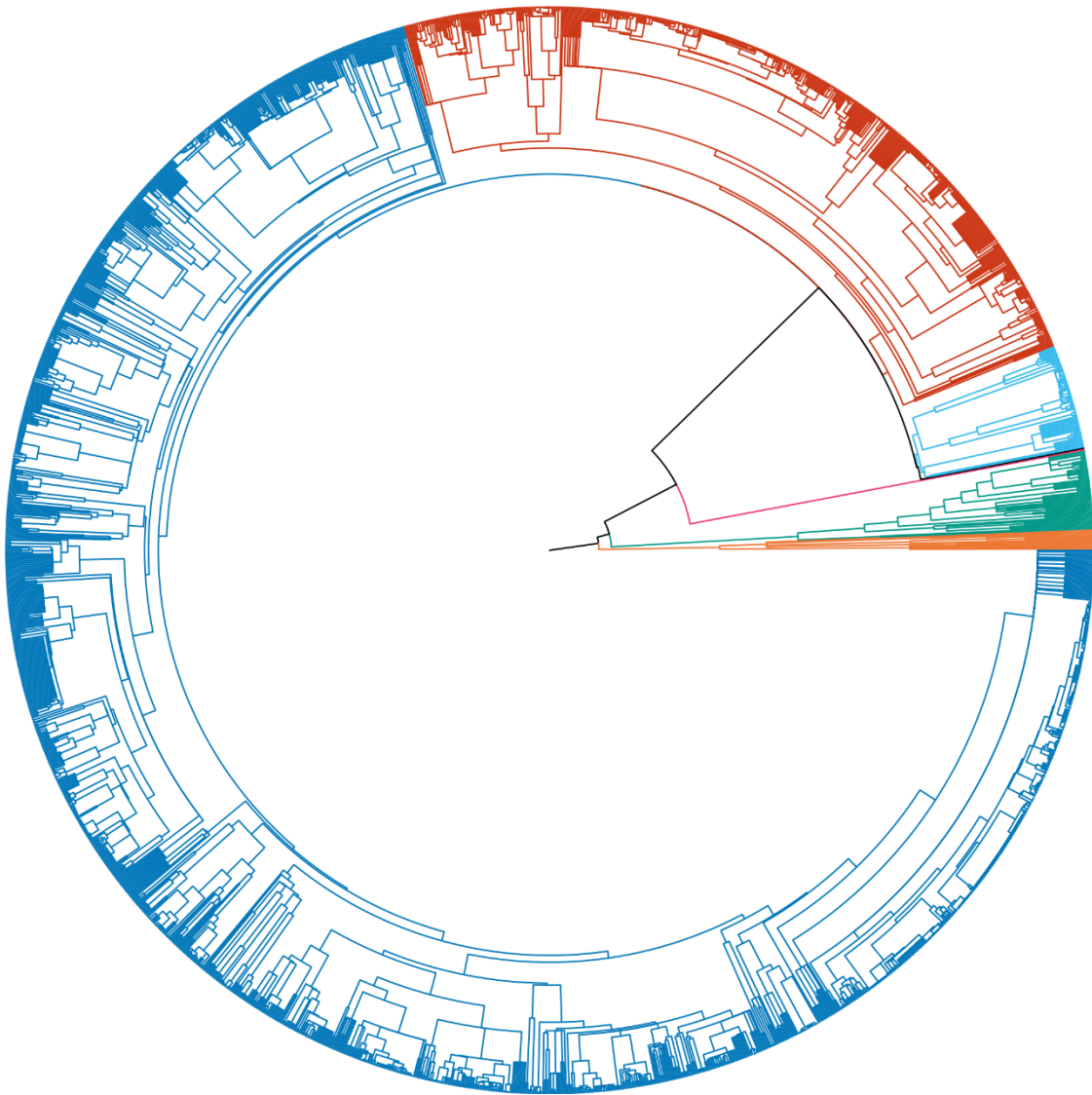
<i>Myrciaria cuspidata</i> O.Berg	X	
<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	X	X
<i>Myrciaria tenella</i> (DC.) O.Berg	X	
<i>Psidium australe</i> Cambess.	X	
<i>Psidium grandifolium</i> Mart. ex DC.	X	
<i>Psidium ovale</i> (Spreng.) Burret	X	
<i>Psidium</i> sp.	X	
Nyctaginaceae		
<i>Guapira opposita</i> (Vell.) Reitz		X
Ochnaceae		
<i>Ouratea sellowii</i> (Planch.) Engl.	X	
<i>Ouratea</i> sp.		X
<i>Ouratea spectabilis</i> (Mart.) Engl.	X	
Peraceae		
<i>Pera glabrata</i> (Schott) Baill.	X	
Polygalaceae		
<i>Polygala lycopodioides</i> Chodat	X	
Primulaceae		
<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	X	X
<i>Myrsine umbellata</i> Mart.	X	X
Proteaceae		
<i>Roupala montana</i> Aubl.	X	X
<i>Roupala montana</i> var. <i>paraensis</i> (Sleumer) K.S.Edwards	X	X
Rhamnaceae		
<i>Frangula sphaerosperma</i> (Sw.) Kartesz & Gandhi	X	X
Rosaceae		
<i>Prunus brasiliensis</i> (Cham. & Schltdl.) D.Dietr.	X	X
<i>Prunus</i> sp.	X	
Rubiaceae		
<i>Borreria paranaensis</i> E.L.Cabral & Bacigalupo	X	
<i>Borreria poaya</i> (A.St.-Hil.) DC.	X	X
<i>Borreria tenella</i> (Kunth) Cham. & Schltdl.		X
<i>Coussarea contracta</i> (Walp.) Müll.Arg.	X	X
<i>Galianthe brasiliensis</i> (Spreng.) E.L.Cabral & Bacigalupo	X	
<i>Galianthe verbenoides</i> (Cham. & Schltdl.) Griseb.	X	
<i>Galium equisetoides</i> (Cham. & Schltdl.) Standl.		X
<i>Ixora venulosa</i> Benth.	X	
<i>Palicourea sessilis</i> (Vell.) C.M.Taylor	X	X
<i>Psychotria leiocarpa</i> Cham. & Schltdl.	X	X
<i>Psychotria suterella</i> Müll.Arg.		X
<i>Rudgea jasminoides</i> (Cham.) Müll.Arg.	X	X
<i>Rudgea sessilis</i> (Vell.) Müll.Arg.	X	X
Rutaceae		
<i>Esenbeckia grandiflora</i> Mart.	X	X
<i>Pilocarpus pauciflorus</i> A.St.-Hil.	X	
<i>Pilocarpus</i> sp.	X	

<i>Zanthoxylum rhoifolium</i> Lam.		X
Salicaceae		
<i>Casearia decandra</i> Jacq.	X	X
<i>Casearia</i> sp.		X
<i>Casearia sylvestris</i> Sw.	X	X
Sapindaceae		
<i>Matayba elaeagnoides</i> Radlk.	X	X
<i>Paullinia carpopoda</i> Cambess.	X	X
Sapotaceae		
<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk.	X	X
<i>Pouteria gardneriana</i> (A.DC.) Radlk.		X
Solanaceae		
<i>Calibrachoa dusenii</i> (R.E.Fr.) Stehmann & Semir	X	X
<i>Calibrachoa paranensis</i> (Dusén) Wijsman		X
<i>Cestrum intermedium</i> Sendtn.		X
<i>Dyssochroma longipes</i> (Sendtn.) Miers		X
<i>Solanum argenteum</i> Dunal		X
<i>Solanum didymum</i> Dunal	X	X
<i>Solanum pseudoquina</i> A.St.-Hil.		X
<i>Solanum</i> sp.		X
<i>Solanum viarum</i> Dunal		X
Symplocaceae		
<i>Symplocos tenuifolia</i> Brand	X	X
<i>Symplocos uniflora</i> (Pohl) Benth.	X	
Theaceae		
<i>Laplacea fruticosa</i> (Schrاد.) Kobuski	X	X
Verbenaceae		
<i>Verbena hirta</i> var. <i>gracilis</i> Dusén	X	
Vochysiaceae		
<i>Qualea cordata</i> Spreng.	X	

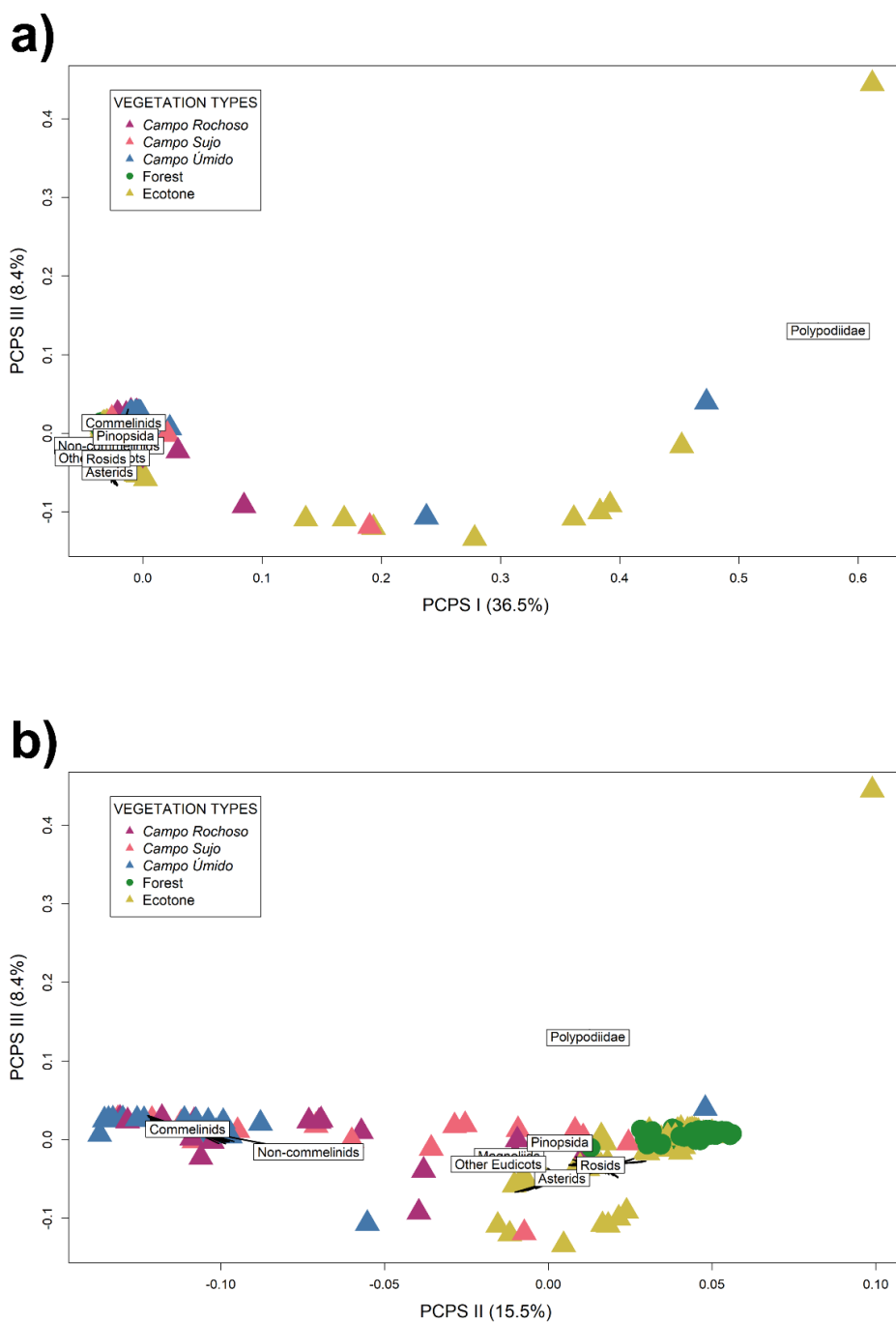
Appendix 2. Reference list used to compile the plant species present in Campos Gerais region.

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Appendix 3. Visualization of the regional plant species phylogenetic tree. We generated the phylogeny by pruning it from a supertree of vascular plants based on Smith & Brown (2018) and Zanne *et al.* (2014). Bluish branches: eudicotyledons; reddish: monocotyledons; cyanish: magnoliids; pinkish: conifers; tealish: ferns; orangish: lycophytes.



Appendix 4. Scatter diagrams of the third eigenvector related to the two main ones generated by Principal Coordinates of Phylogenetic Structure (PCPS) describe the phylogenetic composition of plants among the vegetation types present in the study areas. a: between PCPS I and PCPS III; b: between PCPS II and PCPS III. Triangle points represent plots classified as “Grassland” in the dichotomic mosaic scale. Forest plots are represented as circles.



Appendix 5. Boxplots of correlation between the three first eigenvector of PCPS analysis and our grouping factors. Significance was obtained by a PERMANOVA analysis and a *a posteriori* pairwise comparison test. a: PCPS I variation among vegetation types; b: PCPS I variation between grasslands and forests; c: PCPS II variation among vegetation types; d: PCPS II variation between grasslands and forests; e: PCPS III variation among vegetation types; f: PCPS III variation between grasslands and forests.

