

Original Article

Phylogenetic diversity and structure in moist and dry upland forests in the semi-arid region of Brazil

Diversidade e estrutura filogenética em florestas úmidas e secas de terras altas na região semiárida do Brasil

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Abstract

Understanding the factors influencing variation in the diversity and structure of rich biological communities (e.g., Neotropical upland forests) is essential in the context of climate change. In this study, we examine how environmental filters (temperature, precipitation, and elevation) and distinct habitats (moist upland forests - MUF and dry upland forests - DHF) influence the phylogenetic diversity and structure of 54 tree communities (28 MHF and 26 DHF). We used the standardized effect size (ses) of the metrics phylogenetic diversity (ses.PD), mean pairwise distance (ses.MPD), and mean nearest neighbor distance (ses.MNTD) to quantify changes in tree community diversity and structure. Then, we assessed the relationships of the phylogenetic metrics with the environmental filters as predictors using generalized linear models (GLMs). Our results indicate that increasing temperature negatively affects the phylogenetic indices analyzed, leading to less diverse and more clustered communities. In contrast, increasing precipitation and elevation showed a significant positive relationship with the analyzed indices, directing communities towards greater phylogenetic diversity and random or overdispersed structure. Our findings also reveal that phylogenetic diversity and structure vary with habitat type. For example, while MUFs exhibit higher phylogenetic diversity and random structure, DUFs display lower phylogenetic diversity and clustered structure. In conclusion, our results suggest that the phylogenetic patterns exhibited by upland communities in the semiarid region are strongly related to climatic conditions and the habitat in which they are found. Therefore, if the predicted temperature increases and precipitation decreases in climate change scenarios for the semi-arid region materialize, these communities may face significant biodiversity loss.

Keywords: phylogeny, environmental filter, Brejo de Altitude, Caatinga, Atlantic Forest.

Resumo

Compreender os fatores que influenciam a variação na diversidade e estrutura de comunidades biológicas diversas (por exemplo, florestas de terras altas neotropicais) é essencial no contexto das mudanças climáticas. Por esse motivo, examinamos como os filtros ambientais (temperatura, precipitação e altitude) e habitats distintos (florestas úmidas de altitude - MUF e florestas secas de altitude - DUF) influenciam a diversidade e estrutura filogenética de 54 comunidades de árvores (28 MUF e 26 DUF). Utilizamos o tamanho do efeito padronizado (ses) das métricas diversidade filogenética (ses.PD), distância média entre pares (ses.MPD) e distância média até o vizinho mais próximo (ses.MNTD) para quantificar as mudanças na diversidade e estrutura das comunidades de árvores. Em seguida, avaliamos as relações das métricas filogenéticas com os filtros ambientais como preditores usando modelos lineares generalizados (GLMs). Nossos resultados indicam que o aumento da temperatura possui relação negativa com os índices filogenéticos analisados, direcionando comunidades filogeneticamente menos diversas e mais agrupadas. Já o aumento da precipitação e elevação apresentaram significativa relação positiva com os índices analisados, direcionando comunidades filogeneticamente mais diversas e com estrutura aleatória ou sobredispersas. Nossos achados também mostram que a diversidade e estrutura filogenética variam com o tipo de habitat. Enquanto MUFs apresentam maior diversidade filogenética e estrutura aleatória, DUFs exibem menor diversidade filogenética e estrutura agrupada. Em conclusão, nossos resultados indicam que os padrões filogenéticos apresentados pelas comunidades de terras altas do semiárido possuem forte relação com as condições climáticas e o habitat no qual estão inseridos. Assim, caso o aumento de temperaturas e a redução da precipitação previstos nos cenários de mudanças climáticas para a região semiárida se concretizarem, essas comunidades podem enfrentar uma significativa perda de biodiversidade.

Palavras-chave: filogenia, filtro ambiental, Brejo de Altitude, Caatinga, Floresta Atlântica.

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1. Introduction

Upland ecosystems are among the world's most important environments due to their high biodiversity (Körner, 2004) and provision of essential ecosystem services (e.g., water and food resources, carbon sequestration, soil conservation) (Mengist et al., 2020). The high biodiversity of these environments is linked to the multitude of unique habitats created by the variation of abiotic conditions along their elevation gradients (Körner, 2004; Körner et al., 2017). The most influential abiotic filters contributing to habitat diversification and shaping biodiversity patterns in upland ecosystems encompass temperature, precipitation, and soil properties (Zhang et al., 2016; Chun and Lee, 2018; Sabatini et al., 2018; Luo et al., 2019; Zhu et al., 2019; Ohdo and Takahashi, 2020). In the Neotropics, these abiotic filters stand out as significant drivers of shifts in taxonomic diversity patterns among different plant communities established in uplands, such as Andean forests (Cuesta et al., 2017), Tepuis (Campos et al., 2022a), Inselbergs (Pinto-Junior et al., 2020), Páramos (Campos et al., 2018; Neri et al., 2017), and Caatinga Uplands (Santos et al., 2007a; Ramos et al., 2020; Diniz et al., 2021). Recent studies also indicate that these abiotic filters have a strong relationship with phylogenetic diversity and structure patterns observed in Neotropical upland ecosystems (Mattos et al., 2019; Campos et al., 2021, 2022b; Cisneros et al., 2021).

Phylogenetic diversity refers to the sum of the evolutionary ages of species in a community (Faith, 1992). Simultaneously, the phylogenetic structure is related to the organization of these species (i.e., clustering, overdispersion, and randomness) based on their evolutionary relationships (Webb, 2000; Webb et al., 2002). In communities with clustered structures, species tend to be phylogenetically closer than expected by chance (Webb, 2000), while having similar functional traits that might be conserved in their evolutionary lineages (Connolly et al., 2011). Clustering is commonly determined by environmental filtering, which selects species with conserved functional adaptations suited to local conditions (Wiens and Graham 2005; Cavender-Bares et al., 2009). For example, high temperatures and low precipitation in upland dry forests filter drought-tolerant lineages, promoting phylogenetic clustering (Cisneros et al., 2021).

On the other hand, when biotic interactions (e.g., competition) are more powerful drivers of community assembly than environmental filtering, phylogenetically less related species coexist (i.e., overdispersion), thus enriching the phylogenetic diversity of biological communities (Weiher and Keddy, 1995; Webb et al., 2002). Further, phylogenetic overdispersion can also be an outcome of the effects of environmental filtering on species with convergent trait evolution (Cavender-Bares et al., 2009; Ndiribe et al., 2013; Mori et al., 2021). Conversely, when abiotic and biotic drivers exert balanced or little influence on community assembly, stochastic factors (e.g., dispersal limitation) play a more important role and lead to random phylogenetic structure (Vellend, 2010; Rosindell et al., 2011).

In the biodiversity context, it is evident that there is a strong relationship between climatic variables

(e.g., temperature and precipitation) and phylogenetic diversity and structure (Qian et al., 2017a, b; Luo et al., 2019; Liu et al., 2020; Zhang et al., 2020). Owing to this relationship, global climate change is altering the phylogenetic patterns of plant communities exposed to adverse conditions (Li et al., 2019). The effects of climate on phylogenetic diversity might be more pronounced in tropical upland ecosystems, as they are among the most threatened by such global changes (Mata-Guel et al., 2023). Therefore, a better understanding of the effects of climatic variables on the current phylogenetic patterns can provide insights into how these communities will respond to future climate changes.

Despite the growing number of studies describing the relationships between climatic variables and phylogenetic diversity and structure in upland ecosystems, we identified a significant gap related to the Neotropics. Currently, there are no large-scale studies investigating how the environmental heterogeneity of the Brazilian semi-arid region relates to the phylogenetic patterns of the upland forests in this area. This region is of great interest for conservation, as it is one of South America's most vulnerable locations to climate change (Marengo and Bernasconi, 2015; Marengo et al., 2017). To address this gap, the present study investigates two co-occurring upland ecosystems in the semi-arid region: the *Serras de Caatinga* (dry upland forests - DUF) and the *Brejos de Altitude* (moist upland forests - MUF). The DUFs harbor communities within the phytogeographic domain of the Caatingas (Silva et al., 2014; Moro et al., 2016; Lopes et al., 2017; Ramos et al., 2020; Diniz et al., 2021). In contrast, the MUFs consist of islands of moist vegetation belonging to the Atlantic Forest domain (tropical moist forest), also present in elevated areas of the semi-arid region (Tabarelli and Santos, 2004; Rodal and Nascimento, 2006; Santos et al., 2007b; Rodal et al., 2008; Queiroz et al., 2017; Marques et al., 2021).

With this study, we aimed to investigate the effects of environmental filters (temperature, precipitation, and elevation) and habitat type (DUF and MUF) on the phylogenetic diversity and structure of tree communities in upland ecosystems in the Brazilian semi-arid region. We hypothesize that environmental filters display relevant roles in assembling the tree communities with phylogenetic patterns (clustering or overdispersion) according to their habitat type. Thus, we expect that an increase in the effects of environmental filtering will result in phylogenetically clustered and less diverse communities (DUF), while overdispersed and more diverse communities will occur in less stressful habitats (MUF).

2. Methods

2.1. Study area

The present study comprises 54 tree communities located in five states of the Northeast Region of Brazil: Alagoas, Ceará, Paraíba, Pernambuco, and Rio Grande do Norte (Supplementary Material, Table S1). Together, these states occupy a territorial area of approximately 385,000 km² (IBGE, 2022). The regional climate is BswH'

(warm semi-arid) according to the updated Köppen-Geiger climate classification (Alvares et al., 2014). The states are predominantly occupied by the Caatinga, a mosaic of physiognomies influenced by variations in relief, precipitation, and soils (Moro et al., 2016; Queiroz et al., 2017). In the present study, we focus exclusively on the vegetation found in upland locations in the semi-arid region, particularly MUF and DUF. MUF ecosystems occur in elevated locations in the semi-arid region, such as plateaus, flat-topped hills, mountain ranges, low mountains, and peaks (Tabarelli and Santos, 2004; Santos et al., 2007b; Queiroz et al., 2017; Marques et al., 2021). These ecosystems are refuges of the current Atlantic Forest (moist forest) that have persisted in locations with less arid and more stable conditions throughout the evolutionary history of Brazil's semi-arid region (Silveira et al., 2019). Due to this context, MUFs are considered "islands of moist forest" within a semi-arid matrix, supporting a wide range of ecosystem services and high biodiversity (Pôrto et al., 2004). On the other hand, DUFs are ecosystems that house forests belonging to the phytogeographic domain of the Caatingas, dry forest *sense* of Pennington et al. (2009). Therefore, they are typically associated with mountain ranges, isolated low mountains, and inselbergs (Moro et al., 2016; Lopes et al., 2017), and are considered "biodiversity refuges" due to their high diversity associated with the elevation gradient (Silva et al., 2014; Lopes et al., 2017; Ramos et al., 2020).

2.2. Data acquisition

The floristic data used in the analyzes were obtained from the NeoTropTree (NTT) database (Oliveira-Filho, 2017), which consists of a compilation of checklists of tree species over three meters in height derived from floristic surveys from the published literature and herbarium records. NTT has information on more than 20,000 species of woody plants and 7,000 georeferenced areas that extending from southern Florida (USA) to Patagonia. Each georeferenced area corresponds to a single type of vegetation that can occur within a radius of five kilometers.

We accessed the NTT data tab and selected the geographical data option to collect the necessary information for our study. From this option, it is possible to filter habitats based on information related to the country of occurrence, state or province, and phytogeographic domain, among other criteria. Thus, we initially filtered the study areas by state, taking into consideration the five states mentioned previously. We focused our sampling searches on the five mentioned states as they harbor most MUFs (Tabarelli and Santos, 2004). As an additional criterion, we included communities belonging to the Atlantic Forest and Caatinga domains in the study, which are in locations that presented a minimum elevation of 600 m within the semi-arid region. We used this criterion because DUF (Silva et al., 2014; Moro et al., 2016; Lopes et al., 2017; Ramos et al., 2020; Diniz et al., 2021) and MUF (Tabarelli and Santos, 2004; Santos et al., 2007b; Queiroz et al., 2017; Marques et al., 2021) are intrinsically related to features such as plateaus, flat-topped hills, mountain ranges, low mountains, inselbergs, and peaks.

Based on the criteria established (i.e., five states and 600 m elevation), we selected 28 communities belonging to the Atlantic Forest domain (MUF) and 26 communities belonging to the Caatinga domain (DUF) (Figure 1), totaling 54 communities and a list of 1,015 sampled species.

We used the WorldClim database (Hijmans et al., 2005) to obtain data on mean annual temperature, mean annual precipitation, and elevation (spatial resolution of 30 arc seconds $\approx 1\text{km}^2$) for each sampled area. We used these variables because mean annual temperature and mean annual precipitation are two key climatic variables for species distribution at broad spatial scales (Kreft and Jetz, 2007; Kooyman et al., 2012)

2.3. Phylogenetic reconstruction

We subsequently inserted our species list into the GBOTB.extended mega tree contained in the V.PhyloMaker package algorithm to generate a calibrated phylogeny of our study areas using the phylo.maker function (Jin and Qian, 2019). This mega tree is an updated and corrected version of the phylogeny for plants published by Smith and Brown (2018) combined with the phylogeny published including pteridophytes by Zanne et al. (2014). Since the mega tree was constructed based on fossil and molecular records from GenBank and phylogenetic data from Open Tree of Life, this enables reconstructing phylogenies with high resolution, having all families and most genera resolved.

The phylo.maker function creates phylogenetic hypotheses, which generate evolutionary relationships among different species, in three scenarios (scenarios 1-3) (Jin and Qian, 2019). We used the hypothesis based on scenario 3 to add missing branches to generate our phylogenetic tree. Using the scenario 3, the V.PhyloMaker algorithm defines the length of the taxa branches to be inserted, adding an absent genus between the basal node of its respective family, and an absent species between the basal node of its respective genus (Qian and Jin, 2016). Since scenario 3 consider average distances to bind the tips of the phylogeny, it reduces bias caused by polytomies.

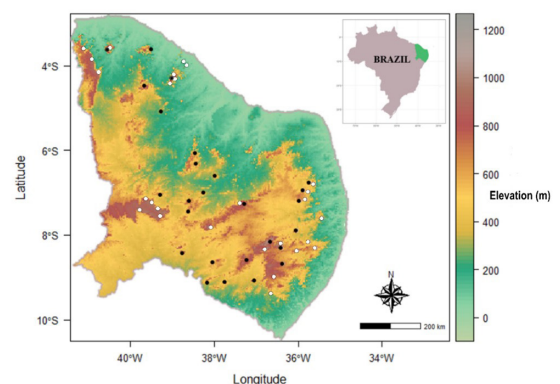


Figure 1. Location of the study areas in the semi-arid region of Brazil. White dots indicate sampling points in moist upland forests; black dots indicate sampling points in dry upland forests.

2.4. Phylogenetic diversity and structure

First, we calculated Faith's Phylogenetic Diversity (PD) (Faith, 1992), Mean Pairwise Distance (MPD), and Mean Nearest Taxon Distance (MNTD) (Webb et al., 2002). Then, we calculated their standardized effect sizes (ses): ses.PD, ses.MPD and ses.MNTD, to correct for the commonly expected collinearity effect with species richness on these metrics. The ses calculation consists of randomly extracting 999 times the same number of species present in each resultant random community, generating means of randomized communities that are compared with the communities observed for each metric (i.e., PD, MPD, and MNTD) (Kembel et al., 2010). The ses was computed using 10,000 randomizations under the null model phylogeny pool (unconstrained null model) (Kembel and Hubbell, 2006). Next, we used the values of ses.MPD, ses.MNTD and of ses.PD, to assess, respectively, if the phylogenetic structure and diversity of the communities are significantly different from the expected by chance. For that, we assessed the significance of the averaged single values of ses.PD, ses.MPD and ses.MNTD of each tree community belonging to DUF and MUF, by applying the 95% confidence interval, which ranged between 1.96 and -1.96. Values within this range (1.96 and -1.96) imply non-significance, while values outside this range deviate from the mean and are considered significant (Forthofer et al., 2006; Zar, 2010). In summary, we considered values less than -1.96 as significantly clustered, greater than 1.96 as significantly overdispersed, and within the range between -1.96 and 1.96 as random (Gotelli and Entsminger, 2003). The phylogenetic structure and diversity metrics were calculated using the functions `ses.pd`, `ses.mpd`, and `ses.mntd` of the `picante` package (Kembel et al., 2010).

2.5. Generalized Linear Models (GLMs)

We conducted Generalized Linear Models (GLMs) with a Gaussian distribution to test whether environmental factors, such as mean annual temperature (°C), mean annual precipitation (mm), and elevation (m), influence and explain the distribution patterns of phylogenetic diversity and structure (ses.PD, ses.MPD, and ses.MNTD) in the tree forest communities. We also added a categorical variable defined as "habitat" as a predictor to verify whether the phytophysognomy itself influences phylogenetic diversity.

We verified the normality of the residuals of the response variables using the Shapiro–Wilk test ($p < 0.05$) to meet the assumptions required by the analysis, while also assessing the distribution of the residuals in Q-Q Plots. We also checked for multicollinearity between the predictor variables by calculating the Variance Inflation Factor (VIF) through the `vif` function of the R package `car` (Fox and Weisberg, 2019). We considered a VIF value < 5 as the threshold to consider acceptable to keep predictors in the same model (Borcard et al., 2018). We also verified the linear relationship between dependent and independent variables through the L2 and SUP tests using the `gof` package (Holst, 2015). All predictors were linearly related to the phylogenetic target variables.

During the pre-tests, we noticed that temperature and elevation were collinear variables ($VIF > 5$). Thus, we decided

to create two models for each response variable. The first one includes the response variables (ses.PD, ses.MPD, and ses.MNTD) and the predictors mean annual temperature, mean annual precipitation and habitat ($v. \text{response} \sim \text{temp.} + \text{precipitation} + \text{habitat}$). Then, we individually evaluated the influence of elevation on the response variables ($v. \text{response} \sim \text{elevation}$) in the second model.

After performing the models, we tested the significance ($p < 0.05$) of the relationships found between the response and predictive variables using ANOVA, calculated from the built-in R function `anova`. All analyzes were developed in the R version 4.2.2 software program (R Core Team, 2022).

3. Results

We found that temperature, precipitation, and elevation influence the phylogenetic diversity and structure of semi-arid upland tree communities (Table 1). All the analyzed environmental filters (temperature, precipitation, and elevation) and habitat types (DUF and MUF) significantly influenced phylogenetic diversity (ses.PD). We observed that phylogenetic diversity (ses.PD) in upland communities (DUF or MUF) decreases with increasing temperature and increases with higher precipitation and elevation (Figure 2A-C). Regarding the index ses.MPD, we found that a significant increase in precipitation has a positive linear relationship with the increase this index values, while a decrease in temperature leads to a reduction in ses.MPD values (Figure 2D, E). Upon analyzing ses.MNTD, we discovered that an increase in temperature is significantly related to a decrease in this index values, while an increase in elevation positively influences ses.MNTD values (Figure 2G, I).

We also found that communities established in distinct habitats (DUF or MUF) exhibit significant phylogenetic

Table 1. Results of the analyses of variance (ANOVA) of the GLMs for the effects of habitat type, temperature, precipitation and elevation on ses.PD, ses.MPD, ses.MNTD.

ses.PD	F	df	P-values
Habitat	32.05	1	< 0.001
Temperature	17.74	1	< 0.001
Precipitation	16.97	1	< 0.001
Elevation	4.70	1	0.03
ses.MPD			
Habitat	42.85	1	< 0.001
Temperature	4.46	1	0.03
Precipitation	24.20	1	< 0.001
Elevation	2.23	1	0.14
ses.MNTD			
Habitat	4.04	1	0.04
Temperature	40.42	1	0.002
Precipitation	2.53	1	0.11
Elevation	4.05	1	0.04

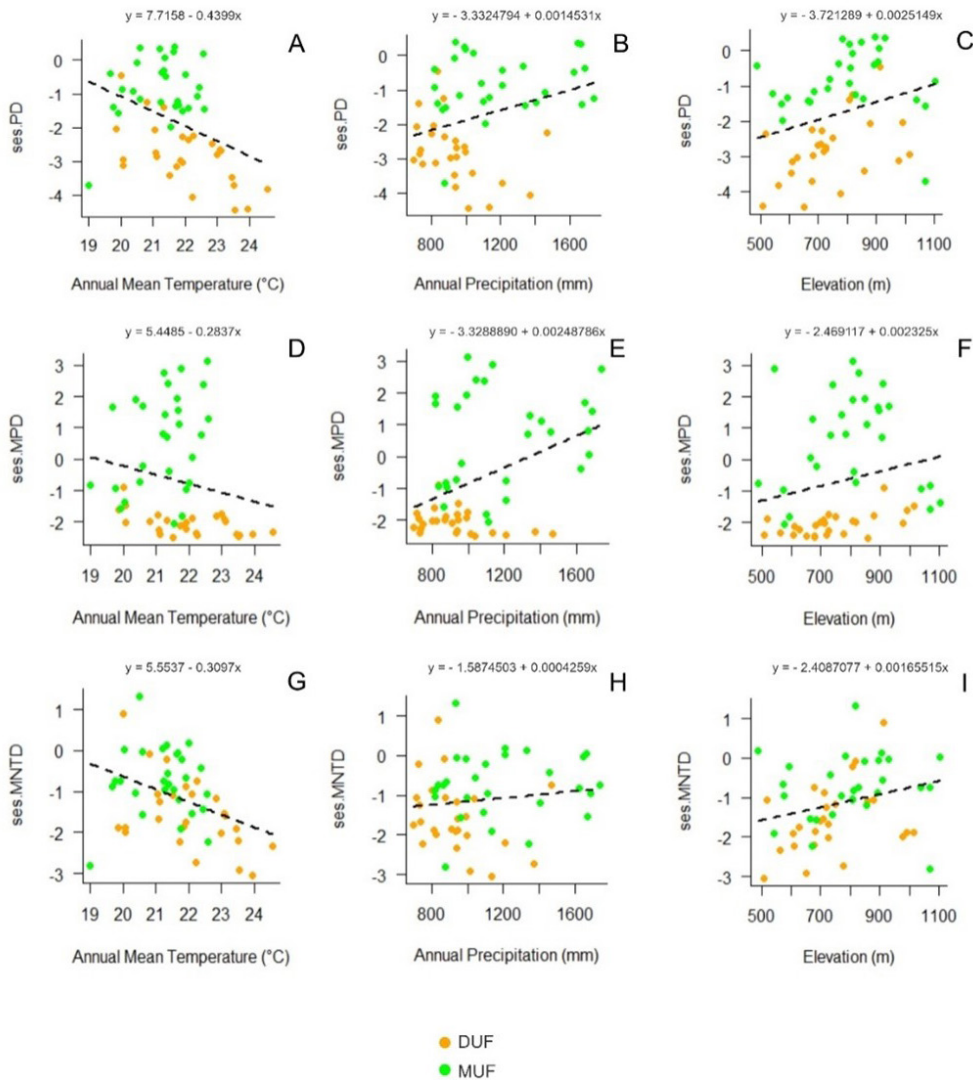


Figure 2. Relationships between the predictive variables (temperature, precipitation and elevation) and the phylogenetic metrics (ses.PD, ses.MPD, ses.MNTD).

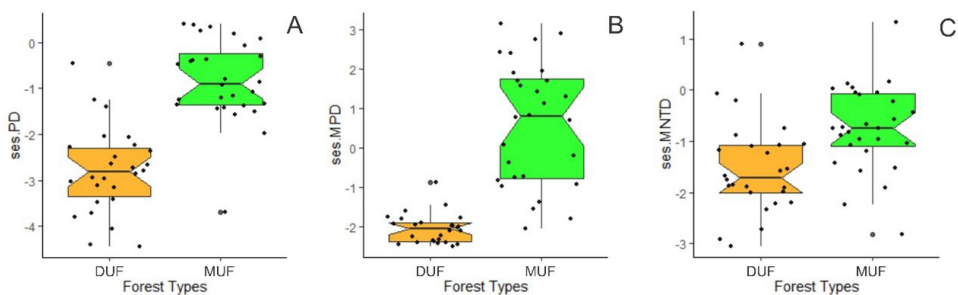


Figure 3. Variation in standardized effect sizes of phylogenetic diversity (ses.PD) (A), mean pairwise distance (ses.MPD) (B) and mean nearest neighbor distance (MNTD) (C) between moist upland forests (MUF) and dry upland forests (DUF).

diversity and structure differences. MUF showed greater phylogenetic diversity (ses.PD) and higher values of ses.MPD and ses.MNTD compared to DUF (Figure 3). Considering the

values of ses.MPD, our results indicate that approximately 80% of MUFs exhibit a random phylogenetic structure. The remaining 20% consisted of communities that displayed

significant phylogenetic overdispersion. When considering the values of *ses.MNTD*, the random phylogenetic structure becomes even more apparent in MUFs, as 90% of their communities showed values distributed between 1.96 and -1.96 for this metric.

On the other hand, the low values of *ses.MPD* and *ses.MNTD* displayed by DUF indicates that many of their communities tend to have a more clustered phylogenetic structure than expected by chance. This tendency becomes clear when we observe that approximately 60% of DUF communities showed *ses.MPD* values below -1.96, indicating phylogenetic clustering based on this index. When considering *ses.MNTD* values, we note that 30% of DUF communities exhibited phylogenetic clustering.

4. Discussion

Our study revealed that temperature, precipitation, and elevation are environmental filters that promote significant changes in the phylogenetic structure and diversity of upland forests in the Brazilian semi-arid region. Consequently, communities established in habitats exposed to harsher environmental conditions (DUF) tend to exhibit low phylogenetic diversity and clustering, as expected. On the other hand, the communities established in habitats under lower pressure of the environmental filters (MUF) harbor higher phylogenetic diversity, and phylogenetic structure ranging from random to overdispersed, partially confirming our expectations. These results highlight the importance of environmental heterogeneity in the semi-arid region for determining distinct phylogenetic patterns in upland communities.

Precipitation and temperature were the primary environmental filters influencing the species phylogenetic relationships. This is congruent with the importance of higher water availability and moderate temperatures as essential drivers of increased phylogenetic diversity in upland forests (Qian et al., 2014; Zhang et al., 2020; Cisneros et al., 2021; Tolmos et al., 2022). Although elevation is also an essential variable influencing the patterns of phylogenetic diversity and structure of upland forests (Mattos et al., 2019; Campos et al., 2021, Campos et al. 2022b), its effect on phylogenetic diversity and structure was less pronounced than precipitation and temperature in our study. Since elevation directly affects local environmental conditions (e.g., temperature, atmospheric pressure, soils), its impact on biological communities is indirect (Körner et al., 2017), thus possibly masking its actual effects in our analysis.

Despite its minor effect on the phylogenetic diversity of our studied upland forests, elevation is a relevant factor due to its influence on variations have temperature and precipitation that lead to orographic rainfall in the semi-arid region (Lyra et al., 2014; Andrade et al., 2016; Mutti et al., 2020). Orographic rainfall occurs when moist air masses encounter elevated areas, and the lower atmospheric pressure and temperature cause water vapor to condense, forming clouds and increasing local precipitation (Roe, 2004). This phenomenon might have been directly linked to the patterns of phylogenetic diversity that we

observed, as the increase in *ses.PD* corresponds to lower temperatures, higher precipitation, and elevation. Moreover, locations exposed to orographic rainfall typically harbor moist ecosystems within the semi-arid region, such as MUF (Queiroz et al., 2017), which exhibited the highest values of *ses.PD*, *ses.MPD* and *ses.MNTD* in our study. Therefore, our findings suggest that orographic rainfall may represent a critical factor in enhancing phylogenetic diversity in upland forests in the semi-arid region, as less stressful environmental conditions and greater resource availability tend to favor an increase in the number of lineages in upland plant communities (Qian et al., 2023).

As stress imposed by environmental filtering increased, exemplified by higher temperatures, we observed a decrease in the values of phylogenetic metrics (i.e., *ses.PD*, *ses.MPD* and *ses.MNTD*). This pattern was expected since factors related to increased water stress tend to reduce phylogenetic diversity in plant communities due to the exclusion of non-tolerant species (Anacker and Harrison, 2012). Thus, our results indicate that the increase in environmental stress in the semi-arid region leads to the assembly of communities mostly composed of phylogenetically close species adapted to harsher conditions, as also observed in other upland forests (González-Caro et al., 2014; Liu et al., 2019; Zhang et al., 2020; Cisneros et al., 2021).

When analyzing the differences in phylogenetic diversity and structure patterns between habitats, we noticed that although MUFs have higher phylogenetic diversity and overdispersion than DUFs, they tend to exhibit random phylogenetic structure, which contradicts part of our initial expectations. This phylogenetic random trend might be an outcome of unmeasured stochastic influence (e.g., dispersal limitation) inherently encompassed in our study (Vellend, 2010). However, the observed MUF communities exhibiting phylogenetic overdispersion regarding the basal clades and older nodes (*ses.MPD*) could be related to the formation process of these habitats. According to Costa et al. (2018), the climate (Last 30,000 years) constrained MUFs to isolated enclaves in northeastern Brazil, while most of their surroundings were occupied by seasonally dry forests (Caatinga). These MUF enclaves maintained more stable and less stressful climatic conditions than their surrounding areas (Silveira et al., 2019). Thus, in this study, for some MUFs this scenario may have favored increased phylogenetic diversity and structural patterns toward overdispersion. Environments with higher productivity, moderate climatic conditions and higher availability of resources tend to support greater species diversity (Kreft and Jetz, 2007; Ricklefs and He, 2016).

The phylogenetic clustering observed in DUF communities possibly also depicts their historical processes linked to the formation of their regional pool of species. Although current semi-arid conditions have only been established in the last 4,500 years (Oliveira et al., 1999), fossil records indicate that some of the most representative plant groups of today's Neotropical dry forests diversified in the Miocene (Pennington et al., 2018). Furthermore, phylogenetic studies show that Neotropical dry forests exhibit a high degree of monophyly and phylogenetic conservatism (Pennington et al., 2009). This is congruent

with our results showing that the phylogenetic clustering in DUF communities is more related to basal nodes and older clades (ses.MPD) of the phylogenetic tree.

Overall, our results indicate that the studied tree communities' phylogenetic components (diversity and structure) are sensitive to variations in temperature and precipitation. This supports a major concern, as studies predict drought events will become more intense and frequent in northeastern Brazil throughout this century (Marengo and Bernasconi, 2015; Marengo et al., 2017). If these predictions are confirmed, MUFs may be one of the most affected ecosystems within the semi-arid context, as the phylogenetic patterns observed in these communities are associated with less stressful environmental conditions. Consequently, a potential increase in temperature and decrease in precipitation could contribute to the extinction of species with low drought tolerance found in MUFs, such as the tree ferns from the genera *Alsophila* and *Cyathea* (Supplementary Material, Table S2), causing significant phylogenetic diversity loss in their communities.

5. Conclusion

Our findings lead us to conclude that greater resource availability (higher precipitation, i.e., water availability) and milder environmental conditions (i.e., lower temperature) were critical factors in increasing phylogenetic diversity, expressed by ses.PD, ses.MPD, and ses.MNTD. Our results also allowed us to conclude that the phylogenetic diversity and structure are also significantly influenced by the habitat type (MUF or DUF) in upland forests of the Brazilian semi-arid region. Thus, these results allow us to better understand the mechanisms driving the phylogenetic diversity and structure of upland forests in the semi-arid region and provide clues on how these communities might be affected by future environmental changes.

Thus, we hope that our contribution to a better understanding of the mechanisms driving the phylogenetic diversity and structure of upland forests in the semi-arid region may encourage further studies. Considering the present, we believe that additional research could explore the influence of other filters, such as soils and chronic anthropogenic disturbances, on the phylogenetic patterns of the communities studied. In light of future risks, studies presenting modeling for different climate change scenarios are important for more accurately understanding how the phylogenetic component of these communities may respond to increased environmental stress. Integrating these approaches could improve our ability to predict and mitigate the impacts of global changes on these communities and their associated ecosystems.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Characterization of the study areas according to geographical location, local name of areas, state of Brazil where are the areas, phytogeographic domains to which the areas belong.

Table S2. Species from the sampled areas in our study categorized by habitat: exclusive to Moist Upland Forests (MUF), exclusive to Dry Upland Forests (DUF), and those found in both habitats (MUF/DUF)

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