LHORAYNNE PEREIRA GOMES

PHYLOGENETIC AND FUNCTIONAL COMMUNITY STRUCTURE OF TREES IN A SEASONAL TROPICAL FOREST

Thesis submitted to the Botany Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae*.

Adviser: Andreza Viana Neri

VIÇOSA – MINAS GERAIS
2023

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T

Gomes, Lhoraynne Pereira, 1992-

G633p
2023

Phylogenetic and functional community structure of trees in a Seasonal Tropical Forests / Lhoraynne Pereira Gomes. – Viçosa, MG, 2023.

1 tese eletrônica (107 f.): il. (algumas color.).

Texto em inglês.
Inclui anexos.
Orientador: Andreza Viana Neri.
Tese (doutorado) - Universidade Federal de Viçosa, Departamento de Biologia Vegetal, 2023.
Inclui bibliografia.
DOI: https://doi.org/10.47328/ufvbbt.2024.089
Modo de acesso: World Wide Web.

1. Comunidades vegetais. 2. Filogenia. 3. Florestas tropicais. 4. Topografia. 5. Habitat (Ecologia). 6. Diversidade das plantas - Conservação. I. Neri, Andreza Viana, 1977-. II. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. III. Título.

CDD 22. ed. 581

Bibliotecário(a) responsável: Bruna Silva CRB-6/2552

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APPROVED: OCTOBER 25, 2023.

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AGRADECIMENTOS

Agradeço primeiramente a Deus, por ter me guiado e trazido até este momento. A minha família, minha base, sempre apoiando as minhas escolhas e estando ao meu lado nesta caminhada. Em especial aos meus pais, Marilza e Dehon, por todo suporte e amor incondicional, e por serem um exemplo de força e coragem. Aos meus irmão Luana e Mardehon por me apoiarem sempre. Ao meu amigo Rodrigo, que encarou essa jornada comigo, dividindo diariamente este caminho de expectativas, aprendizado e conquistas. Só tenho o que agradecer, pela paciência e suporte diário nestes últimos anos.

Ao Celso (chefe), Rodrigo, Alice, Bruna, Nayara Franzini, Elielson, Herval, Miguel, Carlos, Nathália, Michel, Alex, Miller, Arthur, Cecília, Fábia, que foram para campo e me ajudaram na coleta de dados. Sem palavras para agradecer a cada um de vocês que saíram da segurança de suas casas para me ajudar. Vocês foram fundamentais! Ao Celso, uma das pessoas mais generosas que conheci, por todo apoio ao longo desta jornada, ajuda no campo, sempre que precisava e amizade.

Ao grupo da bancada, Rodrigo, Bruna e Nathália pelo suporte. Aos amigos do LEEP e da UFV, Maribel, Nayara Smith, Rodrigo, Alice, Pedro, Bruna, Elielson, Herval, Miguel, Carlos, Nathália, Michel, Alex, Miller, Arthur, Cecília, Fábia, Daniela, Wendelo, Larissa, Josielle, Patanjaly, Natália, Libia, Marina, Samara pela convivência e trocas diárias.

A Universidade Federal de Viçosa e ao Programa de Pós-Graduação em Botânica pela oportunidade, a minha orientadora Andreza Viana Neri, pelo suporte e oportunidade de execução deste estudo. À Coordenação de Aperfeiçoamento de Pessoa de Nível Superior (CAPES) pela bolsa de estudos Código de Financiamento 001 que foi indispensável para a execução desta pesquisa. E a todos os professores que compartilharam comigo um pouco do seu conhecimento.

Finalmente, agradeço a todos que estiveram comigo nestes quatro anos, vocês foram importantes para eu poder chegar até aqui.

Muito obrigada!

ABSTRACT

GOMES, Lhoraynne Pereira, D.Sc., Universidade Federal de Viçosa, october, 2023. **Phylogenetic and functional community structure of trees in a seasonal tropical forest**. Adviser: Andreza Viana Neri.

Habitat partitioning is important for understanding the drivers that influence the assembly of tropical forest communities. Understanding the local-scale effects of environmental gradients on diversity (taxonomic, functional, and phylogenetic) involves understanding the role of each species within the plant communities. In this context, our objectives were as follows: (1) to understand how topography can influence taxonomic and phylogenetic diversity and which variables most influence community assembly on a local scale; (2) to understand how the topographic gradient shapes the functional identity of species, and how they contribute to understanding the mechanisms of community assembly on a local scale; (3) and to verify the functional trait composition of vertical strata and whether the strategies adopted by trees along vertical stratification are related to functional groups, leaf phenology and dispersal syndrome. The study was conducted in three permanent plots of 1 ha within a fragment of the Atlantic Forest. From the floristic list, a phylogenetic tree was created based on 211 species, and phylogenetic diversity was calculated: the average paired distance between all the taxa in the community, the average distance of the closest taxon in the community, and the standardized effect size for these metrics. We calculated the metrics of community weighted average, functional richness, functional uniformity, functional divergence, and metrics of phylogenetic diversity for each plot. Four leaf traits and two wood traits were selected: leaf area (cm^2), specific leaf area (cm^2/g), dry mass content (g/g), wood density (mg/m^3), maximum height (m), and leaf thickness (cm). Multiple linear and generalized linear models were used to evaluate the effects of environmental variables on taxonomic, functional, and phylogenetic diversity. We analyzed the functional identity and diversity across topographic habitats. To analyze the relationship between leaf phenology and dispersal syndrome with the vertical stratification we performed the Qui-square test. We compared the mean values of the traits to understand the functional patterns within the functional groups of leaf phenology, dispersal syndrome, and vertical strata. The MRT grouped the subplots of the whole community into three habitats: lower, intermediate, and high topographic habitats. The diversity of the elevation habitats was significantly different; the intermediate habitats showed higher diversity than the other habitats, and the high habitats had the lowest diversity values. The Low habitats were always different from the other habitats, indicating that PD and MPD decreased with increasing altitude. The regression results showed that richness was negatively influenced by elevation and SB and positively influenced by soil moisture, coarse sand, and organic matter. The topographic gradients showed different functional compositions along the habitats; a high habitat was characterized by species with conservative leaf traits, higher functional divergence, and lower functional richness. The low habitat was characterized for acquisitive leaf traits, less functional divergence, and higher functional richness. Functional richness and functional divergence were the categorical traits that were best explained; at the local scale, edaphic variables appeared to be more important for the variation of the traits and functional diversity, and the texture of the soil was the main driver. Leaf phenology showed a functional pattern of trait mean values of acquisitive-conservative traits between deciduous and evergreen species. The traits mean values of dispersal syndrome shows that zoochory species are correlated with conservative traits and non-zoochory species are correlated with acquisitive traits. Our study demonstrates the importance of local-scale studies, showing that habitats found on local gradients can affect plant diversity at the taxonomic, phylogenetic, and functional levels. This result is very important for understanding how Seasonal Tropical Forests are structured horizontally and vertically and the patterns of functional composition.

Keywords: Topography, community assembly, habitats, environmental variables, vertical stratification

RESUMO

GOMES, Lhoraynne Pereira, D.Sc., Universidade Federal de Viçosa, outubro de 2023. **Estrutura filogenética e funcional da comunidade de árvores de uma Floresta Tropical Estacional**. Orientadora: Andreza Viana Neri.

A estruturação do habitat é importante para a compreensão dos fatores que influenciam a montagem das comunidades de florestas tropicais. A compreensão dos efeitos em escala local dos gradientes ambientais sobre a diversidade (taxonômica, funcional e filogenética) envolve a compreensão do papel de cada espécie dentro das comunidades vegetais. Neste contexto, nossos objetivos foram os seguintes: (1) compreender como a topografia pode influenciar a diversidade taxonômica e filogenética e quais variáveis mais influenciam na montagem da comunidade em escala local; (2) compreender como o gradiente topográfico molda a identidade funcional das espécies, e como eles contribuem para a compreensão dos mecanismos de montagem da comunidade em escala local; (3) e verificar a composição do traço funcional dos estratos verticais e se as estratégias adotadas pelas árvores ao longo da estratificação vertical estão relacionadas aos grupos funcionais, fenologia foliar e síndrome de dispersão. O estudo foi realizado em três parcelas permanentes de 1 ha dentro de um fragmento de Mata Atlântica. A partir da lista florística, uma árvore filogenética foi criada com base em 211 espécies, e a diversidade filogenética foi calculada, a distância média pareada entre todos os táxons da comunidade, a distância média do táxon mais próximo da comunidade, e o tamanho do efeito padronizado para essas métricas. Foram calculadas as métricas de média ponderada da comunidade, riqueza funcional, uniformidade funcional, divergência funcional e métricas de diversidade filogenética para cada parcela. Foram selecionadas quatro características foliares e duas características da madeira: área foliar (cm^2), área foliar específica (cm^2/g), teor de massa seca (g/g), densidade da madeira (mg/m^3), altura máxima (m) e espessura foliar (cm). Para avaliar os efeitos de variáveis ambientais na diversidade taxonômica, funcional e filogenética, foi utilizado um modelo linear múltiplo e um modelo linear generalizado. Analisamos a identidade funcional e a diversidade ao longo dos habitats topográficos. Para analisar a relação entre fenologia foliar e síndrome de dispersão com a estratificação vertical foi realizado o teste Qui-quadrado. Comparamos os valores médios das características para entender os padrões funcionais dentro dos grupos funcionais de fenologia foliar, síndrome de dispersão e estratos verticais. O MRT agrupou as subparcelas de toda a comunidade em três habitats de elevação: habitats topográficos inferiores, intermediários e altos. A diversidade dos habitats de elevação foi significativamente diferente; os habitats intermediários apresentaram maior diversidade do que os outros habitats, e os habitats altos apresentaram os menores valores de diversidade. Os habitats Baixos foram sempre diferentes dos outros habitats, indicando que o PD e o MPD diminuíram com o aumento da altitude. Os resultados da regressão mostraram que a riqueza foi influenciada negativamente pela elevação e SB e positivamente pela umidade do solo, areia grossa e matéria orgânica. Os gradientes topográficos apresentaram diferentes composições funcionais ao longo dos habitats, o baixo habitat foi caracterizado por características foliares aquisitivas, menor divergência funcional e maior riqueza funcional. A riqueza funcional e a divergência funcional foram as características categóricas que melhor foram explicadas; na escala local, as variáveis edáficas se mostraram mais importantes para a variação das características e diversidade funcional, sendo a textura do solo o principal direcionador. A fenologia foliar apresentou um padrão funcional de valores médios de caracteres aquisitivos-conservadores entre espécies descíduas e perenes. Os valores médios das características da síndrome de dispersão mostram que as espécies zoocóricas estão correlacionadas com características conservadoras e as espécies não-zoocóricas estão correlacionadas com características aquisitivas. Nosso estudo demonstra a importância de estudos em escala local, mostrando que habitats encontrados em gradientes locais podem afetar a diversidade de plantas nos níveis taxonômico, filogenético e funcional. Este resultado é muito importante para entender como as Florestas Tropicais Sazonais são estruturadas horizontalmente e verticalmente e os padrões de composição funcional.

Palavras-chave: Topografia, montagem de comunidades, habitats, variáveis ambientais, estratificação vertical.

SUMMARY

GENERAL INTRODUCTION

Tropical forests stand out for their high diversity of plant species, which may be the result of widespread habitat specialization and differentiation of strategies within communities (Kraft et al. 2008) mediated by a set of assembly rules, such as limited species dispersal, environmental filtering by abiotic factors, and biotic interactions that can induce competitive exclusion (Götzenberger et al. 2012; Kraft et al. 2015). One-third of the remaining forests are secondary, and most have less than 60 years of regeneration (Chazdon et al. 2016), mainly because of the negative impacts of land use change (e.g., deforestation, degradation, and fragmentation) (Lewis et al. 2015; Mitchard 2018; Ferreira et al. 2018). Although the succession process is rapid in tropical forests, when there is a source of propagules nearby (Poorter et al. 2021), changes due to land-use changes can negatively affect the diversity of tree communities in forests and, consequently, ecosystem services (Lewis et al. 2015; Walker et al. 2020). The functional ecology approach to plant communities allows us to comprehend the importance of the functional traits of each species and their role in ecosystem processes (Cornelissen et al. 2003). In this sense, this approach can also help to explain the differences in vertical and horizontal space occupation (Vale et al. 2009; Mensah et al. 2016; Ali & Yan 2017). Understanding the relationships between plant communities and abiotic factors will allow us to predict changes in ecosystem functioning (Edwards et al. 2019; Matos et al. 2020; Walker et al. 2020) and facilitate a more active role in the recovery and restoration of ecosystems (Poorter et al. 2021).

Changes in community structure can result from both biotic processes through species interactions (Kraft et al. 2015) and environmental filtering (Liu et al. 2014; Kraft et al. 2015; Bruelheide et al. 2018). Topography, soil fertility, light, and water availability influence the functional structure of communities (Ordoñez et al. 2009; Sterck et al. 2011; Bruelheide et al. 2018; Rodrigues et al. 2019; Poorter et al. 2021). Environmental gradients of resource availability play an important role in the diversity and variability of functional traits (Aguirre-Gutiérrez et al. 2019), and consequently, community structuring (Boukili & Chazdon 2017; Rodrigues et al. 2019). The variables associated with topography, such as elevation, convexity, and slope, are directly related to the gradient of soil fertility and hydrology, and consequently, to the spatial distribution of species (Allié et al. 2015; Chadwick & Asner 2016; Wang et al. 2016; Rodrigues et al. 2021). Studies on the effect of topographic habitats on tree functional traits have demonstrated divergent strategies among community species along topographic gradients (Kraft et al. 2008; Liu et al. 2014). Species richness tends to decrease with elevation and increase with convexity (Liu et al. 2014; Jucker et al. 2018). Wetter areas have higher canopy height values, whereas species with higher wood density are associated with higher and drier areas (Muscarella et al. 2020), indicating that topography can influence both structure and species composition.

The community weighted mean (CWM), which measures the average weight of a trait within the community (Garnier et al. 2004; Lavorel et al. 2007), is one of the main metrics used to understand the relationship between the functional traits of the species that make up the community and resource use strategies, as well as their influence on ecosystem processes (Ali et al. 2017; Ali & Yan 2017; Hernández-Vargas et al. 2019). This metric is directly related to the mass ratio hypothesis (Grime 1998), which proposes that traits of dominant species are primarily responsible for ecosystem functioning. Functional diversity can be defined as a set of metrics that describes the distribution of species and their abundance in the functional space (Mouchet et al. 2010), which is composed of three independent components: functional richness (Fric), functional divergence (FDiv), and functional evenness (FEve) (Villéger et al. 2008; Mouchet et al. 2010). Together, these metrics can be important for interpreting the relationships among diversity, environment, and ecosystem functioning (Villéger et al. 2008) and have been shown to be good predictors for community assembly theories, such as niche complementarity (Mouchet et al. 2010). Different studies in forest ecosystems have highlighted the importance of functional diversity in carbon stocks (Mensah et al. 2016; Ali et al. 2017), showing that both functional diversity and functional dominance can act together on ecosystem processes, but independently (Diaz et al. 2007).

Phylogenetic diversity is another metric that provides information about community structure and diversity as a function of biotic, abiotic, and stochastic processes (Swenson et al. 2007; Cavender-Bares et al. 2009). Since the functional traits of species result from evolutionary history, understanding ecology and ecosystem processes involves the interpretation of functional and phylogenetic data together (Cianciaruso et al. 2009; Mouchet et al. 2010; Reich 2014). When environmental filtering is the dominant mechanism of community assembly and there is a conservation of functional traits in the evolutionary lineage of the closest species, phylogenetic grouping is observed (Kraft et al. 2007; Cianciaruso et al. 2009); however, when competition is the main mechanism, phylogenetically close species that have conserved the trait tend to compete with each other and lead to phylogenetic dispersion (Kraft et al. 2007; Cianciaruso et al. 2009).

Together, the different attributes of biodiversity (taxonomic, functional, and phylogenetic) play a significant role in ecosystem functioning (van der Sande et al. 2018). Insight into the mechanisms that influence dominance and functional diversity, and how these effects shape tree communities at the taxonomic and phylogenetic levels, is fundamental to understanding the future of forests, especially at a local scale, which is directly related to effective preservation and management (Reich 2014; Poorter et al. 2021). Many studies have used the analysis of functional and phylogenetic data together to understand the mechanisms that influence the assembly of communities, showing that the assembly of communities is not random and that both the spatial and functional scales can be determinant in the interpretation of the mechanisms that act in the assembly of communities (Swenson et al. 2007; Cavender-Bares et al. 2009). Silva, Souza and Vitória (2021) showed that a joint analysis of different diversity metrics, including phylogenetic diversity, allows a better understanding of the relationships between the environment and functional ecology of current plant communities, showing functional dominance. However, few studies have analyzed the contribution of different diversity metrics (taxonomic, functional, and phylogenetic) and functional strategies on a local scale topography.

In this context, this study aimed to evaluate how local-scale topography (edaphic-topographic gradient) influences and shapes the diversity (taxonomic, functional, and phylogenetic) and functional traits of the tree community in a secondary fragment of the Atlantic Forest and verify the patterns of functional composition of the vertical stratification. Thus, our main objectives were: (1) to understand how topography can influence taxonomic and phylogenetic diversity and which variables most influence community assembly at the local scale; (2) to understand how the topographic gradient shapes the functional identity of species, and how they contribute to understanding the mechanisms of community assembly at a local scale; and (3) to verify the functional trait composition of the vertical strata and whether strategies adopted by trees throughout vertical stratification are related to functional groups, leaf phenology, and dispersal syndrome.

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CHAPTER 1 – PHYLOGENETIC DIVERSITY AND STRUCTURE ALONG A LOCAL-SCALE TOPOGRAPHY IN A SEASONAL TROPICAL FOREST

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ABSTRACT

Environmental gradients are good predictors of species distribution and can contribute to understanding how and which environmental variables act on community formation of habitats at local scales topography. Phylogenetic diversity can provide information on the processes, whether biotic, abiotic, or stochastic, that are acting on community structure. The aim of this study was to verify whether we can observe differences in diversity structure, taxonomic and phylogenetic, and which environmental variables and how it influences the taxonomic and phylogenetic diversity metrics at a local scale topography. The three permanent plots are in a secondary fragment of Atlantic Forest, classified as Montane Semideciduous Seasonal Forest. The habitats were classified by multivariate regression tree analyses. We estimated species richness for habitats using the first Hill number (q=0, q=1, q=2). From the floristic list, a phylogenetic tree was created based on 211 species and calculated the phylogenetic diversity, the average of pairwise distance between all taxa in the community, the average distance of the closest taxon in the community and the standardized effect size for this metrics. To evaluate the effects of environmental variables on species richness and phylogenetic metrics, we performed a multiple linear model and generalized linear. The results showed that fertility soil shows a gradient between intermediate habitats to high and low habitats. The species richness was significantly different between high habitats and intermediate habitats. The diversity of the elevation habitats was significantly different, the Intermediate habitats show higher diversity than the other habitats, and the High habitats has the lowest diversity values. The local scale gradient effects phylogenetic diversity, with significant differences in PD, MPD, MNTD and ses.MPD. The Low habitats were always different to the other habitats, showing that PD and MPD decreases with increasing altitude. While taxonomic diversity is higher in areas of higher fertility, areas of lower fertility have higher phylogenetic diversity and greater distances between taxa. The regression result showed that richness is negatively influenced by elevation and SB, and positively by soil moisture, Coarse sand, and organic matter. All phylogenetic diversity metrics were negatively influenced by the sum of bases. The model with ses.MNTD was not significant. As expected, water availability is related to an increase in richness and diversity. The edaphic-topographic gradient seems to act on community assembly and diversity metrics may be responding differently to fertility gradients at a small elevational scale. While the results showed that the increase of fertility in this environment worked as a filter and could cause a decrease in richness and consequently the selection of closer species. The results found emphasize the importance of studies of community assembly on a small scale.

Keywords: multivariate regression tree analysis, Atlantic forests, environmental variables

INTRODUCTION

Understand the processes that influence the assembly of communities is one of the main searches in ecology. The high diversity of plant species in tropical forests may be a result of widespread habitat specialization and differentiation of strategies within communities (Kraft et al. 2008). Plants reflect ecological differences in the process of ecosystem evolution and phylogenetic diversity and also can provide information about of community structure as a function of biotic, abiotic, and stochastic processes (Swenson et al. 2007; Cavender-Bares et al. 2009). Thus, environmental gradients and resource availability play an important role in community structuring (Boukili and Chazdon, 2017). In the sense, phylogenetic diversity can help comprehend the ecological processes that influence the assembly of communities (Cavender-Bares et al. 2009). Recognizing differences in assemblage at a local scale is critical for conservation (Saraiva et al. 2018; Bose et al. 2019), restoration planning, and to anticipate potential changes caused by climate change (Poorter et al. 2021).

Environmental gradients can be useful predictors to access species distribution (Jucker et al. 2018; Muscarella et al. 2020) and can contribute to understanding how the environment is influencing community assemblages at local scales (Allié et al. 2015; Rodrigues, Villa, Ali, et al. 2019). One important environmental factor is the topographic gradient (Liu et al., 2014; Rodrigues et al., 2019b; Wang et al., 2016). The variables associated with topography, not only define different topographic habitats (Liu et al. 2014; Rodrigues, Villa, & Neri 2019), but also, suggesting that community structure may be explained by these factors (Allié et al. 2015; Chadwick & Asner 2016; Rodrigues, Villa, Ali, et al. 2019). These variables that make up the topographic gradient are related to microhabitat formation, due to their indirect effects on soil moisture, temperature, light availability, and soil fertility (Comita & Engelbrecht 2009; Blundo et al. 2015) and act to explain species distribution (Muscarella et al. 2020). The patterns that drive the community structure are influenced by the spatial scale. For example, the climate has a strong influence in the community structure on a regional and global scale, but in a local scale the patterns result of ecological process in habitats, for example biological interactions (Webb et al. 2002). The use of phylogenetic metrics has a higher potential to understand how community assembly is drive by these ecological interactions (Webb 2000). Thus, the interaction between local environmental variables and evolutionary history is essential to understand the diversity patterns in tropical forest (Laliberté et al. 2014).

Using different metrics of distance and phylogenetic diversity, as Faith phylogenetic diversity (PD), mean pairwise distance between all species (MPD), and mean pairwise distance the closest relatives (MNTD), it is possibly understand which ecological process influences the community assembly (Webb et al. 2002; Mazel et al. 2016). The ecological process that has best explain the community assembly are deterministic and stochastic theories (Swenson et al. 2007). Deterministic theory highlights environmental filtering and competition between species while stochastic theory emphasizes neutral processes and dispersal limitation as determining factors for the assembly of plant communities (Hubbell 2001; Swenson et al. 2007). When environmental filtering is the dominant mechanism on community assembly and there is a conservation of functional traits in the evolutionary lineage, a phylogenetic clustering is observed, i.e., species are more closely related evolutionarily (Cianciaruso et al., 2009; Kraft et al., 2007; Webb et al., 2002). However, when competition is the main mechanism, phylogenetically close species that have conserved the trait tend to compete with each other, leadings to a phylogenetic overdispersion (Webb et al. 2002; Kraft et al. 2007; Cianciaruso et al. 2009).

At local scale the plant diversity result from an environmental filtering of the regional richness (Laliberté et al. 2014), showing phylogenetic clustering (Okuno et al. 2022). In this scale the habitat heterogeneity is important to niche differentiation (Baldeck et al. 2016; Bose et al. 2019). In a local scale the topographic variables lead to high heterogeneity of soil and the nutrients disponible (Baldeck et al. 2016; Peguero et al. 2023). The soil fertility gradient tends to be influenced by topographic variables, such as elevation and convexity, which influence species distribution at a local scale (Jucker et al. 2018; Rodrigues, Villa, Ali, et al. 2019). The increase in the altitude tend to decrease the soil fertility (Rodrigues et al. 2021a; Morelli et al. 2021) and the fertility tend to increase the phylogenetic diversity (Morelli et al. 2021), indicating that the niche differentiation at local scale effects on phylogenetic structure (Baldeck et al. 2016).

In this context, this research sought to answer the following questions: (i) How the local scale elevation gradient influence soil fertility and texture? (ii) How diversity structure change in a local scale elevation gradient? (iii) Which environmental variables effects taxonomic and phylogenetic structure in a local scale elevation gradient? We hypothesized that: 1) The elevation gradient is expected to have a negative effect on soil fertility and soil moisture. Lower elevation areas tend to have higher soil fertility and soil moisture, while higher elevation areas tend to have lower fertility and soil moisture; 2) The structure of diversity is expected to be affected by soil fertility and moisture gradient, whereby taxonomic and phylogenetic diversity will show a negative correlation with elevation; 3) The edaphic-topographic gradient is expected to influence diversity at a local scale, areas associated with higher fertility and moisture are expected to have higher taxonomic and phylogenetic diversity, and areas with lower fertility are expected to have lower taxonomic and phylogenetic diversity.

MATERIAL AND METHODS

Study site

The study was conducted in a secondary forest, the "Mata da Biologia", in the municipality of Viçosa (20°45'14 "S, 42°51'53 "W) in the state of Minas Gerais, southeastern Brazil (Fig. S1). It is classified as Montane Semideciduous Seasonal Forest (Veloso et al. 1991), the fragment has approximately 75 ha (Paula et al. 2002). The area was clear-cut in the early 1920s (Lopes et al. 2002; Paula et al. 2002) and subsequently used for shade coffee plantations until 1926 (Paula et al. 2002). Since then, the area has been abandoned, left to regenerate naturally (Paula et al. 2002), and is in an intermediate stage of succession (Lopes et al., 2002; Paula et al. 2003).

Located in a region of mountainous and strongly undulated relief, the fragment lies between 620 and 820 m, and presents a soil gradient between Red-Yellow Latosols, at the top of the highest regions and on the steepest slopes, and nutrient-rich Cambisols in the valleys (Ferreira-Júnior et al. 2007). According to the Köppen classification, the region's climate is characterized as Humid Subtropical (Cwa) with hot summers and dry winters, mainly between May and August (Alvares et al. 2013), with an average annual temperature of approximately 21°C and average annual precipitation of 1250 mm (Avila-Diaz et al. 2020).

Sample design

Three 1-ha permanent plots were established in the forest fragment with contrasting topographical conditions. Each permanent plot was subdivided into 100 subplots of 10 x 10 m to better capture topography effect on the local scale. In each plot, all living arboreal individuals with a circumference at breast height (CAP) equal to or greater than 10 cm were recorded and measured. All individuals were identified, and species nomenclature follows the Angiosperm Phylogeny Group IV (APG IV 2016) classification system.

Topographic variables

For each subplot, 10 x 10 m, three topographic variables (elevation, slope, and convexity) were measured and calculated using a total station with the assistance of a surveying engineer. Elevation was calculated using the average elevation value of each of the four corners of the plot. The slope (°) corresponds to the average angular deviation from the horizontal of each of the four triangular planes, formed by connecting three of its corners. Convexity was determined by subtracting the elevation of the plot center from the average elevation of the eight surrounding plots (Wang et al. 2016).

Edaphic variables

For soil characterization, the methodology presented by Ferreira-Júnior (2017) was followed. The soil sampling was made systematically at three points at a depth of 0-10 cm. Afterwards, they were homogenized to obtain one composite sample per subplot. The samples were analyzed in the Soil Laboratory of the Soil Department of the Federal University of Viçosa. The physical-chemical attributes analyzed were the following: pH (potential hydrogen), Ca (calcium), Mg (magnesium), K (potassium), Na (sodium), P (phosphorus), pAl (potential acidity), MO (organic matter), SB (base sum), m(saturation percentage by aluminum), V (saturation percentage by exchange), t(Cation Exchange Capacity), fine sand, coarse sand, clay, silt content, soil density and CGA (soil moisture) will be analyzed according to the methodology proposed by EMBRAPA (2011).

Phylogenetic metrics

A phylogenetic tree was created based on the species list of the three sampled areas, with the help of the package "V.PhyloMaker" (Jin & Qian 2019) in the R program. The package uses the "GBOTB.extended.tre" mega-tree, which contains 74,533 species of vascular plants (Jin & Qian 2019). We use "scenario 3" to create the phylogenetic tree, as it has demonstrated robust results for ecological studies at the level of environmental gradients (Qian & Jin 2016). Based on the generated tree we calculated for each subplot the phylogenetic diversity (PD - the sum of the lengths of all the branches of the taxa that are members of the community) (Faith 1992), as well as the average pairwise distance between all taxa in the community (MPD), the average distance of the closest taxon in the community (MNTD) and the standardized effect size for PD, MPD, and

MNTD (ses.PD, ses.MPD, and ses.MNTD). We calculated these phylogenetics metrics using the “picante” package (Kembel et al. 2010).

Statistical analyses

We performed a Multiple Regression Tree analysis (MRT; De’ath 2002) to classify the subplots (10 x 10 m) in different categories based on species similarity and topographic variables (elevation, slope, and convexity). MRT can be defined as a constrained cluster analysis that seeks to relate species composition to environmental data (De’ath 2002) and can be used to identify the variables that most influence species grouping (Larsen & Speckman 2004). With the results of the MRT classification, we grouped the subplots into different topographic habitats (Wang et al. 2016). The MRT analysis was performed using the function “mvpart” from the ‘mvpart’ package (De’ath 2002).

We used Principal component analysis (PCA) to evaluate possible correlations between topography habitats and soil variables. PCA allows both simplification and verification of the most important variables of the data (Abdi & Williams 2010). The PCA was performed using the "FactoMineR" package (Husson et al. 2017).

We estimated diversity for each habitat by plotting rarefaction and extrapolation curves that considered the number of sampled individuals and the number of sample units. We estimated species richness using the first Hill number ($q = 0$), species diversity using the exponential of Shannon entropy ($q = 1$), and the inverse of Simpson’s concentration index ($q=2$; Chao *et al.* 2014). We used the package *iNEXT* (Hsieh et al. 2016) to calculate rarefaction and extrapolation curves based on the number of sampled individuals and the number of sample units. We estimated 95% confidence intervals through 100 bootstrap replications. Non-overlapping confidence intervals indicated significantly different species numbers with $p < 0.05$ (Colwell et al. 2012; Rodrigues et al. 2021b).

To verify differences of phylogenetic metrics between topographic habitats were tested the metrics for normality using the Shapiro test. And then, parametric data was tested with the ANOVA test for observe if the mean difference between habitats, and when the result was significant, we applied the T test. The non-parametric data was test for differents mean using the Kruskal-Wallis test and when the result was significant, we applied the Wilcoxon-test. To attest than the mean values of ses.Pd, ses.MPD, and ses.MNTD wass different of zero, we performed the one-sample T test.

To evaluate the effects of environmental variables on phylogenetic metrics (PD, ses.PD, ses.MPD, and ses.MNTD), we performed a multiple linear model (LM) and generalized linear model, family poisson for evaluate the effect of environmental variables on richness. Variables were selected to avoid collinearity between variables (cor < 0.7) using the function "ggcorr" from "GGally" package (Schloerke et al. 2021), and multicollonearity (VIF < 5) using the "car" package (Fox & Weisberg 2019). The topographic variables (elevation and slope) and edaphic variables (MO, Sandc, soil density, CGA and SB) were used as explanatory variable in the final model to verify the effect on the variables response (Richness, PD, ses.PD, ses.MPD, and ses.MNTD). The LMs were performed using the "lme4" package (Bates et al. 2015). We used "q-qplot" to validate the model's assumptions from "car" package (Fox & Weisberg 2019). The graphics were performed using the "GGplot2" and "sjPlot" package (Wickham 2016; Lüdecke 2023). All analyses were performed in R environment (R Core Team 2023).

RESULTS

Taxonomic and phylogenetic structure at local scale topography

A total of 6536 individuals (DHB ≥ 10 cm) were sampled in three ha sample plots. A total of 211 species were identified, 188 at the species level, 20 at the genus level, and 2 at the family level. These species belong to 124 genera and 44 families (Fig.S2).

The MRT grouped the subplots of the whole community into three habitats, where the elevation was the main cut-off variable (Fig.S2). Habitat L (low topographic habitat) corresponds to 87 subplots with an elevation below 694.7 meters, Habitat I (intermediate topographic habitat - I), corresponds to 139 subplots with an elevation between 694.7 and 715.1, and Habitat H (higher topographic habitat – H) corresponds to 74 subplots with elevation above 715.1 m. The first node (breakpoint= 674.7 m) explains 7% of standardized species variance and the second node (breakpoint = 715.1 m) explains 3% of standardized species variance. The nodes explained 10.4% of the total standardized species variance.

The PCA with topography and soil texture variables explained 70.6 % (PCA1=57.9%; PCA2=12.7%) of the subplot's variances, showing a soil moisture gradient between higher topographic habitats to lower topographic habitats (Fig. 1). The PCA with topography and soil fertility variables explained 71.6% (PCA1=57.9%; PCA2=12.7%) of the variance (Fig. 2). This analysis showed a fertility gradient between intermediate habitats and the others, with a positive correlation with SB, V, and pH with de axis 1.

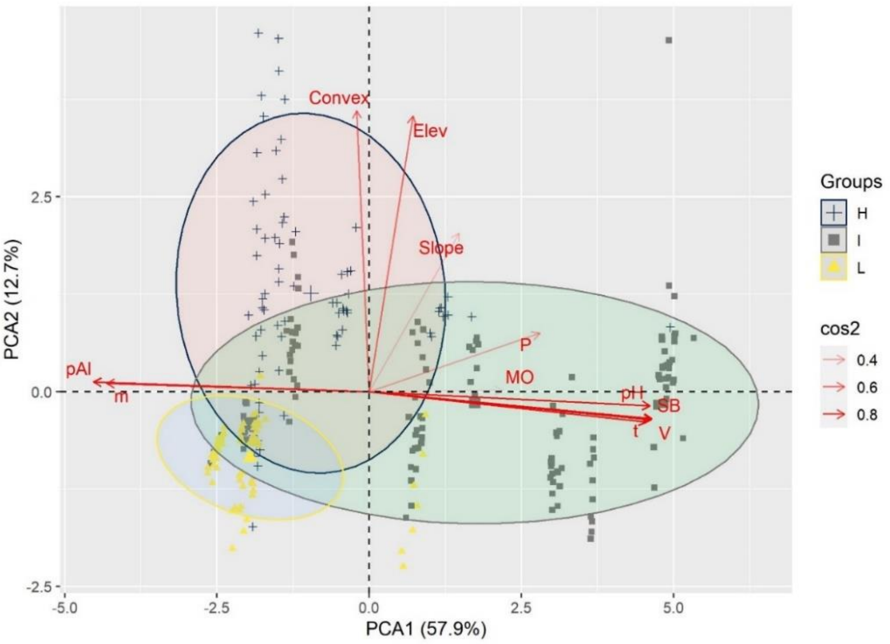

Fig. 1 - Principal correspondence analysis (PCA) of relations between the habitat's subplots and topographic variables, and physical soil attributes. The topographic variables area elevation (Elev), slope, and convexity (Convex). The physical soil variables are fine sand, coarse sand, clay, silt content, soil density and soil moisture (CGA). The evaluated habitats were Higher topographic habitat (H; blue plus); intermediate topographic habitat (I; grey square); and low topographic habitat (L; yellow triangle).

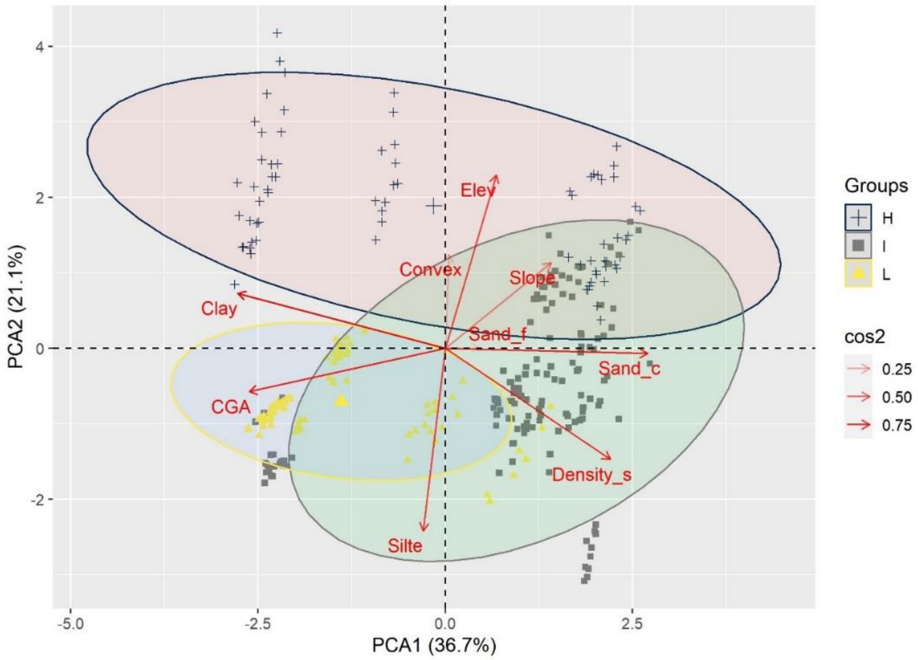

Fig.2- Principal correspondence analysis (PCA) of relations between the habitat's subplots and topographic variables, and chemical soil attributes. The topographic variables area elevation (Elev), slope, and convexity (Convex). The chemical soil variables are pH (hydrogen potential), MO (organic matter), SB (base sum), m (saturation percentage by aluminum), P (phosphorus), pAl (potential acidity), V (saturation percentage by exchange), t(Cation Exchange Capacity). The evaluated habitats were Higher topographic habitat (H; blue plus); intermediate topographic habitat (I; grey square); and low topographic habitat (L; yellow triangle).

The species richness was not significantly different between topographic habitats (q=0), while the diversity index showed differences between habitats (q=1 and q=2). The Intermediate habitats showed higher diversity than the other habitats, and the Higher habitats had the lowest diversity values (Fig. 3).

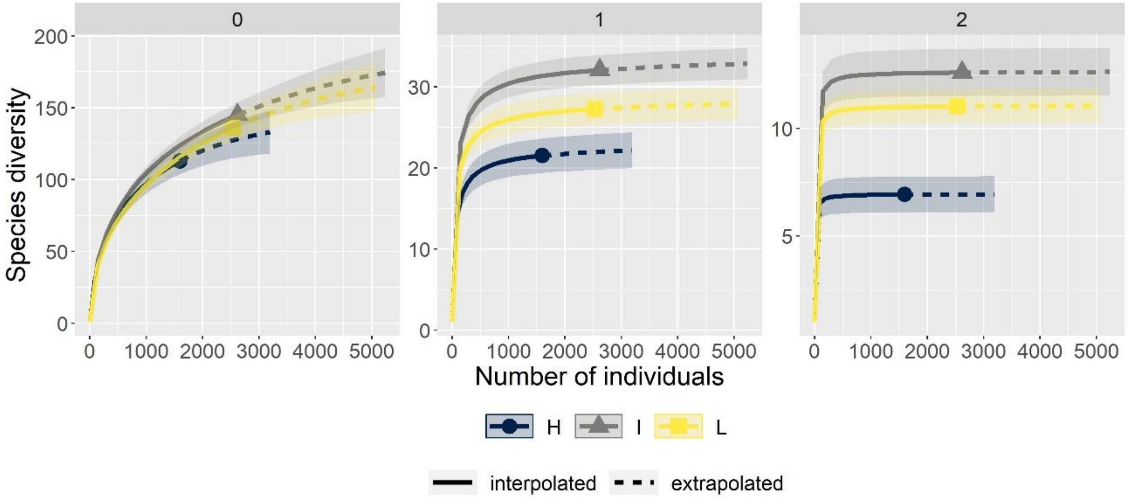

Fig. 3 - Rarefaction curves based on the number of individuals (solid lines); extrapolation curves (dashed lines) of species richnes (0) species diversity using the exponential of Shannon entropy (1), and the inverse of Simpson's concentration index (2) in the three topographic habitats. Higher topographic habitat (H; blue); intermediate topographic habitat (I; grey); and low topographic habitat (L; yellow). The rarefaction and extrapolation curves represent mean values, followed by coloured bands that represent standard deviation with 95% confidence intervals.

The local scale gradient effects phylogenetic diversity, with significant differences in PD, MPD, MNTD and ses.MPD (Fig. 4). The ses.PD main values don't show significant differences between habitats neither the zero. The habitat Low were always different to the other habitats, showing that PD decreases with increasing altitude (L=1232 Ma; I= 930 Ma; H= 926 Ma). The MPD shows that the species are more closely related at higher and intermediate topographic habitats (L=239 Ma; I=234 Ma; H=235 Ma). The ses.MPD analyses of the intermediate topographic habitats were significantly different from zero, indicating phylogenetic clustering, while in lower topographic habitats the mean was positive, indicating overdispersion (Fig. 4; Table 1). The MNTD shows that the close species are more closely related at low topographic habitat (L= 153 Ma; I= 171 Ma; H= 174 Ma). Although ses.MNTD did not show significant differences between habitats, the mean of higher habitats indicates phylogenetic overdispersion and the other habitats the mean values don't shows differentiation of zero (Fig. 4; Table 1).

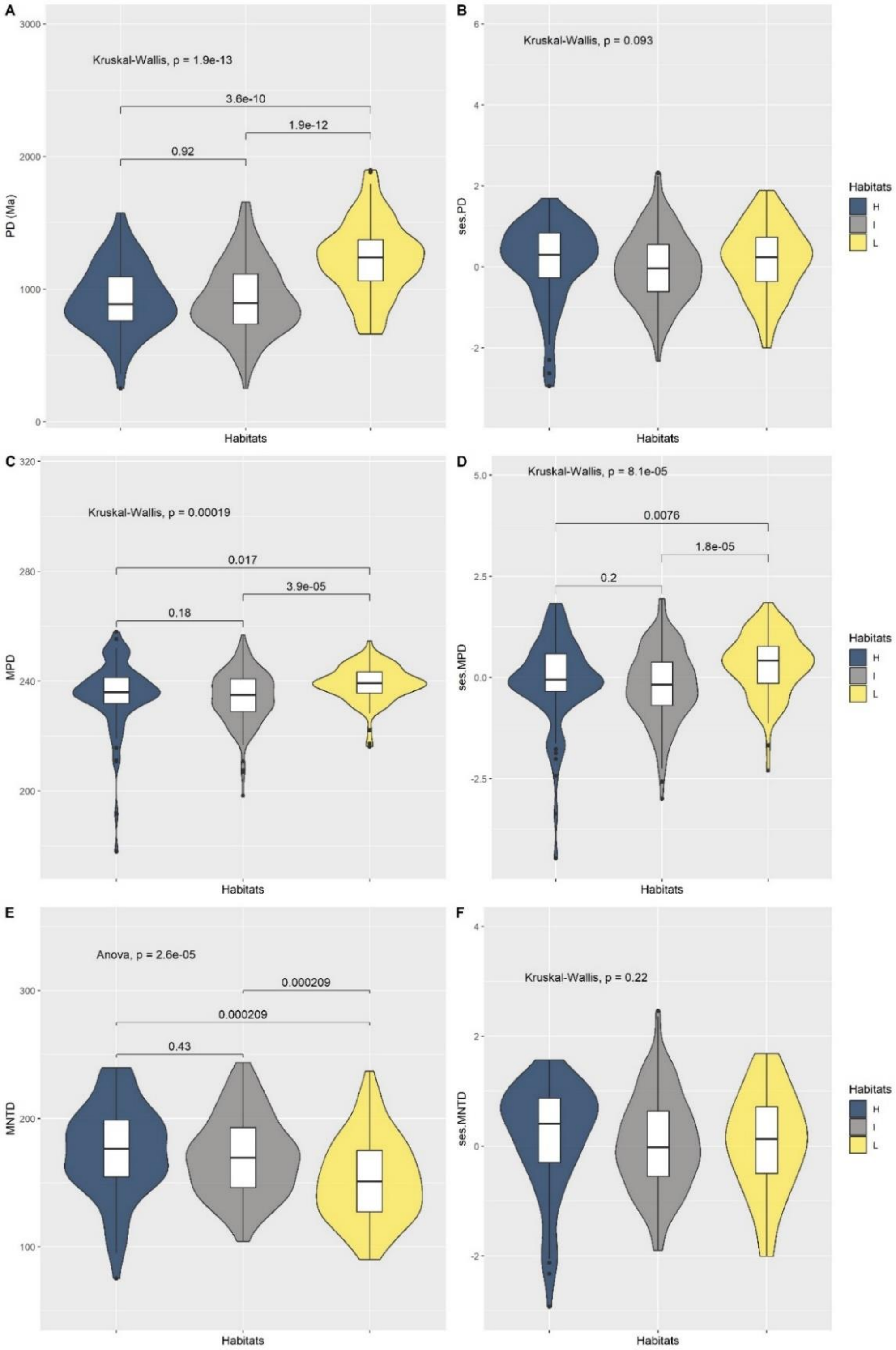

Fig. 4 - Variation in the phylogenetic diversity (PD; A), as the average pairwise distance between all taxa in the community (MPD; C), the average distance of the closest taxon in the community (MNTD; E) and the standardized effect size for PD (ses.PD; B), MPD (ses.MPD; D), and MNTD (ses.MNTD; F) in the three topographic habitats. The evaluated habitats were Higher topographic habitat (H; blue); intermediate topographic habitat (I; grey); and low topographic habitat (L; yellow).

Table 1 – T test for each mean value of ses.PD, ses.MPD and ses.MNTD for each topographic habitat to differentiate from zero.

	ses.PD		**ses.MPD**		**ses.MNTD**	
HABITAT	Mean	*p*	Mean	*p*	Mean	*p*
High	0.106	0.053	-0.095	0.855	0.154	**0.024**
Intermediate	-0.015	0.840	-0.188	**0.016**	0.053	0.471
Low	0.172	0.066	0.317	**0.0002**	0.061	0.533

Significant results, mean different of zero, are indicated in bold ($p < 0.05$).

The effect of a local topographic gradient on taxonomic and phylogenetic diversity

The regression showed that species richness is negatively influenced by elevation and SB, and positively by CGA, Coarse sand and organic matter (AIC=1488.7; Fig. 5A). The model with PD was significant and explained 35% of the variation in phylogenetic diversity (F=23.66, p=<2.2^{-16}; Fig.5B). In which soil moisture, coarse sand and organic matter was positively correlated and base sum the elevation negatively influences PD at local topographic scale. The variation of ses.PD was also influenced mainly by soil variables, positively by soil density and negatively by base sum (Fig.5C). Although the model was significant (F= 2.51, p=0.02) these variables only explained 4% of the variation in ses.PD. We found that ses.MPD was positively influenced by soil density, moisture, and coarse sand, and negatively by base sum. the model was significant (F=5.80, p=2.66^{-06}) and explained 10% of the variation in ses.MPD (Fig.5D). The model with ses.MNTD was not significant (F1.16, p=0.32).

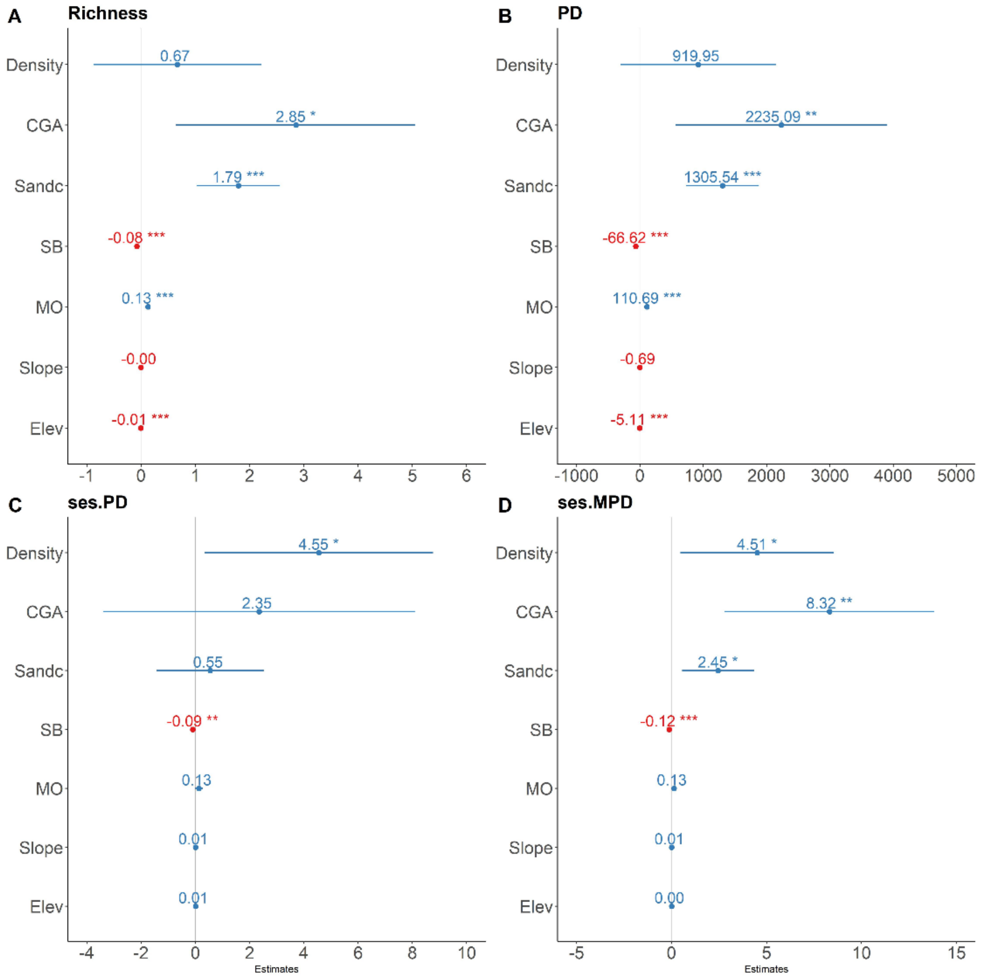

Fig. 5 - Effects of elevation (Elev), slope, MO (organic matter), SB (base sum), coarse sand, soil density, and soil moisture (CGA) of species richness (A) phylogenetic diversity (PD; A), and the standardized effect size for PD (ses.PD; C), MPD (ses.MPD; D) in local scale elevation gradient in a Montane Semideciduous Seasonal Forest.

DISCUSSION

The results emphasize the importance of studying communities on a local scale, both at the taxonomic and phylogenetic levels. Topography and differences in soil characteristics affect community assembly so that habitats show differences in taxonomic and phylogenetic diversity. These results suggest that even at a local topographic scale, we can find differences in the edaphic factors that act on the community, shaping the taxonomic and phylogenetic diversity of the tree communities.

Taxonomic and phylogenetic structure at local scale topography

The results support the hypotheses that the taxonomic structure of forest is affect by the local scale topography (Liu et al. 2014; Wang et al. 2016; Rodrigues, Villa, & Neri 2019). The elevation seems to be the important drive of composition and richness at local scale (Liu et al. 2014; Wang et al. 2016; Jucker et al. 2018). Others study shows an elevation patterns of differentiation of composition and decrease of species richness along the elevation gradient, with the lower topographic habitats showing more richness and the higher topographic habitats with lower species richness (Liu et al. 2014; Jucker et al. 2018; Rodrigues, Villa, Ali, et al. 2019).

Our results showed that elevational habitats exhibit significant differences in local scale of phylogenetic structures. The results sustain that local scale variations can promote phylogenetics diversity (Kembel & Hubbell 2006; Morelli et al. 2021; Campos et al. 2022), showing that phylogenetic diversity and structure could present a altitudinal patterns at local scale topographic gradient (Kembel & Hubbell 2006; Morelli et al. 2021), the increase of altitude tend to decrease PD (Morelli et al. 2021). Lower elevation areas showed higher phylogenetic diversity and higher distances between species and lower distances between species of closely related taxa (Morelli et al. 2021). These results demonstrate that ecological processes influence phylogenetic structure at a local topographic gradient, in higher habitat tended to be terminal phylogenetic overdispersed, intermediate habitats the species that occurs together tended to be tree-wide phylogenetic clustering, and lower habitats the species exhibited tree-wide overdispersion (Kembel & Hubbell 2006; Mazel et al. 2016). Phylogenetic dispersal metrics tend to represent a temporal scale, MPD tends to be more sensitive and representative of the base of the tree, and MNTD is more representative of the final portion of the tree (Mazel et al. 2016; Webb et al. 2002), indicating that there may be homogenization and/or niche differentiation along the temporal scale and topographic gradient.

The effect of a local topographic gradient on taxonomic and phylogenetic diversity

Our results showed that taxonomic diversity was positively correlated with higher soil fertility habitats, but this did not follow the expected gradient with elevation (Rodrigues, Villa, Ali, et al. 2019). Topographic variables tend to influence the edaphic gradient, both in terms of soil moisture availability and fertility (Allié et al. 2015; Chadwick and Asner 2016; Rodrigues et al. 2021b). Taxonomic diversity seems to respond better to local variation in soil fertility, influenced by topographic variation, which, at a local scale, plays an important role in habitat differentiation (Rodrigues et al. 2019; Liu et al. 2014; Rodrigues et al. 2021b). Phylogenetic diversity responds to elevation and moisture gradients, with lower elevations and higher surface soil moisture showing higher phylogenetic diversity (Morelli et al. 2021). These patterns indicate the important role of environmental variability in taxonomy (Rodrigues et al. 2019) and phylogenetic community structure (Baldeck et al. 2016).

The results showed that soil fertility had a negative effect on species richness and phylogenetic diversity, contradicting our hypothesis. These results are opposite to those expected for soil fertility from both the effect of elevation on the fertility gradient (Rodrigues et al. 2021b) and the positive effect on taxonomic richness and phylogenetic diversity (Morelli et al. 2021; Peguero et al. 2023). Increased productivity (soil fertility) is not always associated with a continuous increase in richness (Godberg and Miller, 1990), in some ecosystems, increased fertility can lead to a competitive exclusion (Laliberté et al. 2014).

The terminal phylogenetic structure (ses.MNTD) was less sensitive to the topographic and edaphic gradient, whereas species richness, ses.PD, and ses.MPD were significantly influenced by environmental variables. The phylogenetic structure among habitats is mainly related to ses.MPD and is correlated with the humidity gradient; wetter habitats are related to more distant species, phylogenetic overdispersion, while drier habitats are related to closer species, phylogenetic clustering. The results shows that moisture gradient appears to be one of the main factors influencing the phylogenetic structure of habitats. The texture soil could be important to the variation of phylogenetic diversity metrics (Villa et al. 2020). Even at a local topographic scale, moisture differentiation is significant (Daws et al. 2002), and is important mainly during drought periods, influencing floristic patterns (Daws et al. 2002; Oliveira-Filho and Fontes, 2000). Hydrological heterogeneity can lead plants to specialize in habitats (Daws et al. 2002), which demonstrates the influence of habitats heterogeneity on community phylogenetic structure, even at a local scale (Baldeck et al. 2016; Morelli et al. 2021).

CONCLUSION

We found that local scale topography is important for the variation in the taxonomic and phylogenetic diversity and structure at a local scale. The results reinforce the importance of topographic variables on the fertility and moisture availability, and for the differentiation of habitats in a local scale. This result shows the importance of research in a local scale, both topographic and edaphic gradient to determine how the different habitats effects on taxonomic composition and phylogenetic community structure.

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SUPPLEMENTARY DATA

Fig. S1 - Geographic location of the study area and the permanent plots in the Mata da Biologia in Viçosa, state of Minas Gerais, Brazil.

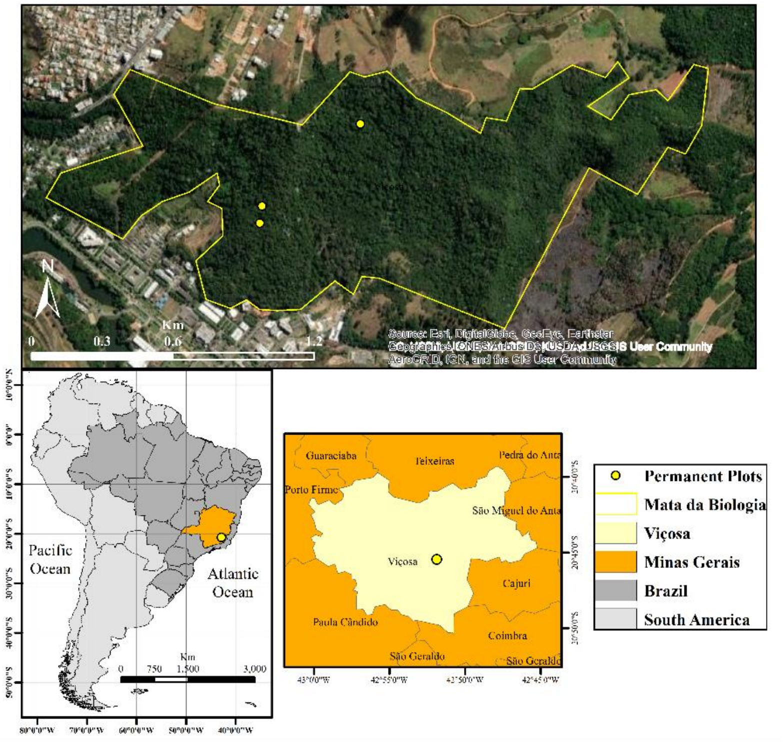


Table S1 **-** List of species used in the phylogenetic analysis.

Species	**Family**
Abarema langsdorffii (Benth.) Barneby & J.W.Grimes	Fabaceae
Albizia polycephala (Benth.) Killip ex Record	Fabaceae
Alchornea glandulosa Poepp. & Endl.	Euphorbiaceae
Alchornea triplinervia (Spreng.) Müll.Arg.	Euphorbiaceae
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	Sapindaceae
Allophylus racemosus Sw.	Sapindaceae
Allophylus semidentatus (Miq.) Radlk.	Sapindaceae
Amaioua guianensis Aubl.	Rubiaceae
Anadenanthera colubrina (Vell.) Brenan	Fabaceae
Anadenanthera peregrina (L.) Speg.	Fabaceae
Andira fraxinifolia Benth.	Fabaceae
Andira inermis (W.Wright) DC.	Fabaceae
Andira sp	Fabaceae
Aniba firmula (Nees & Mart.) Mez	Lauraceae
Annona cacans Warm.	Annonaceae
Annona dolabripetala Raddi	Annonaceae
Annona sp	Annonaceae
Annona sylvatica A.St.-Hil.	Annonaceae
Aparisthmium cordatum (A.Juss.) Baill.	Euphorbiaceae
Aparisthmium sp	Euphorbiaceae
Apuleia leiocarpa (Vogel) J.F.Macbr.	Fabaceae
Aspidosperma olivaceum Müll.Arg.	Apocynaceae
Aspidosperma sp	Apocynaceae
Astronium fraxinifolium Schott	Anacardiaceae
Astronium glaziovii Mattick	Anacardiaceae
Attalea dubia (Mart.) Burret	Arecaceae
Bathysa nicholsonii K.Schum.	Rubiaceae
Bauhinia forficata Link	Fabaceae
Brosimum guianense (Aubl.) Huber	Moraceae
Brunfelsia uniflora (Pohl) D.Don	Solanaceae
Cabralea canjerana (Vell.) Mart.	Meliaceae
Calyptranthes sp	Myrtaceae
Campomanesia xanthocarpa (Mart.) O.Berg	Myrtaceae
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae
Cariniana legalis (Mart.) Kuntze	Lecythidaceae
Cariniana sp	Lecythidaceae
Carpotroche brasiliensis (Raddi) A Gray	Achariaceae
Casearia arborea (Rich.) Urb.	Salicaceae
Casearia decandra Jacq.	Salicaceae
Casearia gossypiosperma Briq.	Salicaceae
Casearia lasiophylla Eichler	Salicaceae
Casearia mariquitensis Kunth	Salicaceae

Casearia obliqua Spreng.	Salicaceae
Casearia sp	Salicaceae
Casearia sylvestris Sw.	Salicaceae
Casearia ulmifolia Vahl ex Vent.	Salicaceae
Cassia ferruginea (Schrad.) Schrad. ex DC.	Fabaceae
Cecropia glaziovii Snethl.	Urticaceae
Cedrela fissilis Vell.	Meliaceae
Ceiba speciosa (A.St.-Hil.) Ravenna	Malvaceae
Chomelia brasiliana A.Rich.	Rubiaceae
Chrysophyllum flexuosum Mart.	Sapotaceae
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Sapotaceae
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Sapotaceae
Citronella paniculata (Mart.) R.A.Howard	Cardiopteridaceae
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	Moraceae
Coffea sp	Rubiaceae
Copaifera langsdorffii Desf.	Fabaceae
Varronia bullata L.	Boraginaceae
Cordia sellowiana Cham.	Boraginaceae
Cordia silvestris Fresen.	Boraginaceae
Cordia taguahyensis Vell.	Boraginaceae
Coutarea hexandra (Jacq.) K.Schum.	Rubiaceae
Coutarea sp	Rubiaceae
Croton floribundus Spreng.	Euphorbiaceae
Croton urucurana Baill.	Euphorbiaceae
Cryptocarya moschata Nees & Mart.	Lauraceae
Cryptocarya sp	Lauraceae
Cupania ludowigii Somner & Ferrucci	Sapindaceae
Cupania platycarpa Radlk.	Sapindaceae
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae
Dalbergia nigra (Vell.) Allemão ex Benth.	Fabaceae
Didymopanax morototoni (Aubl.) Decne. & Planch.	Araliaceae
Elachyptera festiva (Miers) A.C. Sm.	Celastraceae
Endlicheria paniculata (Spreng.) J.F.Macbr.	Lauraceae
Eriotheca candolleana (K.Schum.) A.Robyns	Malvaceae
Erythroxylum pelleterianum A.St.-Hil.	Erythroxylaceae
Eugenia florida DC.	Myrtaceae
Eugenia leptoclada O.Berg	Myrtaceae
Eugenia ligustrina (Sw.) Willd.	Myrtaceae
Eugenia sp	Myrtaceae
Eugenia stictopetala Mart. ex DC.	Myrtaceae
Eugenia uniflora L.	Myrtaceae
Euterpe edulis Mart.	Arecaceae
Ficus enormis Mart. ex Miq.	Moraceae
Garcinia gardneriana (Planch. & Triana) Zappi	Clusiaceae
Genipa infundibuliformis Zappi & Semir	Rubiaceae

Guapira hirsuta (Choisy) Lundell	Nyctaginaceae
Guapira opposita (Vell.) Reitz	Nyctaginaceae
Guarea kunthiana A.Juss.	Meliaceae
Guarea macrophylla Vahl	Meliaceae
Guarea pendula R.S.Ramalho, A.L. Pinheiro & T.D.Penn.	Meliaceae
Guatteria australis A.St.-Hil.	Annonaceae
Guatteria sp	Annonaceae
Guatteria villosissima A.St.-Hil.	Annonaceae
Guettarda scabra (L.) Vent.	Rubiaceae
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Bignoniaceae
Himatanthus phagedaenicus (Mart.) Woodson	Apocynaceae
Hirtella triandra Sw.	Chrysobalanaceae
Inga marginata Willd.	Fabaceae
Inga striata Benth.	Fabaceae
Inga vera subsp. *affinis* (DC.) T.D.Penn.	Fabaceae
Ixora gardneriana Benth.	Rubiaceae
Ixora venulosa Benth.	Rubiaceae
Jacaranda macrantha Cham.	Bignoniaceae
Jacaranda micrantha Cham.	Bignoniaceae
Lacistema pubescens Mart.	Lacistemataceae
Licania spicata Hook.f.	Chrysobalanaceae
Luehea grandiflora Mart.	Malvaceae
Luehea paniculata Mart.	Malvaceae
Mabea fistulifera Mart.	Euphorbiaceae
Machaerium aculeatum Raddi	Fabaceae
Machaerium acutifolium Vogel	Fabaceae
Machaerium brasiliense Vogel	Fabaceae
Machaerium floridum (Mart. ex Benth.) Ducke	Fabaceae
Machaerium nyctitans (Vell.) Benth.	Fabaceae
Machaerium oblongifolium Vogel	Fabaceae
Machaerium sp	Fabaceae
Machaerium stipitatum Vogel	Fabaceae
Machaerium villosum Vogel	Fabaceae
Maclura tinctoria (L.) D.Don ex Steud.	Moraceae
Maprounea guianensis Aubl.	Euphorbiaceae
Matayba elaeagnoides Radlk.	Sapindaceae
Matayba grandis Radlk.	Sapindaceae
Matayba guianensis Aubl.	Sapindaceae
Melanoxylon brauna Schott	Fabaceae
Miconia pusilliflora (DC.) Naudin	Melastomataceae
Micropholis gardneriana (A.DC.) Pierre	Sapotaceae
Mollinedia argyrogyna Perkins	Monimiaceae
Mollinedia schottiana (Spreng.) Perkins	Monimiaceae
Monteverdia aquifolium (Mart.) Biral	Celastraceae

Monteverdia ilicifolia (Mart. ex Reissek) Biral	Celastraceae
Monteverdia schumanniana (Loes.) Biral	Celastraceae
Myrcia multiflora (Lam.) DC.	Myrtaceae
Myrcia sp	Myrtaceae
Myrcia splendens (Sw.) DC.	Myrtaceae
Myrcia teuscheriana (O.Berg) M.F.Santos	Myrtaceae
Myrciaria floribunda (H.West ex Willd.) O.Berg	Myrtaceae
Myrciaria glomerata O.Berg	Myrtaceae
Myroxylon peruiferum L.f.	Fabaceae
Myrtaceae sp	Myrtaceae
Nectandra lanceolata Nees	Lauraceae
Nectandra oppositifolia Nees & Mart.	Lauraceae
Nectandra rigida (Kunth) Nees	Lauraceae
Ocotea corymbosa (Meisn.) Mez	Lauraceae
Ocotea dispersa (Nees & Mart.) Mez	Lauraceae
Ocotea glauca (Nees & Mart.) Mez	Lauraceae
Ocotea odorifera (Vell.) Rohwer	Lauraceae
Ocotea pulchella (Nees & Mart.) Mez	Lauraceae
Ocotea sp	Lauraceae
Ocotea teleiandra (Meisn.) Mez	Lauraceae
Ocotea velutina (Nees) Rohwer	Lauraceae
Ocotea villosa Kosterm.	Lauraceae
Ouratea polygyna Engl.	Ochnaceae
Palicourea mamillaris (Müll.Arg.) C.M.Taylor	Rubiaceae
Palicourea sessilis (Vell.) C.M.Taylor	Rubiaceae
Peltophorum dubium (Spreng.) Taub.	Fabaceae
Persea americana Mill.	Luaraceae
Persea sp	Lauraceae
Persea willdenovii Kosterm.	Lauraceae
Picramnia parvifolia Engl.	Picramniaceae
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Fabaceae
Piptadenia paniculata Benth.	Fabaceae
Platymiscium pubescens Micheli	Fabaceae
Platypodium elegans Vogel	Fabaceae
Plinia peruviana (Poir.) Govaerts	Myrtaceae
Pouteria caimito (Ruiz & Pav.) Radlk.	Sapotaceae
Pradosia lactescens (Vell.) Radlk.	Sapotaceae
Protium warmingianum Marchand	Burseraceae
Prunus myrtifolia (L.) Urb.	Rosaceae
Pseudobombax grandiflorum (Cav.) A.Robyns	Malvaceae
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima	Fabaceae
Psychotria carthagenensis Jacq.	Rubiaceae
Pterocarpus rohrii Vahl	Fabaceae
Qualea multiflora subsp. *pubescens* (Mart.) Stafleu	Vochysiaceae
Randia armata (Sw.) DC.	Rubiaceae

Rubiaceae sp	Rubiaceae
Rudgea sessilis (Vell.) Müll.Arg.	Rubiaceae
Sapium glandulosum (L.) Morong	Euphorbiaceae
Schefflera sp	Araliaceae
Schizocalyx cuspidatus (A.St.-Hil.) Kainul. & B. Bremer	Rubiaceae
Seguieria americana L.	Phytolaccaceae
Seguieria langsdorffii Moq.	Phytolaccaceae
Senna multijuga (Rich.) H.S.Irwin & Barneby	Fabaceae
Senna sp	Fabaceae
Simira sampaioana (Standl.) Steyerm.	Rubiaceae
Siparuna guianensis Aubl.	Siparunaceae
Solanum pseudoquina A.St.-Hil.	Solanaceae
Sorocea bonplandii (Baill.) W.C.Burger et al.	Moraceae
Sparattosperma leucanthum (Vell.) K.Schum.	Bignoniaceae
Swartzia myrtifolia Sm.	Fabaceae
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae
Symplocos sp	Symplocaceae
Tabernaemontana laeta Mart.	Apocynaceae
Tapirira guianensis Aubl.	Anacardiaceae
Trichilia elegans A.Juss.	Meliaceae
Trichilia lepidota Mart.	Meliaceae
Trichilia lepidota subsp. *schumanniana* (Harms) T.D. Penn.	Meliaceae
Trichilia pallida Sw.	Meliaceae
Trichilia silvatica C.DC.	Meliaceae
Vernonanthura divaricata (Spreng.) H.Rob.	Asteraceae
Vitex megapotamica (Spreng.) Moldenke	Lamiaceae
Xylopia sericea A.St.-Hil.	Annonaceae
Xylosma prockia (Turcz.) Turcz.	Salicaceae
Xylosma venosa N.E.Br.	Salicaceae
Zanthoxylum rhoifolium Lam.	Rutaceae
Zanthoxylum riedelianum Engl.	Rutaceae
Zanthoxylum sp	Rutaceae
Zeyheria tuberculosa (Vell.) Bureau ex Verl.	Bignoniaceae
Zollernia ilicifolia (Brongn.) Vogel	Fabaceae

Fig.S2 - Phylogenetic tree of the pool of species of the topographic gradient in a local scale.

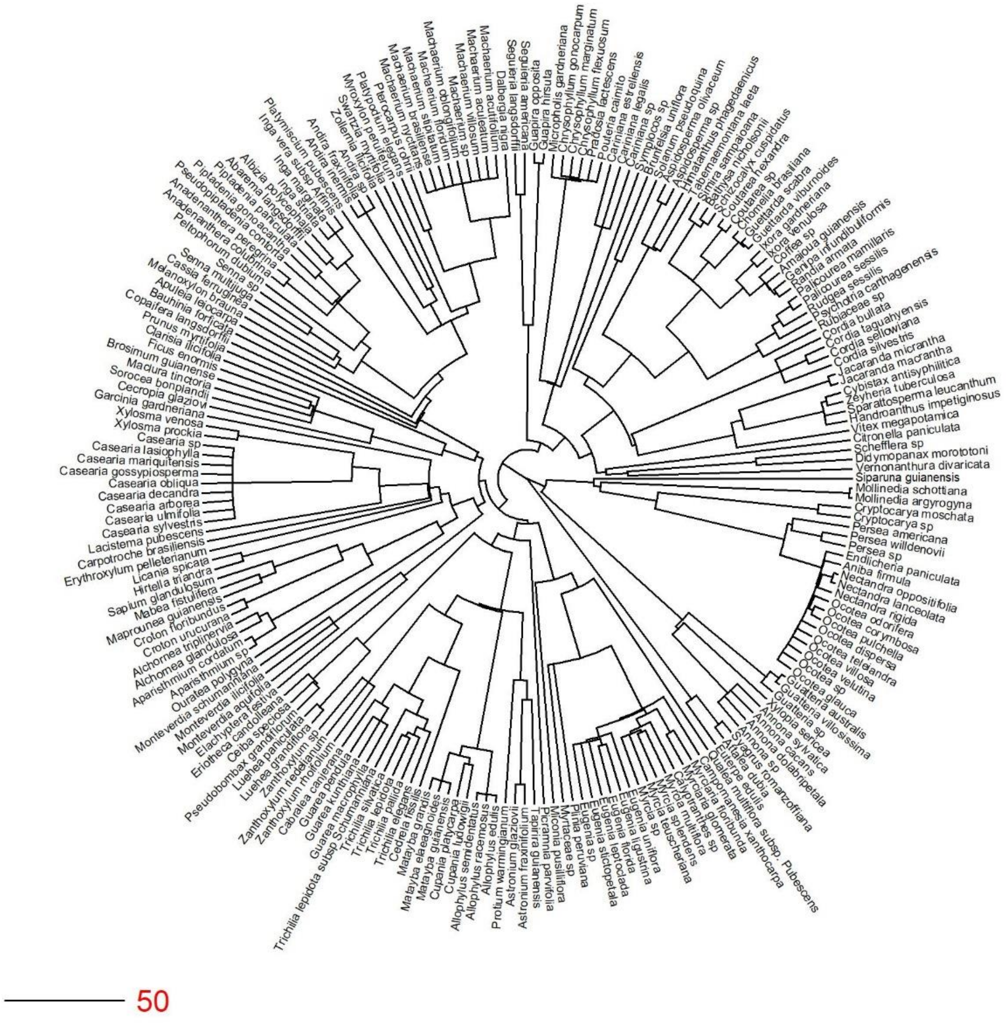


Fig.S3 - Multiple regression analysis tree results for the topographic gradient in a local scale.

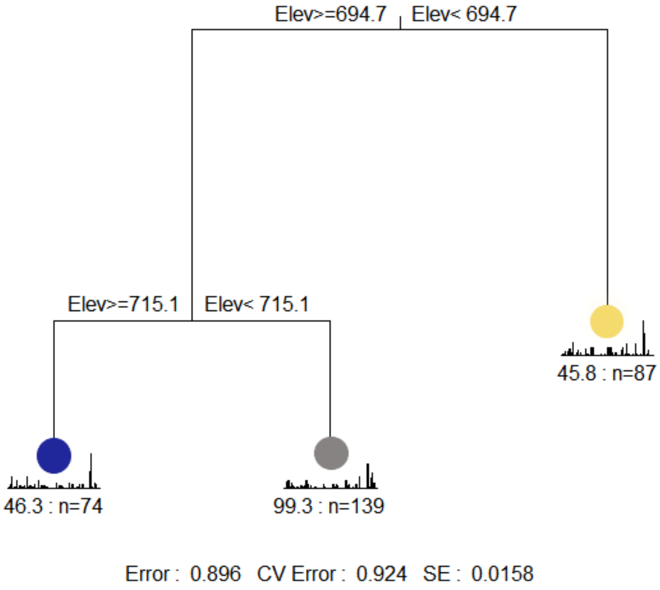
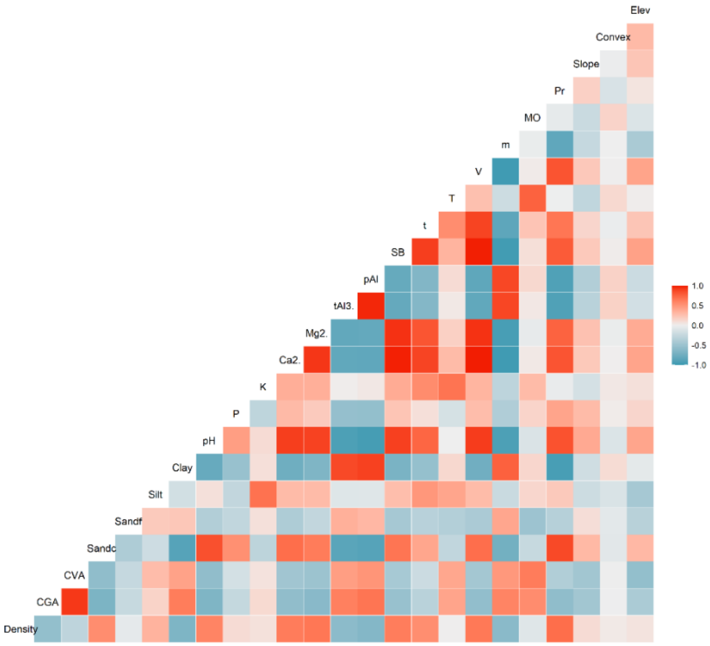


Fig.S4. Pearson correlation among all individual variables the topographic gradient in a local scale. For analysis: available P, K, Ca, Na, Mg, exchangeable acidity (HAl), pH (H_2O), organic matter (MO), sum of exchangeable bases (SB); effective cation exchange capacity (t), soil humidity (CGA and CVA) and soil bulk density (Density) and the soil texture as sand, clay and silt contents were included, Elevation (Elev), Slope, Convexity (Convex).



CHAPTER 2 – SOIL IS THE MAIN DRIVE OF FUNCTIONAL COMPOSITION AND STRUCTURE AT LOCAL SCALE TOPHOGRAPY IN A SEASONAL TROPICAL FOREST

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ABSTRACT

The topographic gradient is a good tool for understanding the correlation between the functional composition and environmental variables, and the functional-environmental approach can assist understanding the process that affects the community structure in Tropical Forests. The aim of the present study was to understand how topographic gradients shape the functional identity of species and how they contribute to the understanding of the mechanisms that drive community assembly at a local scale. The three permanent plots located in a Montane Semideciduous Seasonal Forest fragment. Each permanent plot was subdivided into 100 subplots of 10 m × 10 m to better capture the effect of topography on the local scale. We sampled all trees 10 cm or more in circumference at breast height. The topographic and edaphic variables were also measured. For 37% of the sample species, which accounted for 93% of all plant individuals sampled, we measure leaf area (LA; cm^2), specific leaf area (SLA; cm^2/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m^3), maximum height (Hmax; m), leaf thickness (LT; mm), and species was classified according to leaf phenology, dispersal syndrome, and the regeneration strategy. We estimated the community-weighted mean and functional diversity metrics for 300 subplots. We analyzed the functional identity and diversity along the topographic habitats. Generalized linear models were used to evaluate the effects of environmental variables on the community weighted mean and functional diversity metrics. The topographic gradients showed different functional compositions along the habitats, high habitat was characterized by species with conservative leaf traits, higher functional divergence, and lower functional richness. The low habitat was characterized for acquisitive leaf traits, less functional divergence, and higher functional richness. The maximum height, specific area, and leaf thickness were the traits that were best explained by edaphic and topographic variables. Evergreen phenology, zoochory dispersal, and non-zoochory dispersal were the categorical traits that were best explained. Functional richness and functional divergence were the categoric traits that were best explained; at the local scale, edaphic variables appeared to be more important for the variation of the traits and functional diversity, and the texture of the soil was the main driver. Our results showed that in the local topographic gradient, the edaphic variables were more important than the topographic variables in understanding the variation of traits and the impacts on the functional community structure at the local scale.

Key words: Community-weighted-mean, Atlantic Forest, functional diversity.

INTRODUCTION

Multiple process affects the community structure in tropical forests (McGill 2003). At the local scale, niche relationships and habitat diversity are among the main mechanisms that determine diversity and functional composition (Shmida & Wilson 1985; Kraft et al. 2008; Bruelheide et al. 2018). According to niche theory, competition and environmental filtering determine which species survive (Shmida & Wilson 1985). The competition exclusion hypothesis states that a new propagule that arrives at a site only can survive in the absence of a neighbor of a different species (cite). The environmental filtering suggests that a new propagule arriving at a site result in a subset of species or traits that can survive a given spatially defined abiotic regime (Kraft et al. 2015). Therefore, the ability of a new species to recruit depends on its ability to occupy underutilized niches (McGill 2003; Tilman 2004; Kraft et al. 2015). The functional trait approach can assist comprehend the process that effect on the assembly community (Kraft et al. 2008). Since the functional traits of plant species result from an evolutionary response to niche exploration (Reich 2014; Silva et al. 2021), understanding these mechanisms is extremely important, as they impact the plant growth, reproduction, and survival (Violle et al. 2007) affecting the structure of forest communities.

In tropical forests, abiotic factors play an important role in the spatial distribution, growth and consequently productivity of plants (Fortunel et al. 2018; Zemunik et al. 2018; Schwartz et al. 2020). For example, topographic gradients are directly associated with soil fertility and moisture gradients at a local scale (Allié et al. 2015; Chadwick & Asner 2016; Rodrigues et al. 2021). In tropical forest, increasing elevation tends to a decrease in soil fertility and moisture (Allié et al. 2015; Rodrigues et al. 2021). Lower areas seem to be more fertile and associated with acquisitive traits,while higher areas are associated with lower resource availability and more conservative traits (Liu et al. 2014; Fortunel et al. 2018). Forest areas with high soil fertility have more varied resource-use strategies than those with low fertility (cite). However, poor soil tends to lead to the convergence of strategies (Liu et al. 2014). Studies on the relationships between traits and environment, such as along topographic habitats (Kraft et al. 2008; Liu et al. 2014; Rodrigues et al. 2019) are tools for understanding the mechanisms that influence the assembly of communities (Xia et al. 2015), since variation in functional traits is the result of an evolutionary response to the exploitation of that edaphic niche (Joswig et al. 2022).

Plants exhibit a trait pattern that can be defined as the resource acquisition-conservation trade-off (Diaz et al. 2004). Which is independent of geographic location and taxonomic affinity to observe trait patterns (Diaz et al. 2004; Poorter et al. 2008). This means that the traits can facilitate rapid resource acquisition by the plant, allowing a high capacity to move, acquire, and use water and nutrients to fix carbon (cite). However, the traits can destine to tissue protection to resist resource scarcity and conserve carbon (Diaz et al. 2004; Reich 2014). Considering the Tropical Forests, habitat filtering appears be the main drive at local scale (Kraft et al. 2008; Liu et al. 2014). Therefore, co-occurring species share similar traits that are necessary for tolerance to the abiotic environmental (Kraft et al. 2008; Kraft et al. 2015). The Seasonal Atlantic Forests tend to be associated with high specific leaf area, leaf nitrogen content, wood density, and lower leaf thickness (Silva et al. 2021), these patterns of traits are associated with acquisition strategy (Díaz et al. 2016). These characteristics could be an adaptation to thermal variation associated with a seasonal frequency of rainfall and to low fertile and sandy soils (Silva et al. 2021). In view of global change scenarios is essential to understand trait-environment relationships and the main drivers of species' distribution at local scale to predict the ability of plants to adapt and acclimatize to these changes (Heilmeier 2019).

The Atlantic Forest is a complex phytogeography (Veloso et al. 1991). The latitudinal and interiorization floristic gradients are the result of spatial variations in precipitation and temperature within the biome (Oliveira-Filho & Fontes 2000; Eisenlohr & de Oliveira-Filho 2015). Climatic factors have shaped not only the floristic composition (Eisenlohr & de Oliveira-Filho 2015), but also the functional assemblage of the Atlantic Forest (Silva et al. 2021). The Semideciduous Seasonal Forest (SSF), the second largest type of vegetation in the Atlantic Forest, is mainly found in the interior of the southeastern and central regions of the Atlantic domain (Morellato & Haddad 2000). This vegetation that occurs in areas with seasonal climate, with cold and dry winters, and is characterized by the deciduousness of trees between 20% and 50% (IBGE 2012). The duration of the dry period strongly influences the distribution of FES occurrence, as well as floristic patterns (Oliveira-Filho & Fontes 2000), being associated with species of broad dispersion, non-co-familial, and different functional characteristics (Souza et al. 2021). The environmental factors shaped not only the floristic composition (Eisenlohr & de Oliveira-Filho 2015) as well, the functional assemblage of the Atlantic Forest (Silva et al. 2021).

In this context, the of the present research is to comprehend how the topographic gradient shapes the functional identity of species, and how they contribute to understanding the mechanisms of community assembly on a local scale. We hypothesized that:1) areas with higher resource availability along the elevation gradient are expected to predominate acquisitive traits and have higher functional diversity, whereas areas with lower resource availability predominate conservative traits and lower functional richness; 2) areas with greater resource availability along the elevation gradient are expected to have higher species of zoochorous dispersion and perennials; therefore, we expected a negative correlation of the topographic gradient with zoochorous and perennial species and a positive correlation with non-zoochoryc dispersion and deciduous species; and 3) the edaphic-topographic gradient would influence functional traits and functional diversity on a local-scale, and edaphic variables are the main drivers of this variation.

MATERIAL AND METHODS

Study site

The study was conducted in a secondary forest, the "Mata da Biologia", in the municipality of Viçosa (20°45'14 "S, 42°51'53 "W) in the state of Minas Gerais, southeastern Brazil (Fig. S1). It is classified as Montane Semideciduous Seasonal Forest (Veloso et al. 1991), the fragment has approximately 75 ha (Paula et al. 2002). The area was clear-cut in the early 1920s (Lopes et al. 2002; Paula et al. 2002) and subsequently used for shade coffee plantations until 1926 (Paula et al. 2002). Since then, the area has been abandoned, left to regenerate naturally (Paula et al. 2002), and is in an intermediate stage of succession (Lopes et al., 2002; Paula et al. 2003).

Located in a region of mountainous and strongly undulated relief, the fragment lies between 620 and 820 m, and presents a soil gradient between Red-Yellow Latosols, at the top of the highest regions and on the steepest slopes, and nutrient-rich Cambisols in the valleys (Ferreira-Júnior et al. 2007). According to the Köppen classification, the region's climate is characterized as Humid Subtropical (Cwa) with hot summers and dry winters, mainly between May and August (Alvares et al. 2013), with an average annual temperature of approximately 21°C and average annual precipitation of 1250 mm (Avila-Diaz et al. 2020).

Sample design

Three 1-ha permanent plots were established in the forest fragment with contrasting topographical conditions. Each permanent plot was subdivided into 100 subplots of 10 x 10 m to better capture topography effect on the local scale. In each plot, all living tree individuals with a circumference at breast height (CAP) equal to or greater than 10 cm were recorded and measured. All individuals were identified, and species nomenclature follows the Angiosperm Phylogeny Group IV (APG IV 2016) classification system.

Topographic variables

For each subplot, 10 x 10 m, three topographic variables (elevation, slope, and convexity) were measured and calculated using a total station with the assistance of a surveying engineer. Elevation was calculated using the average elevation value of each of the four corners of the plot. The slope (°) corresponds to the average angular deviation from the horizontal of each of the four triangular planes, formed by connecting three of its corners. Convexity was determined by subtracting the elevation of the plot center from the average elevation of the eight surrounding plots (Wang et al. 2016). Multiple regression analysis (MRT; De'ath 2002) was used to group the subplots (10 x 10 m) based on species similarity and topographic variables (elevation, slope, and convexity), and thus classify the subplots into different topographic habitats (Wang et al. 2016). MRT can be defined as a constrained cluster analysis that seeks to relate species composition to environmental data (De'ath 2002) and can be used to identify the variables that most influence species grouping (Larsen & Speckman 2004). The MRT analysis was performed using de function "mvpart" from the 'mvpart' package (De'ath 2002). The MRT grouped the subplots of the whole community into three habitats, Habitat L (lower topographic habitat) corresponds to 87 subplots with an elevation below 694.7 meters. Habitat I (intermediate topographic habitat -I), corresponds to 139 subplots with an elevation between 694.7 and 715.1, and Habitat H (higher topographic habitat – H) corresponds to 74 subplots with elevation above 715.1 m (Fig.S1).

Edaphic variables

For soil characterization, the methodology presented by Ferreira-Júnior (2017) was followed. The soil sampling was made systematically at three points at a depth of 0-10 cm. Afterwards, they were homogenized to obtain one composite sample per subplot. The samples were analyzed in the Soil Laboratory of the Soil Department of the Federal University of Viçosa. The physical-chemical attributes analyzed were the following: pH (hydrogen potential), Ca (calcium), Mg (magnesium), K (potassium), Na (sodium), P (phosphorus), H+Al (potential acidity), MO (organic matter), SB (base sum), m(saturation percentage by aluminum), V (saturation percentage by exchange), t(Cation Exchange Capacity), fine sand, coarse sand, clay, silt content, soil density and CGA (soil moisture) was analyzed according to the methodology proposed by EMBRAPA (2011). Principal component analysis (PCA) was used to evaluate possible correlations between topographic habitats and soil variables. The PCA was performed using the "FactoMineR" package (Husson et al. 2017). PCA of the topography and soil texture variables showed a soil moisture gradient between higher topographic habitats and lower topographic habitats. PCA showed a fertility gradient between intermediate habitats and the others, with a positive correlation with SB, V, and pH.

Functional traits

For 37% of the sample's species, which account for 93% of all plant individuals sampled, we measure six functional traits were chosen for this research, four leaf traits and two wood traits: leaf area (LA; cm^2), specific leaf area (SLA; cm^2/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m^3), maximum height (Hmax; m) and leaf thickness (LT; mm). These traits were selected because they can reflect the whole-plant trade-off (Díaz et al. 2016). The leaves used in this study was collected from the highest branches of the individuals. Between three and 15 individuals of each species was collected to obtain an average value for the trait, considering the three hectares. The LA was calculated by measuring five leaves (excluding the petiole) for everyone, from images using the ImageJ program (Schneider et al. 2012). The leaf area of the compound leaves was calculated by summing the area of all leaflets. The leaf dry mass was calculated using dried leaves previously dried at 60° C for 72 h. The leaf thickness was calculated using a digital pachymeter with a resolution of 0.01 mm (Stainless Hardened), avoiding measurement in contact with the primary and secondary vein. The specific leaf area was calculated from leaf area/dry leaf mass (cm^2/g). All leaf traits were measures following (Pérez-Harguindeguy et al. 2013). Wood density data was obtained from the Global Wood Density Database (Zanne et al. 2009; Chave et al. 2014). Maximum height potential was calculated as the upper 95-percentile height for those trees whose height was equal to or greater than 10% of the observed maximum height of the population (King et al. 2006; Ali et al. 2019). Species was classified according to leaf phenology (strictly deciduous and semi-deciduous, 1; evergreen, 0), dispersal syndrome (zoochoric, 1; non-zoochoric, 0), and the regeneration strategy (shade tolerant, 1; pioneer, 0). These data were obtained through research to different bibliographic sources.

Functional metrics

To understand the composition of traits in the community and among functional groups we calculated for each plot the community-weighted-mean (CWM) for all leaf and wood traits (Garnier et al. 2004; Lavorel et al. 2007). The CWM was performed using the “functcomp” function from "FD" package (Laliberté & Legendre 2010; Laliberté & Legendre 2014). To quantify functional diversity and understand how the environment may influence trait diversity we calculated functional richness (FRic), represents the amount of functional space occupied by a set of species, functional divergence (FDiv), defines how far species abundance diverges from the center of the functional space, functional eveness (FEve), represents the evenness of the distribution of species abundance in the functional space (Mouchet et al. 2010), and functional dispersion (FDis), defines the weighted mean distance of individual species to the center of the functional space for all species, while weights correspond to the relative abundances of the species (Laliberté & Legendre 2010), for each plot. This metrics was calculated using the “fundiversity” package (Grenié & Gruson 2023).

Statistical analyses

We used Principal component analysis (PCA) to evaluate possible correlations between topographic habitats and functional traits, and functional diversity metrics. PCA allows both simplification and verification of the most important variables of the data (Abdi & Williams 2010). The PCA was performed using the "FactoMineR" package (Husson et al. 2017).

To calculate functional diversity metrics, we used the Gower distance between species to perform a Principal Coordinates Analysis (PCoA). These analyses were carried out using the "vegan" and "ape" packages (Paradis & Schliep 2019; Oksanen et al. 2019). We extracted the two axes of the PCoA to calculate the functional diversity metrics. The final values were standardized between 0 and 1. The CWM and functional diversity metrics were tested for normality using the Shapiro test, parametric data was tested with the Anova test and non-parametric data was test using the Kruskal-Wallis test for mean differences between habitats. When the results were significantly, we use T test to parametric data and Wilcox test to non-parametric data to calculate the pairwise mean comparation pairwise. This analysis was performed using the “ggpubr” package (Kassambara 2023) and “ggplot2” package (Wickham 2016).

To evaluate the effects of environmental variables on CWM of traits and functional diversity metrics, we performed a generalized linear model (GLM). Variables were selected to avoid collinearity between variables (cor < 0.7) using the function “ggcorr” from “GGally” package (Schloerke et al. 2021), and multicollonearity (VIF < 5) using the “car” package (Fox & Weisberg 2019). The topographic variables and edaphic variables (OM, Sandc, moisture, P and SB) were used as explanatory variable in the final model to verify the effect on the variable’s response. We used Gamma residuals distribution for continuous data (i.e., values of CWM funtional traits values) and for all others, we used family quasibinomial to avoid overdispersion. The GLMs were performed using the “stats” package (R Core Team 2023). We used “q-qplot” to validate the model’s assumptions from “car” package (Fox & Weisberg 2019). To calculate the coefficient of determination, R^2, we used the “rsq” package (Zhang 2022). The graphics and tables were performed using the “GGplot2” and “sjPlot” package (Wickham 2016; Lüdecke 2023). All analyses were performed in R Environmental (R Core Team 2023).

RESULTS

Patterns of functional traits along a local-scale topography

The variation in the functional composition space of tree species pools between habitats largely overlapped for the CWM traits (Fig. 1). The PCA of the CWM traits explained 61.4 % (PCA1= 47.6%; PCA2= 13.8%) of the subplot’s variances (Fig. 1). The High habitat was negatively correlated with LA and positively correlated with LDMC. The first axis indicated a variation of pioneer, non-evergreen species with non-zoochoryc dispersion and high SLA, to shade-tolerant, evergreen species with zoochoryc dispersion and high Th. The second axis indicated a variation from species with conservative traits, high LDMC, and high WD to species with acquisitive strategies, high LA, low LDMC, and low WD. The High habitat was more correlated with conservative traits, with low LA, high LDMC, and high WD.

The PCA with functional diversity metrics explained 71.3% (PCA1= 46.7%; PCA2=24.6%) of the variance (Fig. 2). The first axis indicates a variation in the community with high Fric and FDis, and the second axis indicates a variation in the community with high FDis and

FEve. The PCA showed that the Low habitats were positively correlated with Fric, and the Low and Intermediate habitats were negatively correlated with FRic.

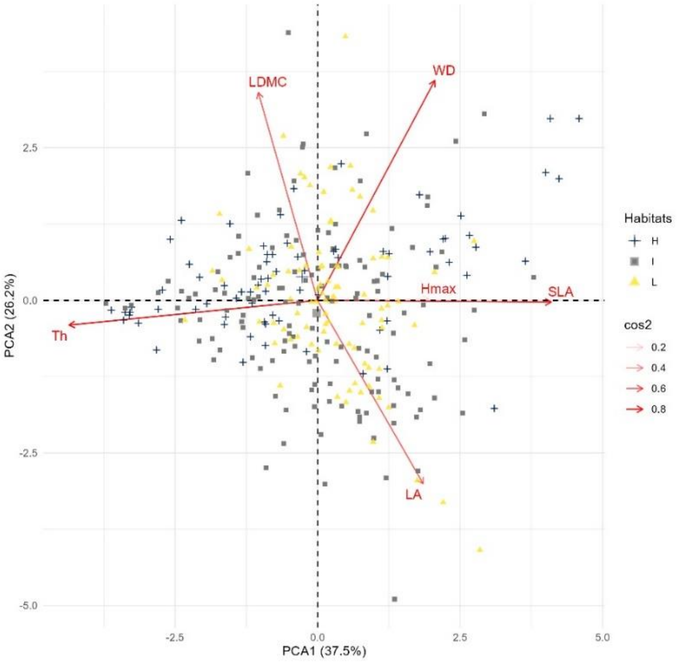

Fig. 1 - Principal correspondence analysis (PCA) of relations between the habitat's subplots and CWM functional traits values. The CWM functional traits are leaf area (LA; cm²), specific leaf area (SLA; cm²/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m³), maximum height (Hmax; m) and leaf thickness (Th; mm). The evaluated habitats were High (H; blue plus); intermediate (I; grey square); and low topographic habitat (L; yellow triangle).

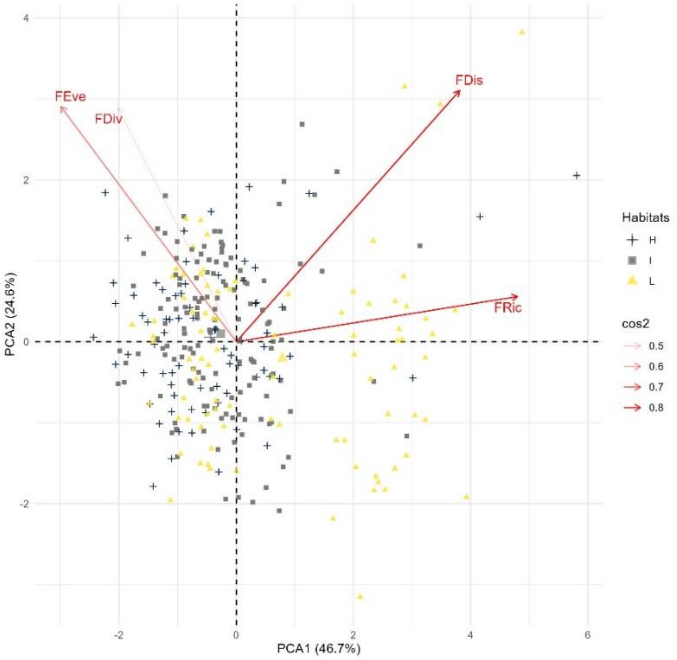

Fig. 2 - Principal correspondence analysis (PCA) of relations between the habitat's subplots and functional diversity. The functional diversity metrics are functional richness (FRic), functional divergence (FDiv), functional eveness (FEve), and functional dispersion (FDis). The evaluated habitats were High (H; blue plus); intermediate (I; grey square); and low topographic habitat (L; yellow triangle).

The functional composition of tree species in the CWM was significantly different between topographic habitats (Fig. 3). The functional composition indicated a gradient between High and Low habitats. The High topographic habitat was characterized for species with conservative leaf traits, high Th, LDMC, low LA and SLA. The Low habitat was characterized by species with acquisitive leaf traits, low Th, LDMC, high LA, and SLA. The wood traits showed that WD did not differ between habitats, and Hmax increased with increasing elevation.

The habitats show a gradient of decreased of pioneer species with increasing elevation and increased of the non-zoochoryc dispersion species with the increasing the elevation (Fig. 4). The functional diversity metrics of the species pool show significant different between topographic habitats (Fig. 5). The topographic gradient shows a clear variation between the habitats for Fric and FDiv, the decrease in elevation increased the Fric and decrease the FDiv (Fig. 5A and 5B). The Low habitat has low FEve and high FDis comparing to the High habitat (Fig. 5C and 5D).

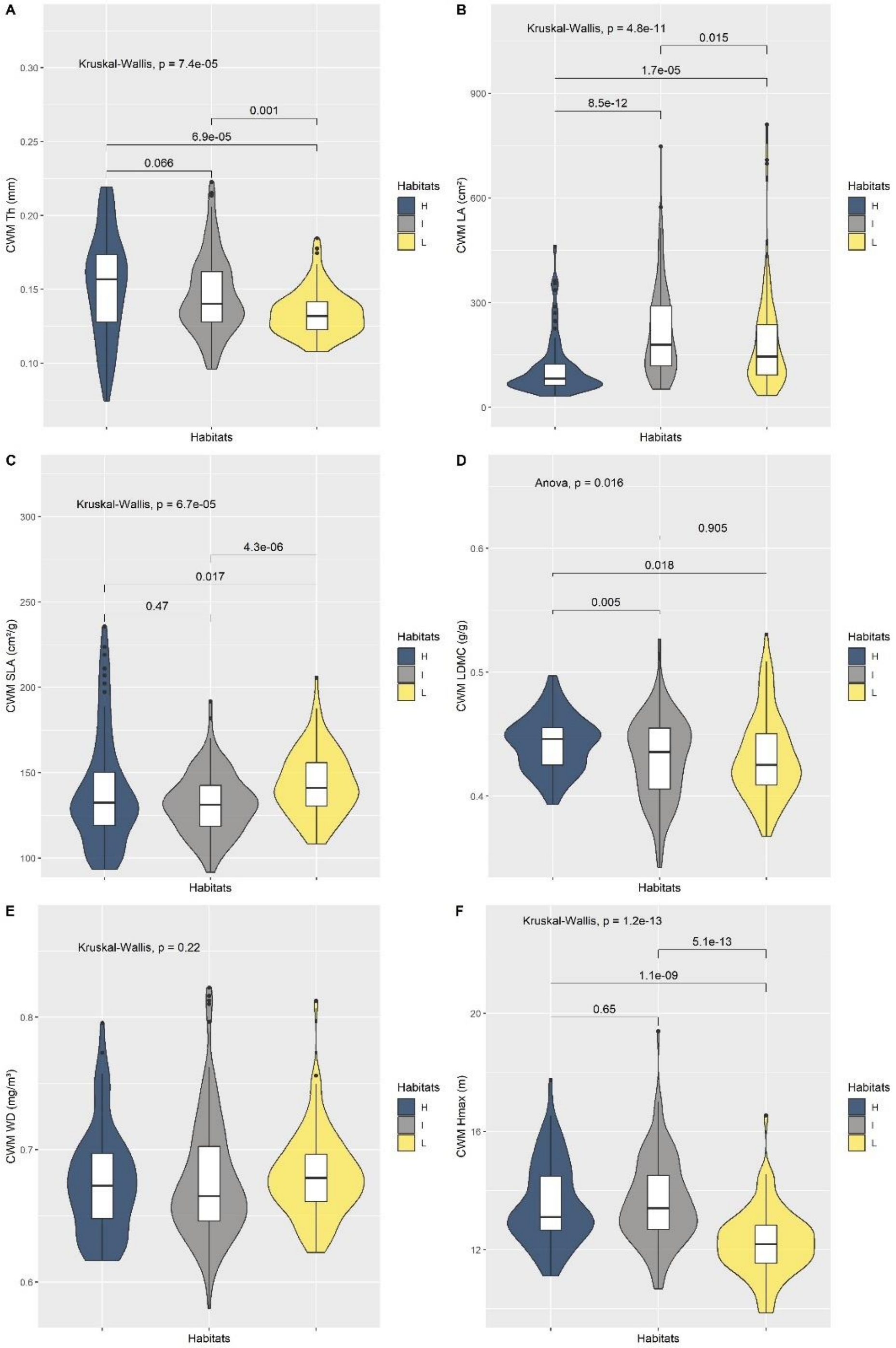

Figure. 3 - Variation in the CWM functional traits values along the topographic habitats (A-F). The CWM functional traits are leaf thickness (A; CWM Th), leaf area (B; CWM LA), specific leaf area (C; CWM SLA), leaf dry mass content (D; CWM LDMC), wood density (E; CWM WD), maximum height (F; CWM Hmax). The evaluated habitats were High (H; blue); intermediate (I; grey); and low topographic habitat (L; yellow).

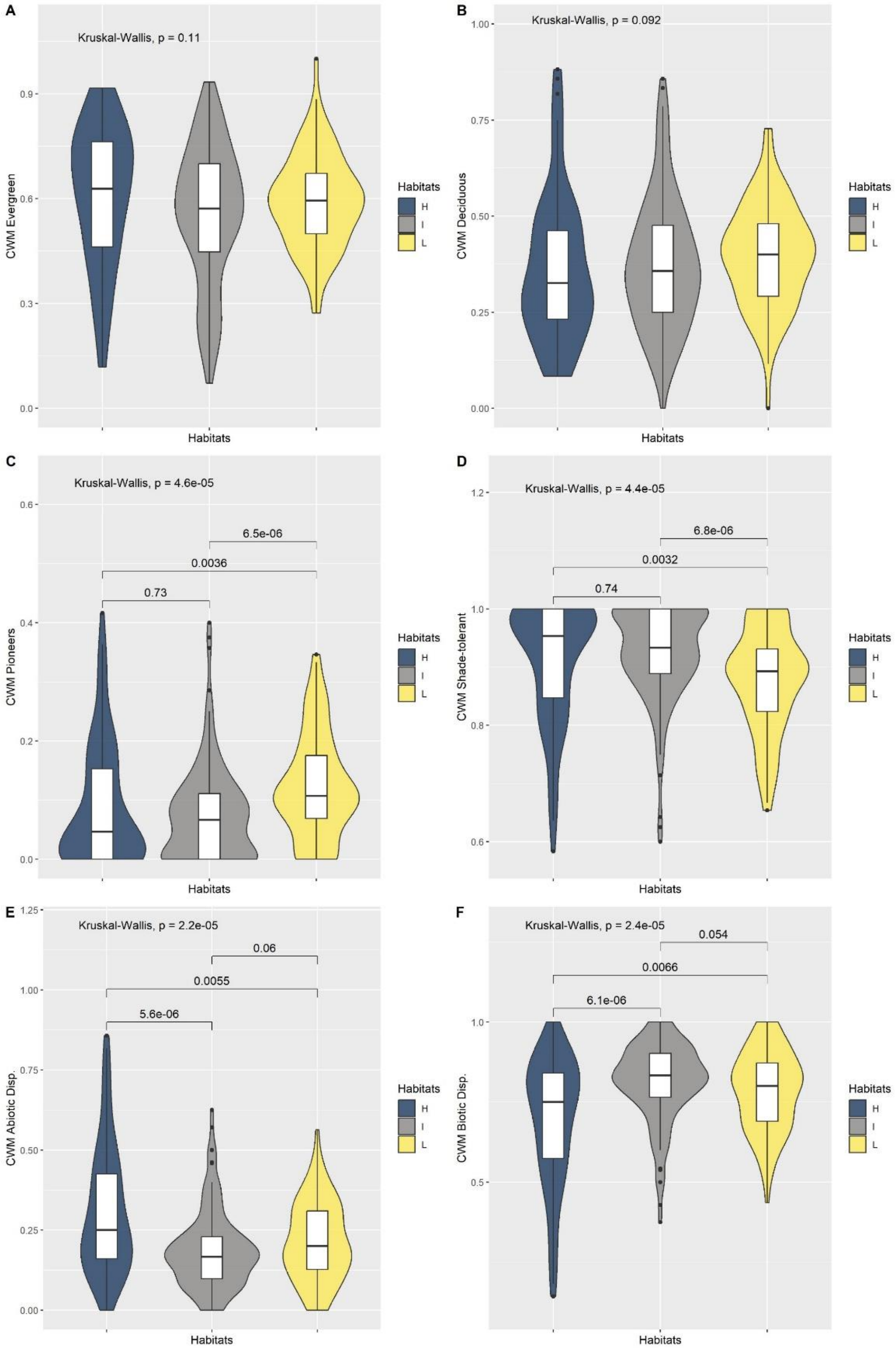

Figure. 4 - Variation in the CWM functional groups proportion values along the topographic habitats (A-F). The CWM functional groups are evergreen phenology (A; CWM Evergreen), deciduous phenology (B; CWM Deciduous), pioneer succession group (C; CWM Pioneers), shade-tolerant succession group (D; CWM Shade-tolerant), non-Zoochorus dispersal (E; CWM Non-Zoochorus Disp.), Zoochory dispersal (F; CWM Zoochory Disp.). The evaluated habitats were High (H; blue); intermediate (I; grey); and low topographic habitat (L; yellow).

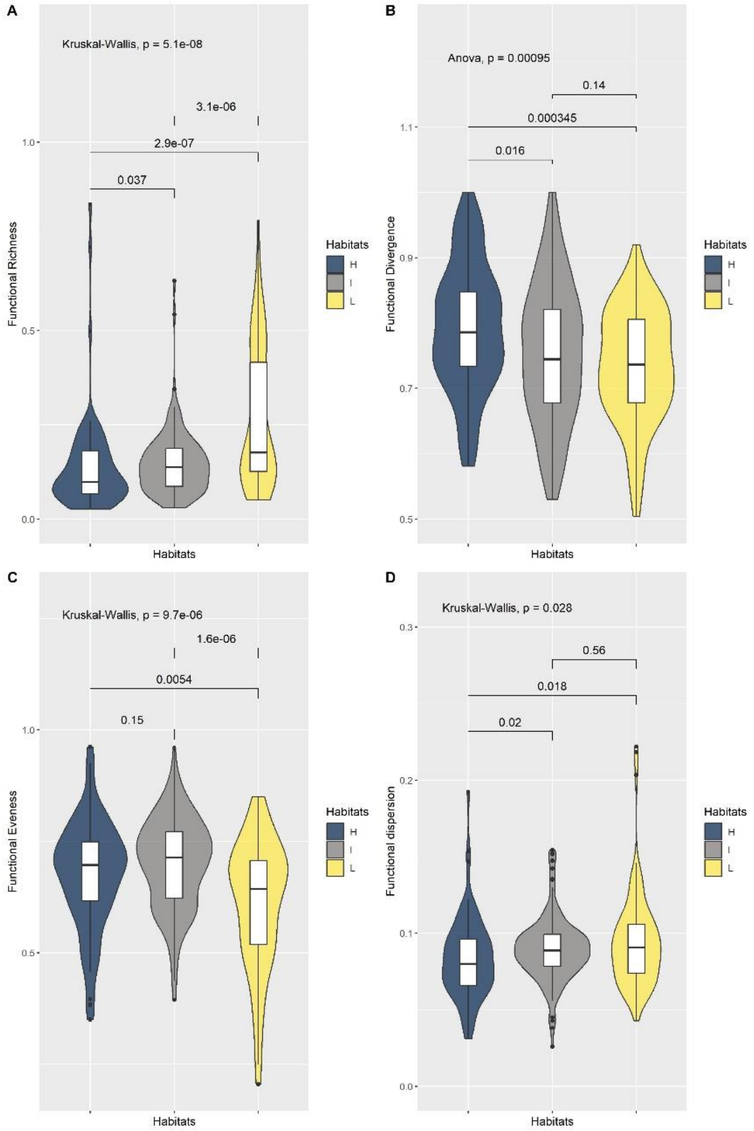

Figure. 5 - Variation in the functional diversity metrics values along the topographic habitats (A-D). The evaluated habitats were High (H; blue); intermediate (I; grey); and low topographic habitat (L; yellow).

Effect of local topography on functional structure

The topographic-edaphic variables explained 12 to 42% of the variation in the CWM trait variation for leaf and wood traits across the topographic gradient (Fig. 6). The Sand and BS indicates were the most influential variables, both edaphic variables, these variables showed effect all CWM leaf and wood traits. LA, SLA, WD and Hmax decreased with increasing sand content, while Th and LDMC increased. The increasing in the sand content lead variation of acquisitive to conservative strategy of the leaf traits. Additionally, increased the BS with increasing SLA, LDMC, WD and decreasing LA, Th and Hmax. WD was only related to edaphic variables and increased with increasing BS and P, and decreased with increasing Sand and OM. The convexity indicates was the most influential topographic variable and only related with leaf traits. Convexity led to a decreasing of LA, SLA and increasing of Th and LDMC. The increasing in the convexity lead variation of acquisitive to conservative strategy of the leaf traits.

The topographic-edaphic variables explained 11 to 27% of the variation in the CWM categoric trait variation across the topographic gradient (Fig. 7). The results indicator that the edaphic variables are more important to explain the variation in local scale than topographic variables. The Sand and P indicates were the most influential variables. Evergreen, Shade-tolerant species, zoochory dispersion species decreased with increasing the sand content, while increased the deciduous, pioneer, and non-zoochoryc dispersion species. Although, Evergreen, Shade-tolerant species, zoochoryc dispersion species increased with increasing the P content, while decreased the deciduous, pioneer, and non-zoochoryc dispersion species.

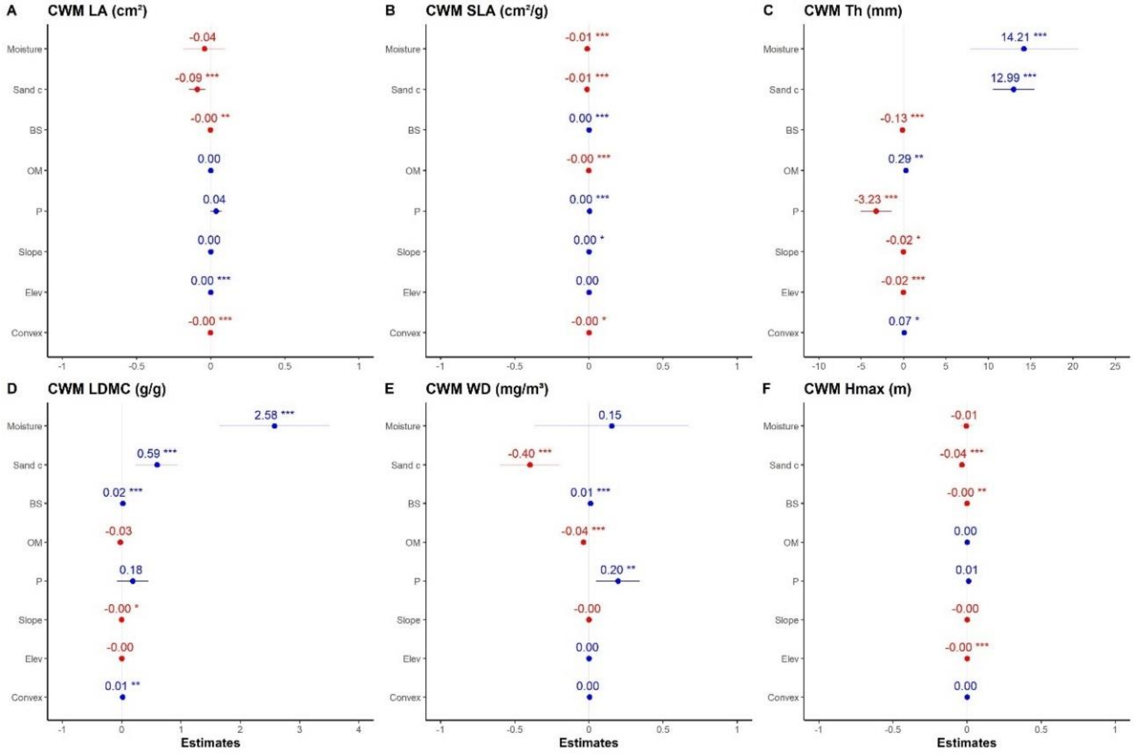

Figure. 6 - Effects of elevation (Elev), slope, convexity (Convex), organic matter (OM), base sum (SB), coarse sand (Sand c), and soil moisture (Moisture) in the CWM functional traits values in local-scale topographic gradient in Atlantic Forest. The CWM functional traits are leaf area (A; CWM LA; $R^2 = 0,31$), specific leaf area (B; CWM SLA; $R^2 = 0,40$), leaf thickness (C; CWM Th; $R^2 = 0,40$), leaf dry mass content (D; CWM LDMC; $R^2 = 0,28$), wood density (E; CWM WD; $R^2 = 0,12$), maximum height (F; CWM Hmax; $R^2 = 0,42$). Standardized coefficients with 95% CIs are shown. Values with asterisk (*; **; ***) indicate significant responses. Negative coefficients indicate a negative effect, and positive coefficients indicate a positive effect.

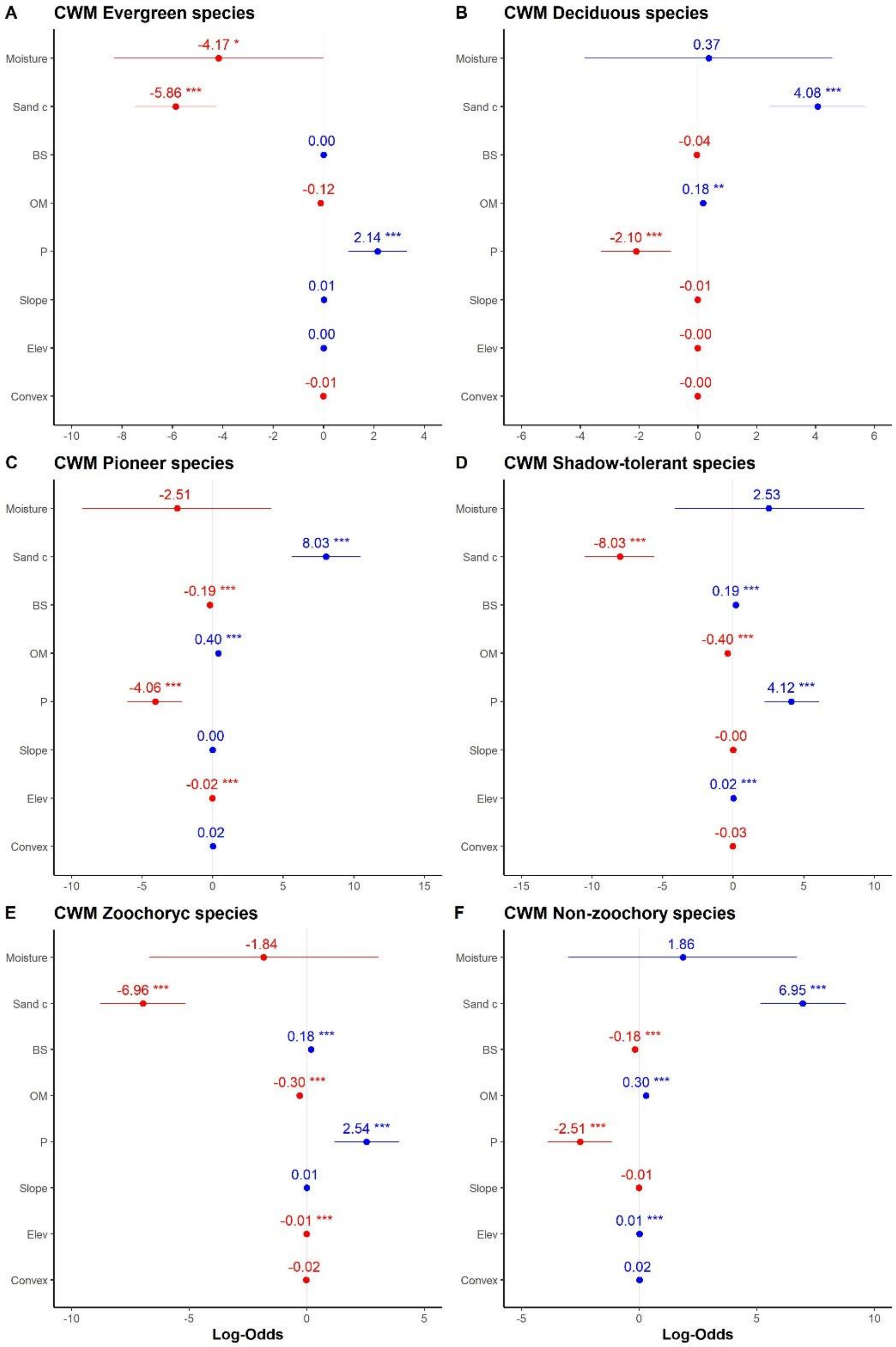

Figure. 7 - Effects of elevation (Elev), slope, convexity (Convex), organic matter (OM), base sum (SB), coarse sand (Sand c), and soil moisture (Moisture) in the CWM functional groups proporcion values in local-scale topographic gradient in Atlantic Forest. The CWM functional groups are evergreen phenology (A; $R^2 = 0,27$), deciduous phenology (B; $R^2 = 0,11$), pioneer succession group (C; $R^2 = 0,16$), shade-tolerant succession group (D; $R^2 = 0,16$), zoochoryc dispersal (E; $R^2 = 0,26$), and non-zoochoryc dispersal (F; $R^2 = 0,26$). Standardized coefficients with 95% CIs are shown. Values with asterisk (*; **; ***) indicate significant responses. Negative coefficients indicate a negative effect, and positive coefficients indicate a positive effect.

The functional diversity metrics were six to 31% explained by the topographic-edaphic variables across the topographic gradient in a local scale (Fig. 8). The results showed that functional dispersion ($R^2 = 0,06$; Fig. 8D) and functional evenness ($R^2 = 0.08$; Fig. 8C) were poorly explained by the variables. The functional richness shows be effect by most of the variables, and the main predictor were sand and phosphorus, while sand increased this metrics, P decreased the functional richness (Fig. 8A). Soil moisture had an important effect in functional divergence, with a negative effect (Fig. 8B). The sand was the main predictor in general, with positive effects in functional richness, dispersion, and negative effect in functional divergence (Fig. 8A, B, D).

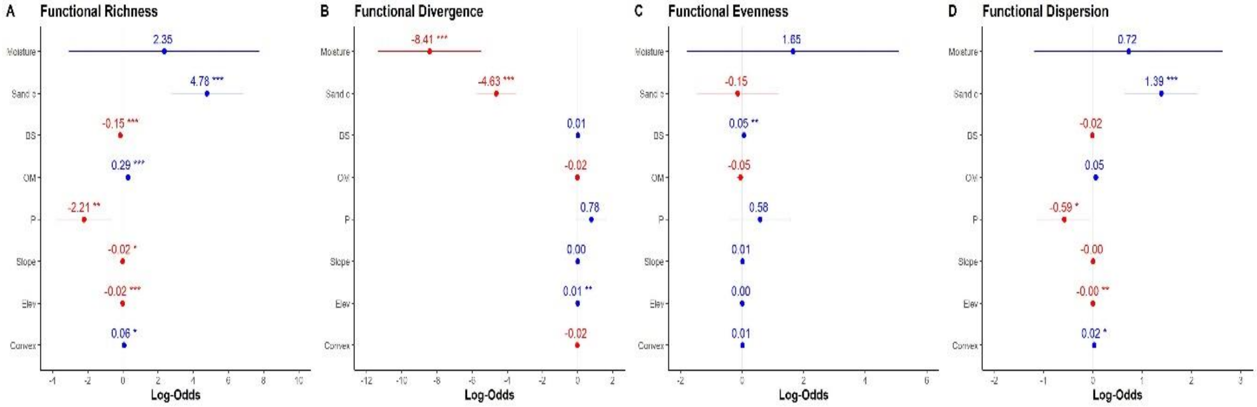

Figure. 8 - Effects of elevation (Elev), slope, convexity (Convex), organic matter (OM), base sum (SB), coarse sand (Sand c), and soil moisture (Moisture) in the functional diversity metrics local-scale topographic gradient in Atlantic Forest. The functional diversity metrics are functional richness (A; $R^2 = 0,23$), functional divergence (B; $R^2 = 0,31$), functional evenness (C; $R^2 = 0,08$), and functional dispersion (D; $R^2 = 0,06$). Standardized coefficients with 95% CIs are shown. Values with asterisk (*; **; ***) indicate significant responses. Negative coefficients indicate a negative effect, and positive coefficients indicate a positive effect.

DISCUSSION

In this study, we aim to understand whether the topographic gradient on a local scale can alter the functional composition of the community. The results shows that leaf traits show a trade-off along of the topography and respond to the edaphic variations along to the topographic gradient. Our results show that in the local-scale topographic gradient, the edaphic variables were more important than the topographic variables to the understanding of the variation of traits and the impacts on the functional community structure at local scale.

Patterns of functional traits along a local-scale topography

The results show a clear pattern between functional traits in a local scale topographic gradient. This results are in agreement with our fist hypothesis and with others research in tropical forests (Báez et al., 2022; Liu et al., 2014b), and shows that a local scale topographic gradient can have different functional strategies (Kraft et al., 2008), despite the lower elevation range. As predicted, topographic gradients can model the fertility and soil water gradient at local-scale and consequently, shape the functional strategies of tree species (Allié et al., 2015; Fortunel et al., 2018; Rodrigues et al., 2021a). Our results show a pattern for leaf traits along the topographic habitats. The traits Th, SLA, and LDMC reveal differences between upper and lower habitats, with values associated with acquisitive strategy in the lower habitat (Kraft et al., 2008). As expected the upper topographic habitats are related to conservative and lower habitats are related with acquisitive strategies (Kraft et al., 2008; Liu et al., 2014b). Wood traits did not show a relationship with the trade-offs. Contrary to what was expected, the results showed that there was no difference between habitats for WD, and the maximum height was higher in upper areas. This contradicts the findings of other studies in topographic gradients (Jucker et al., 2018; Rodrigues, Villa, Ali, et al., 2019), that showed significant patterns with high tree maximum height and low wood density at lower topographic habitats. This result may be related to the higher proportion of pioneer species in lower areas. Species with high light demand tend to have a higher mortality rate (Wright et al., 2010) and, consequently, may cause a lower average maximum height in lower areas (Fortunel et al., 2018). The results of the functional trait analysis reinforce that in a local-scale topographic gradient, the plants have different strategies, mainly for leaf traits, that the traits change between acquisitive traits in lower habitats and conservative traits in high topographic habitats. And may be is showing that wood and leaf functional strategies could be decoupled (Baraloto et al., 2010).

Our results showed that the forest has higher proportions of evergreen and zoochoryc dispersed species. Contrary to our hypothesis, the results show no differences between the topographic habitats for the leaf habit, both evergreen and deciduous leaf phenology habit. Tropical Forests along the succession process tends increasing species with conservative traits (Lohbeck et al., 2015; Pinho et al., 2018), which drives species turnover. In fact, this change leads to the recruitment of evergreen species that are more shade tolerant, and a decrease in deciduous species (Poorter et al., 2021). However, for dispersal syndrome, the topographic habitats have some significant differences. In general, the proportion of zoochoryc dispersal species is higher, but that upper areas have higher proportions of non-zoochoryc dispersal than the other habitats. In Atlantic Forest, species with zoochoryc dispersal tend to be higher than non-zoochoryc (Tabarelli & Peres, 2002). This reproductive strategy is associated with conservative strategy in Tropical forests (Lohbeck et al., 2015), moreover, with evergreen species that is the main leaf phenology strategy.

Effect of local topography on functional structure

In local scale the edaphic variables appear has more importance for the variation of the traits, both for leaf and wood traits. The sand coarse content and the BS has a significant relationship with all traits and with the topographic gradient. The results shows that sand content is negative correlated with water availability. The increasing in the sand content indicates a variation of acquisitive to conservative strategy of the leaf traits. The fertility and water availability of the soil has similar trend, the lowest habitats has more fertile and water availability in soil (Ferreira-Júnior et al., 2007). Species in the areas with more fertile soil are related with acquisitive strategies and species in the areas with low fertility are related with conservative traits (Hodgson et al., 2011; Jager et al., 2015; Ordoñez et al., 2009). So, our results suggests that the low water availability besides be more related to values of leaf traits more associated to conservative strategy, in this areas tend to an increasing of deciduous species and non-zoochoryc dispersion, which is particularly associated to drought- avoidance strategy (Poorter et al., 2021).

The results suggest a clear correlation for functional richness and divergence along the topographic habitats. These findings reinforce that environmental gradients can cause effect in functional diversity (Suárez-Castro et al., 2022). Functional divergence define the degree of differentiation of traits values between the most abundant species within the community (Mason et al., 2005). This suggest that in the high habitat the species tend to diverge on traits values (Mason et al., 2012). While in the low habitat the species tends to converge on similar traits values (Mason et al., 2012). This results contrast with results findings in other research (Liu et al., 2014b; Mason et al., 2012), they found that functional divergence and evenness tends to be higher in lower topographic habitats. In this high habitat, competition between species may be greater and may cause greater divergence in traits values (Mason et al., 2005; Mouchet et al., 2010; Suárez-Castro et al., 2022).

Functional richness and divergence were the metrics that were most explained by environmental variables, and the main drives were water availability and sand content. The analyses suggest that the highest the water availability and sand content in the soil, the higher the functional space of the species and the lower the divergence between them. Water availability can directly effects plants distribution and tree growth at local scale (Engelbrecht et al., 2007; Hofhansl et al., 2021; Pontara et al., 2016). Our results show that soil water availability leads to functional clustering and low water availability leads to a dispersion of trait values among the dominant species (Mason et al., 2005). This implies that these species tend to have a greater variation in functional traits and occupy different niches. The species associated to the upper habitat are high tolerances to low resource (Comita & Engelbrecht, 2009).

CONCLUSION

Our research highlights the trait approach to understand the effects of local -scale environment variables to predict the distribution of species and their functional characteristics along a local topographic gradient. We found difference in the functional dominance between habitats. These findings improve our knowledge regarding the different strategies along a local gradient. The leaf traits appear to be more sensible to the edaphic variables along the local topographic gradient. We showed that local gradients can affects the patterns of leaf traits, functional diversity, and show the importance of understand trait-environmental relationship.

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SUPPLEMENTARY DATA

Fig.S1. Multiple regression analysis tree results for the topographic gradient in a local scale.

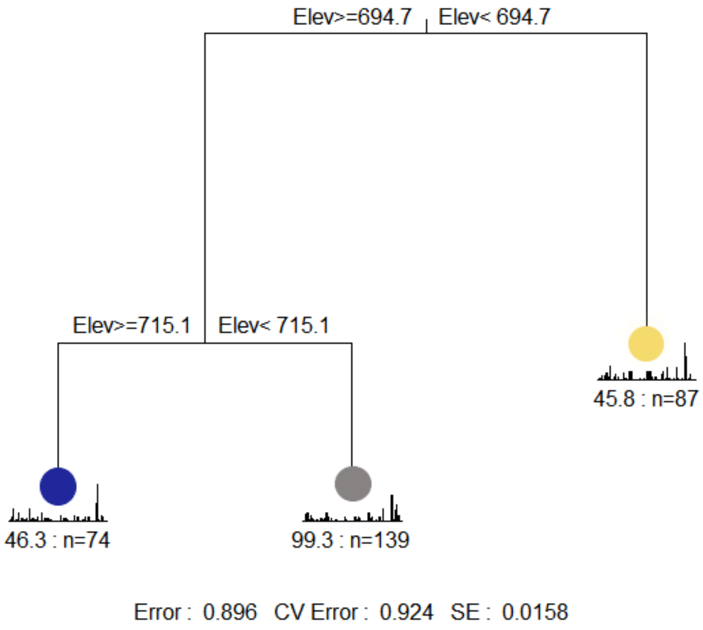


Table S1. Information of the leaf and wood traits

Functional traits	Abbreviation	Units	Min	Max	Mean	Standard deviation	Coefficient of variation (%)
Leaf thickness	Th	mm	0.05	0.25	0.12	0.05	36.97177157
Lef area	LA	cm²	7.57	2987.31	176.08	392.28	222.7820048
Specific leaf area	SLA	cm²/g	46.94	300.40	148.72	45.64	30.68888895
Leaf dry mass content	LDMC	g/g	0.26	0.63	0.43	0.07	16.86794585
Wood density	WD	mg/g³	0.39	1.05	0.67	0.13	19.99110233
Maximum height	Hmax	m	6.28	28	13.25	3.80	28.67485045

Fig.S2. Pearson correlation among all individual variables the topographic gradient in a local scale. For analysis: available P, K, Ca, Na, Mg, exchangeable acidity (HAl), pH (H_2O), organic matter (MO), sum of exchangeable bases (SB); effective cation exchange capacity (t), soil humidity (CGA and CVA) and soil bulk density (Density) and the soil texture as sand, clay and silt contents were included, Elevation (Elev), Slope, Convexity (Convex).

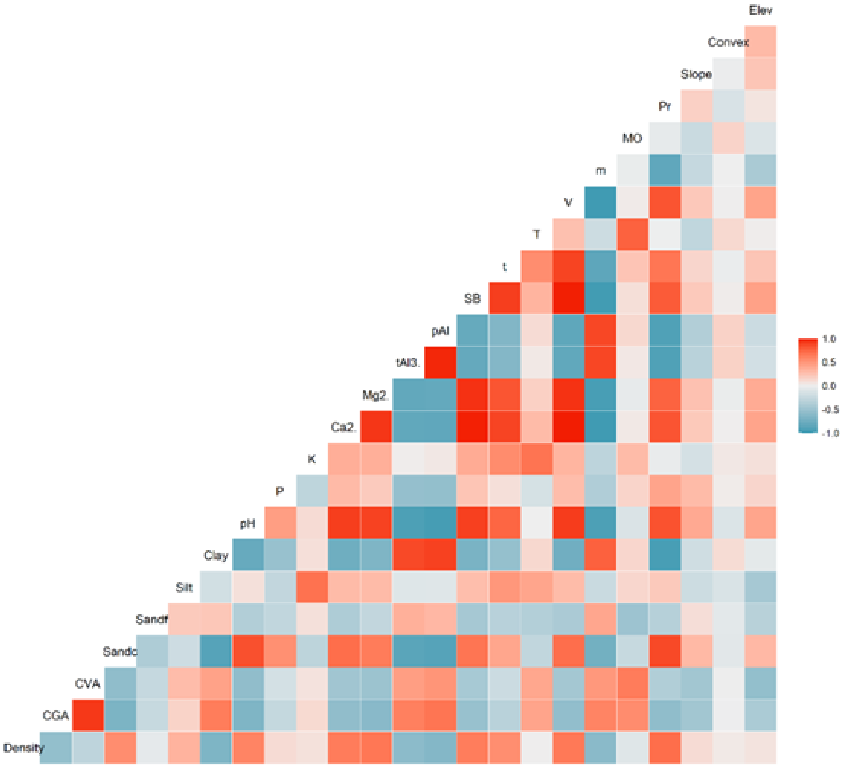


Fig. S3 - Principal correspondence analysis (PCA) of relations between the habitat's subplots and topographic variables, and physical soil attributes. The topographic variables area elevation (Elev), slope, and convexity (Convex). The physical soil variables are fine sand, coarse sand, clay, silt content, soil density and soil moisture (CGA). The evaluated habitats were Higher topographic habitat (H; blue plus); intermediate topographic habitat (I; grey square); and low topographic habitat (L; yellow triangle).

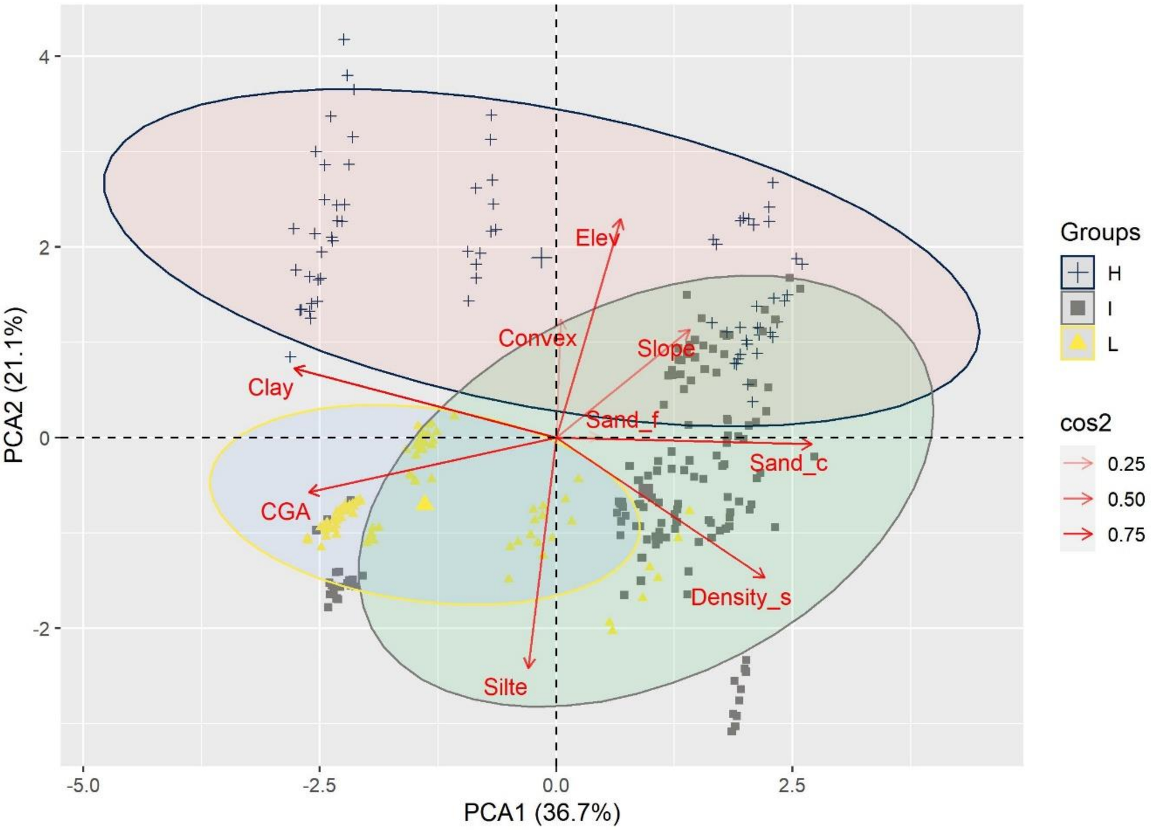
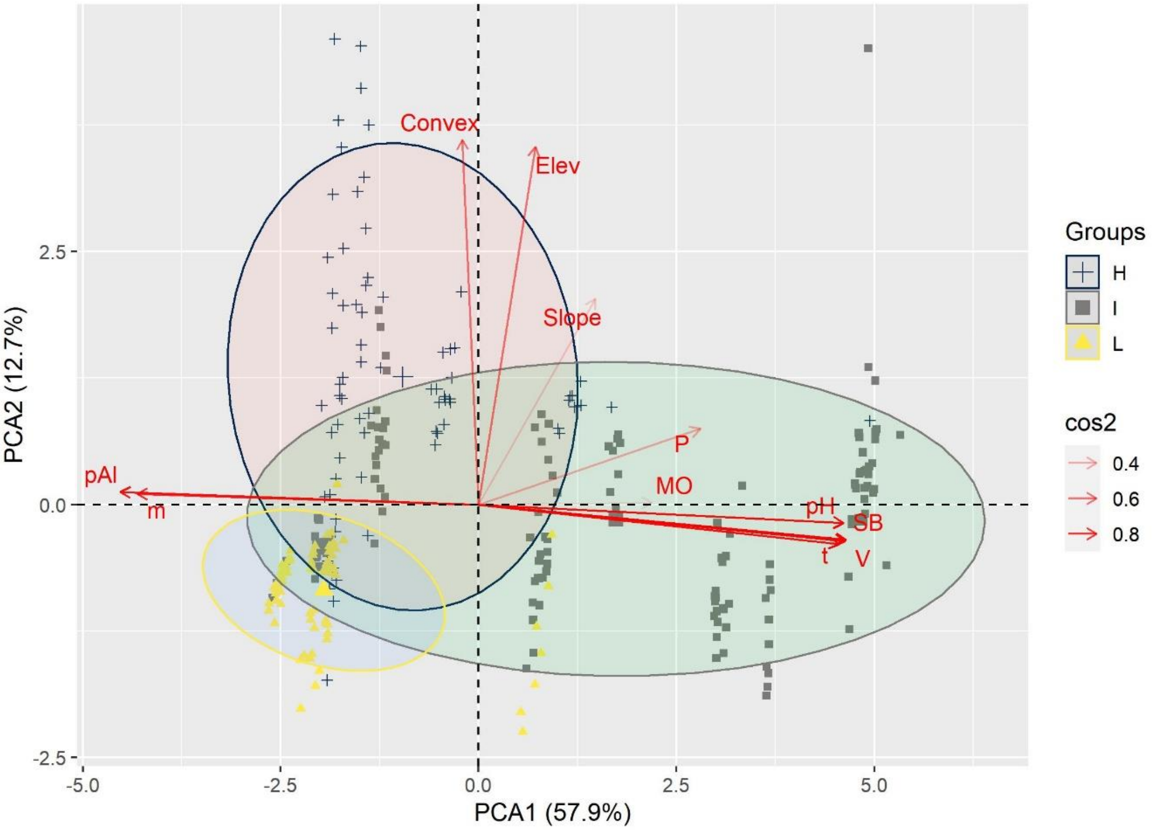


Fig. S4- Principal correspondence analysis (PCA) of relations between the habitat's subplots and topographic variables, and chemical soil attributes. The topographic variables area elevation (Elev), slope, and convexity (Convex). The chemical soil variables are pH (hydrogen potential), MO (organic matter), SB (base sum), m (saturation percentage by aluminum), P (phosphorus), pAl (potential acidity), V (saturation percentage by exchange), t(Cation Exchange Capacity). The evaluated habitats were Higher topographic habitat (H; blue plus); intermediate topographic habitat (I; grey square); and low topographic habitat (L; yellow triangle).



CHAPTER 3 – PATTERNS OF TRAITS IN DIFFERENT FUNCTIONAL GROUPS OF SEASONAL TROPICAL FOREST

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ABSTRACT

Vertical stratification allows for the study of habitat partitioning and general patterns of functional groups on the vertical scale of forests. The functional approach contributes to understanding community structure and identifying the drivers that influence community assembly. The study was conducted in a montane semideciduous seasonal forest in the Atlantic Forest. For 74 species, 35% of the sample's species, which account for 90% of all plant individuals sampled, we measure leaf area (LA; cm²), specific leaf area (SLA; cm²/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m³), maximum height (Hmax; m), leaf thickness (Th; mm), and classified according to leaf phenology (deciduous, semi-deciduous, and evergreen) and dispersal syndrome (zoochory, anemochory, and autochory). Each species was classified as vertical stratum, understory, intermediate, and overstory. To analyze the relationship between leaf phenology and dispersal syndrome with the vertical stratification we performed the Qui-square test. We compared the mean values of the traits to understand the functional patterns within the functional groups of leaf phenology, dispersal syndrome, and vertical strata. The results showed that both leaf phenology and dispersal syndrome showed a dependent relationship with vertical stratification and leaf phenology with dispersal syndrome. Leaf phenology showed a functional pattern of trait mean values of acquisitive-conservative traits between deciduous and evergreen species. The traits mean values of dispersal syndrome shows that zoochory species are correlated with conservative traits and non-zoochory species are correlated with acquisitive traits. out of these results for leaf phenology and dispersal syndrome, the vertical stratification with mean values does not show patterns between strata. Our results highlight the relationship between leaf phenology and dispersal syndromes, and with vertical stratification. This result is very important to understand how seasonal tropical forests are structured vertically and the patterns of functional composition.

Keywords: Vertical strata, Dispersal syndrome; Leaf phenology

INTRODUCTION

Habitat partitioning is an essential question in ecology (Wisheu 1998). Trees exhibit shared preferences for environmental gradients, therefore the habitat partitioning observed in forests is due to the plasticity of each species, which leads to a differentiated distribution (Wisheu 1998). This promotes a niche separation within the forest (Sterck et al. 2011). Evaluation of the variability of the functional traits of the species can improve the understanding of the mechanisms that influence the taxonomic and functional composition of the communities and the functioning of the forests (Liu et al. 2014). Studies that relate species richness and functional traits can contribute to the management of biodiversity conservation and ecosystem services (Díaz & Cabido 2001), helping to explain the differences in growth between species, resilience in resource gradients, the spatial distribution of species (Reich 2014), and therefore the structuring of the community. This approach based on the functional traits of tree communities, can also help explain the differences in vertical occupation (Vale et al. 2009; Ali & Yan 2017). Thus, the study of vertical structures contributes to a better understanding of the relationship between community structure and ecosystem functions (Ali & Yan 2017).

Community structure can be influenced by many factors such as traits, environmental gradients, biotic interactions, and performance (Mcgill et al. 2006). The functional trait approach initially differentiates species by traits and how these traits influence species performance but can also identify general patterns of functional groups inside the community and between communities in different environmental gradients (Mcgill et al. 2006). In Tropical forests tree species shows a trade-off between acquisitive species and conservative species in response to light and water availability (Sterck et al. 2011). The light competition is one of the drives that effects the vertical stratification inside of forests (Falster & Westoby 2003). The vertical classification of strata refers to grouping species of the community according to the average mature height (Smith 1973). Acquisitive species have higher leaf nitrogen concentration, leaf area index, are found in positions of higher light levels, and grow potentially fast (Sterck et al. 2011). While conservative species are more tolerant to shade and drought, and occurs in environmental with low availability of resources (Sterck et al. 2011). Therefore, smaller species tend to show slower growth rates and a conservative strategy; taller species tend to be more competitive, show faster growth rates, and an acquisitive strategy (Laurans et al. 2014).

In the tropical forests, the climate and special factors are the main drives of differentiation of floristic composition (Eisenlohr & Oliveira-Filho 2014; Rezende et al. 2018). Seasonal Tropical Forest composition is driven by potential evapotranspiration and seasonal precipitation (Eisenlohr & Oliveira-Filho 2014; Rezende et al. 2018) and this differentiation drives the changes in leaf phenology and the dispersal syndrome patterns (Reich 1995; Perina et al. 2019). The precipitation gradient leads to a trade-off in leaf phenology strategy (Reich 1995; Aguirre-Gutiérrez et al. 2019) leading to an increase of deciduous species with decreasing of precipitation and soil water availability. Deciduous species is defined by maintain the leaf no more than one growing season (van Ommen Kloeke et al. 2012). The presence of deciduous species in the canopy layer changes the light availability in consequence of the leaf fall in the dry season (Souza et al. 2014). One strategy of understory species is the management of the leaves for a better photosynthesis rate in the dry season (Reich 1995). The phenophases are not totally independent in seasonal forests, for some deciduous species the phenophases are almost chronological, occurring in the leafless phase (van Schaik et al. 1993). In the Seasonal Atlantic Forests, zoochorous species have the peaks of mature fruits in the wet season, while the anemochorus and autochorus species are in the dry season (Perina et al. 2019). Understanding the trade-offs that influence the plant height strategy and the correlation with leaf phenology and dispersal syndrome strategies, and identifying traits beyond the height could predict the tree height of vegetation under different events such as disturbances and climate change (Falster & Westoby 2003; Perina et al. 2019).

The aim of this research is verifying the functional traits composition of the vertical strata and if strategies adopted by trees throughout vertical stratification are related to functional groups (leaf phenology and dispersal syndrome). By differentiating the species into groups of vertical strata (Smith 1973), we hypothesized that (1) species classified as overstorey are mostly deciduous and semi-deciduous and have a higher proportion of anemochoric and autochoric species, while understory species are mostly evergreen and with zoochoric. (2) We hypothesize that deciduous and semi-deciduous species have higher acquisitive trait values, mainly leaf traits, and, mostly, show anemochory and autochory dispersal strategies. While evergreen species will have more conservative trait values and a higher proportion of species with zoochoric dispersal, compared to other leaf phenology strategies. And consequently, (3) the understory will present more conservative trait values and the overstorey will present more acquisitive trait values, and this trade-off along vertical stratification will be driven by leaf phenology and dispersal syndrome.

MATERIAL AND METHODS

Study site

The study was conducted in a secondary forest, the "Mata da Biologia", in the municipality of Viçosa (20°45'14 "S, 42°51'53 "W) in the state of Minas Gerais, southeastern Brazil (Fig. S1). It is classified as Montane Semideciduous Seasonal Forest (Veloso et al. 1991), the fragment has approximately 75 ha (Paula et al. 2002). The area was clear-cut in the early 1920s (Lopes et al. 2002; Paula et al. 2002) and subsequently used for shade coffee plantations until 1926 (Paula et al. 2002). Since then, the area has been abandoned, left to regenerate naturally (Paula et al. 2002), and is in an intermediate stage of succession (Lopes et al., 2002; Paula et al. 2003).

Located in a region of mountainous and strongly undulated relief, the fragment lies between 620 and 820 m, and presents a soil gradient between Red-Yellow Latosols, at the top of the highest regions and on the steepest slopes, and nutrient-rich Cambisols in the valleys (Ferreira-Júnior et al. 2007). According to the Köppen classification, the region's climate is characterized as Humid Subtropical (Cwa) with hot summers and dry winters, mainly between May and August (Alvares et al. 2013), with an average annual temperature of approximately 21°C and average annual precipitation of 1250 mm (Avila-Diaz et al. 2020).

Sample design

Three 1-ha permanent plots were established in the forest fragment with contrasting topographical conditions. Each permanent plot was subdivided into 100 subplots of 10 x 10 m to better capture topography effect on the local scale. In each plot, all living arboreal individuals with a circumference at breast height (CAP) equal to or greater than 10 cm were recorded and measured. All individuals were identified, and species nomenclature follows the Angiosperm Phylogeny Group IV (APG IV 2016) classification system (Souza et al. 2014).

Functional traits

For 74 species, 35% of the sample's species, which account for 90% of all plant individuals sampled, we measure six functional traits that were chosen for this study, four leaf traits and two wood traits: leaf area (LA; cm^2), specific leaf area (SLA; cm^2/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m^3), maximum height (Hmax; m) and leaf thickness (Th; mm). These traits were selected because they can reflect the whole-plant trade-off (Díaz et al. 2016). The leaves used in this study were collected from the highest branches of the individuals. Between three and 15 individuals of each species were collected to obtain an average value for the trait, considering the three hectares. The LA was calculated by measuring five leaves (excluding the petiole) for all species, from images using the ImageJ program (Schneider et al. 2012). The leaf area of the compound leaves was calculated by summing the area of all leaflets. The leaf dry mass was calculated using dried leaves previously dried at 60° C for 72 h. The leaf thickness was calculated using a digital pachymeter with a resolution of 0.01 mm (Stainless Hardened), avoiding measurement in contact with the primary and secondary veins. The specific leaf area was calculated from leaf area/dry leaf mass (cm^2/g). All leaf traits were measured following Pérez-Harguindeguy et al., (2013). Wood density data were obtained from the Global Wood Density Database (Zanne et al. 2009; Chave et al. 2014). Maximum height potential was calculated as the upper 95-percentile height for those trees whose height was equal to or greater than 10% of the observed maximum height of the population (King et al. 2006; Ali et al. 2019). Species were classified according to leaf phenology (deciduous, semi-deciduous, and evergreen) and dispersal syndrome (zoochory, anemochory, and autochory). These data were obtained through research to different bibliographic sources.

Vertical Stratification Classification

To describe the vertical structure of the community, we classified the vertical stratum according to the formula (Vale et al. 2009):

$$\text{Understory: } Q3s \leq Mc$$
$$\text{Intermediate: } Mc < Q3s \leq Q3c$$
$$\text{Overstorey: } Q3s > Q3c$$

Where Q3s corresponds to the third quartile of the heights of the individuals sampled from the species, Mc corresponds to the median of the heights of the individuals sampled from the community and Q3c corresponds to the third quartile of the heights of the individuals sampled from the community.

Statistical analyses

To analyze the relationship between leaf phenology and dispersal syndrome with the vertical stratification we performed the Qui-square test. We used the number of individuals in the contingence table. The analysis was performed using the “stats” (R Core Team 2023) and “corrplot” package (Wei & Simko 2021).

We used Principal component analysis (PCA) to evaluate possible correlations between functional groups (dispersal syndrome, leaf phenology and vertical strata) and traits. PCA allows both simplification and verification of the most important variables of the data (Abdi & Williams 2010). The PCA was performed using the "FactoMineR" package (Husson et al. 2017).

To evaluate possible differences between mean traits values by functional groups, we tested the mean traits values for normality using the Shapiro test. The parametric data was tested with the ANOVA test and non-parametric data was test using the Kruskal-Wallis test for significant differences between groups. When the results were significant, we used T test for parametric data and Wilcox test for non-parametric data to calculate the pairwise mean comparation. This analysis was performed using the “ggpubr” package (Kassambara 2023) and “ggplot2” package (Wickham 2016). To assess possible significant relationship between maximum height (explanatory variable) and the traits (response variable), we performed a linear regression. The graphics were built using “ggplot2” package (Wickham 2016). All analyses were performed in R environment (R Core Team 2023).

RESULTS

Of the 74 species sampled, 41 were classified as belonging to the overstory stratum, corresponding to 33.9% (2,216 ind.) of the individuals in the community. 28 species were classified in the intermediate strata, corresponding to 39.1% (2,557 ind.) of the individuals. Only five species were classified as understory, corresponding to 17.4% (1,136 ind.) of the community. Most canopy species have some level of leaf deciduousness (68,3%) and are mostly dispersed by animals (56,1%). The intermediate stratum species, on the other hand, are mostly evergreen (60,7%) and dispersed by animals (82,1%). And the understory was composed mostly by evergreen species (80,0%) and totally by zoochoric species (Fig. 1). The deciduous species showed mostly non-zoochoric dispersal, and the main dispersal strategy was autochory (47.1%). The semideciduous and evergreen species showed mostly zoochoric strategy (Fig. 2).

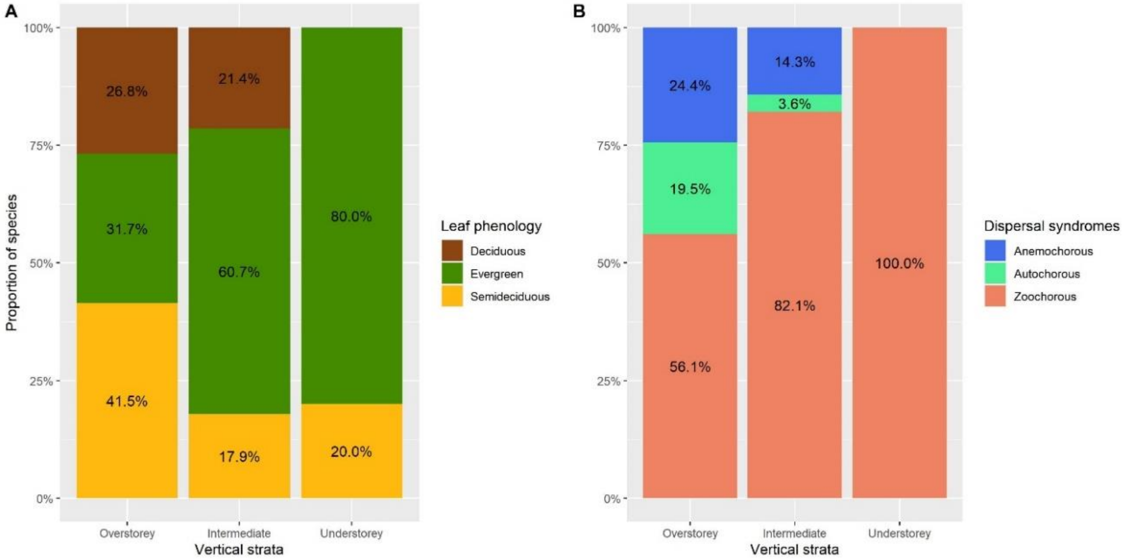

Figure 1 – The proportion of species of leaf phenology (A) and dispersal syndrome (B) per with vertical strata.

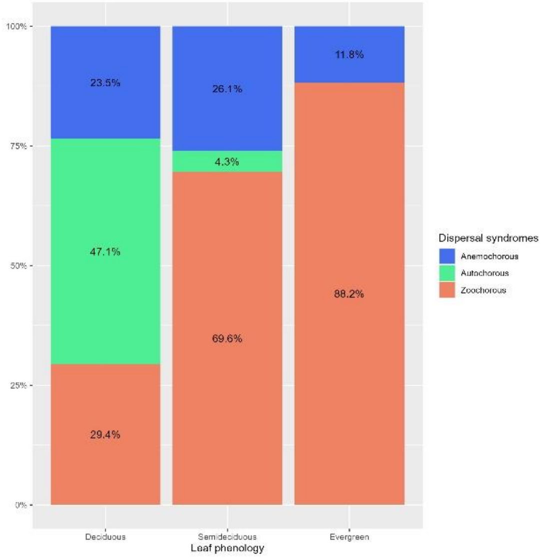

Figure 2 – The proportion of species of dispersal syndrome per with leaf phenology.

The leaf phenology and the vertical strata are dependents (X-squared = 1859.8, df = 4, p-value < 2.2e-16). The deciduous habit is positively and strongly associated with overstory, while the evergreen species are negatively and strongly associated with overstory, although understory shows positive and median association with evergreen species (Fig. 3A; Fig. S1A). The dispersal syndrome and vertical stratification also shows dependency (X-squared = 1690, df = 4, p-value < 2.2e-16). The autochory species are positively and strongly associated with the overstory (Fig. 3B;

Fig. S1B). The dispersal syndrome and leaf phenology are dependents (X-squared = 4475.8, df = 4, p-value < 2.2e-16). The autochory dispersal syndrome is positively and strongly associated with deciduous species (Fig. 4). The zoochory shows positive correlation with evergreen species and negative correlation with deciduous and semideciduous species (Fig. S2).

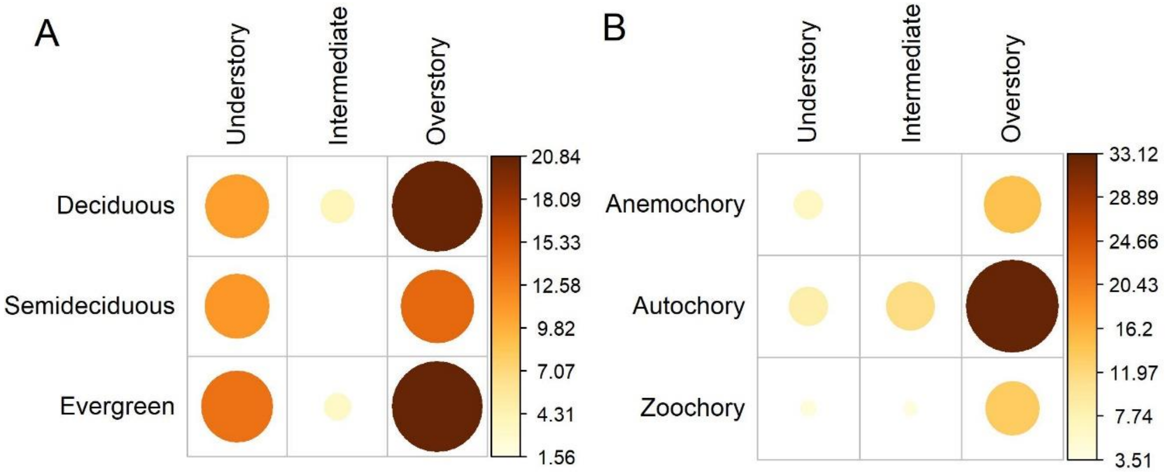

Figure 3 – The contribution of each category of leaf phenology (A) and dispersal syndrome (B) to the association with the categories of vertical stratification.

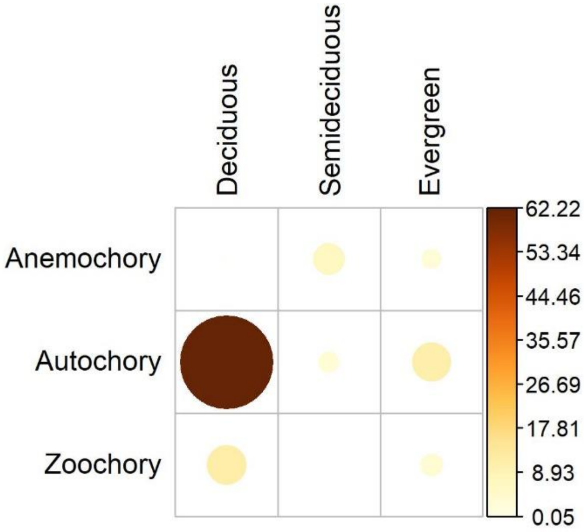

Figure 4 – The contribution of each dispersal syndrome to the association with the categories of leaf phenology.

Distribution of species in the trait space

The three axes represent 72.2% of the variance in leaf phenology and dispersal syndrome functional groups (Fig. S3). The Leaf phenological functional space shows a gradient between deciduous, semideciduous, and evergreen species (Fig. S3A and B). Deciduous species with high SLA and lower Th, and taller species. Semideciduous species are taller with lower Th values. The Evergreen species showed shorter species with higher Th and lower SLA (Fig. 5B, C, and D). The dispersal syndrome functional trait space shows a separation between dispersal strategies (Fig. S3C and D). Zoochory species shows to be smaller with higher WD and greater thickness (Fig. 6). The anemochory syndrome has higher SLA, thin leaves and lower WD (Fig. 6). Autochory species present high LDMC, SLA, WD, thin leaves, and the tallest species (Fig. 6D).

The three axes represented 80.8% of the variance in vertical stratification groups (Fig. S4). The first axis (PCA1) was mainly positively correlated with LA and SLA and negatively with WD. The second main axis (PCA2) separates species with high SLA and LDMC from species with high Th. Although the functional space appeared to separate overstory and understory species from intermediate strata species, there were no significant differences in the mean trait values between the vertical strata groups (Fig. 7).

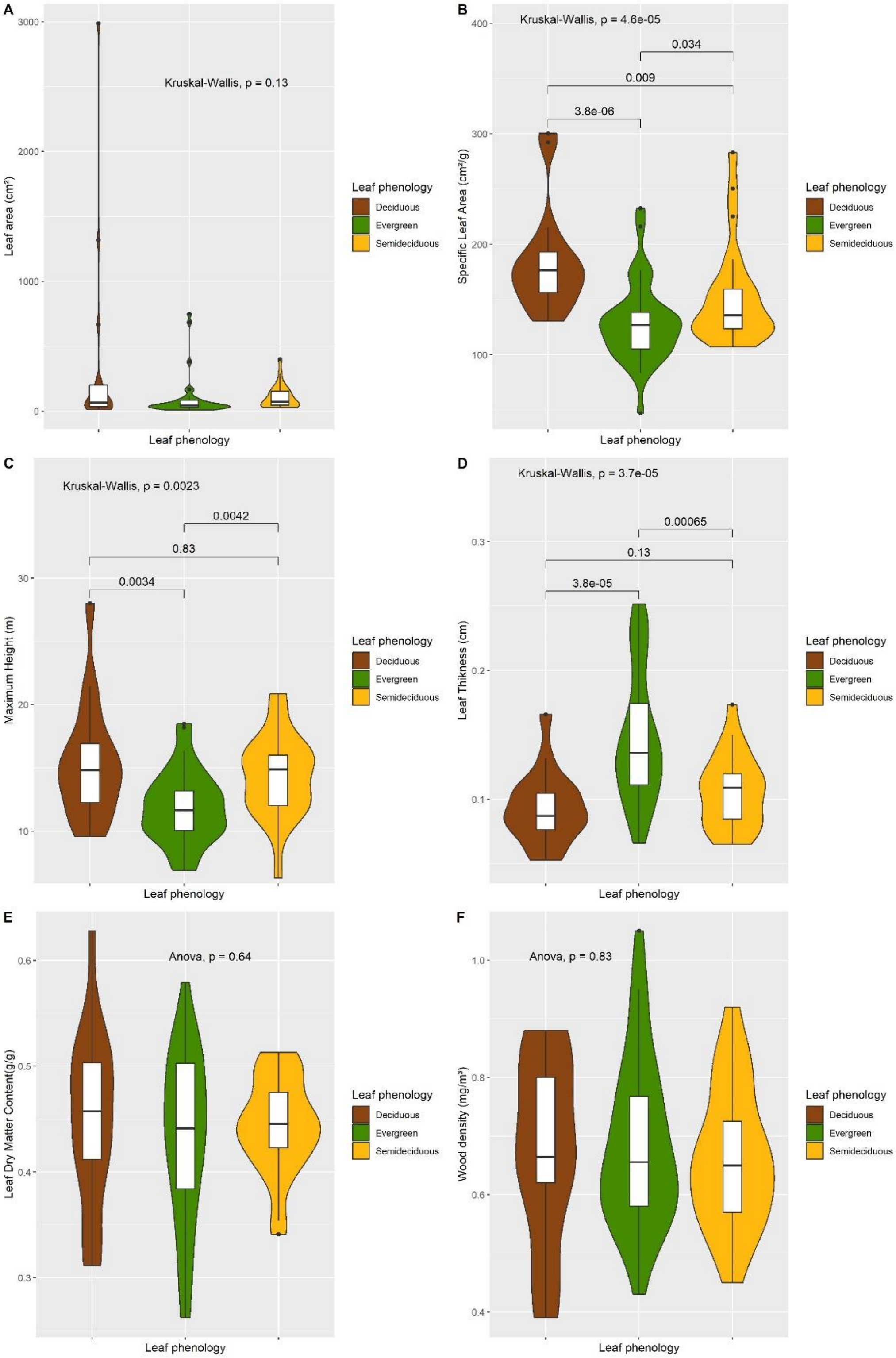

Figure 5 - Variation in the mean trait's values for Leaf phenology group. The functional traits are leaf area (A), specific leaf area (B), maximum height (C), leaf thickness (D), leaf dry mass content (E), and wood density (F). The evaluated Leaf phenology was deciduous (brown); semideciduous (yellow); and evergreen (green).

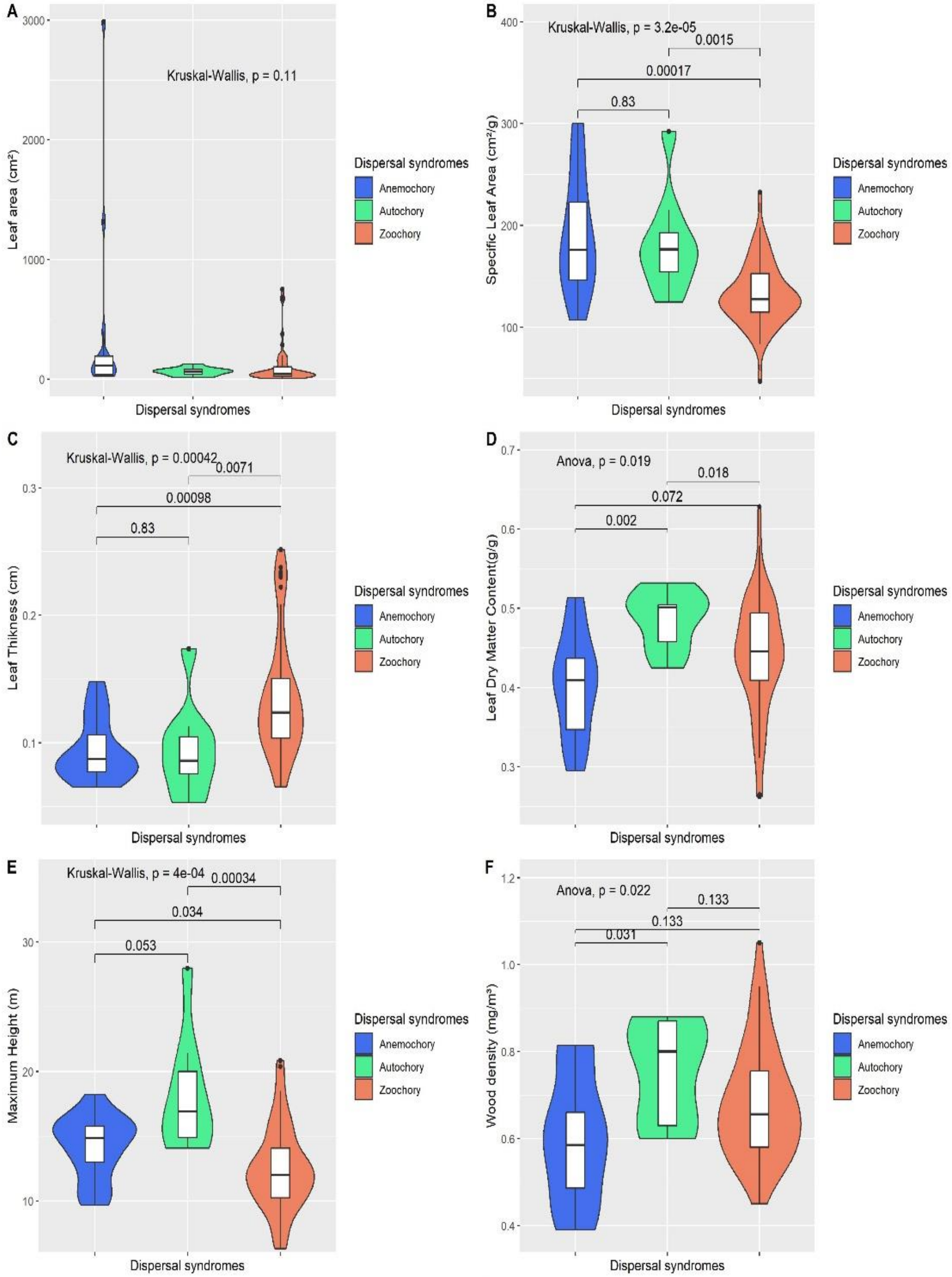

Figure 6 - Variation in the mean trait’s values for Dispersal syndrome group. The functional traits are leaf area (A), specific leaf area (B), leaf thickness (C), leaf dry mass content (D), maximum height (E), and wood density (F). The evaluated dispersal syndromes were Anemochory (blue); autochory (light green); and zoochory (salmon).

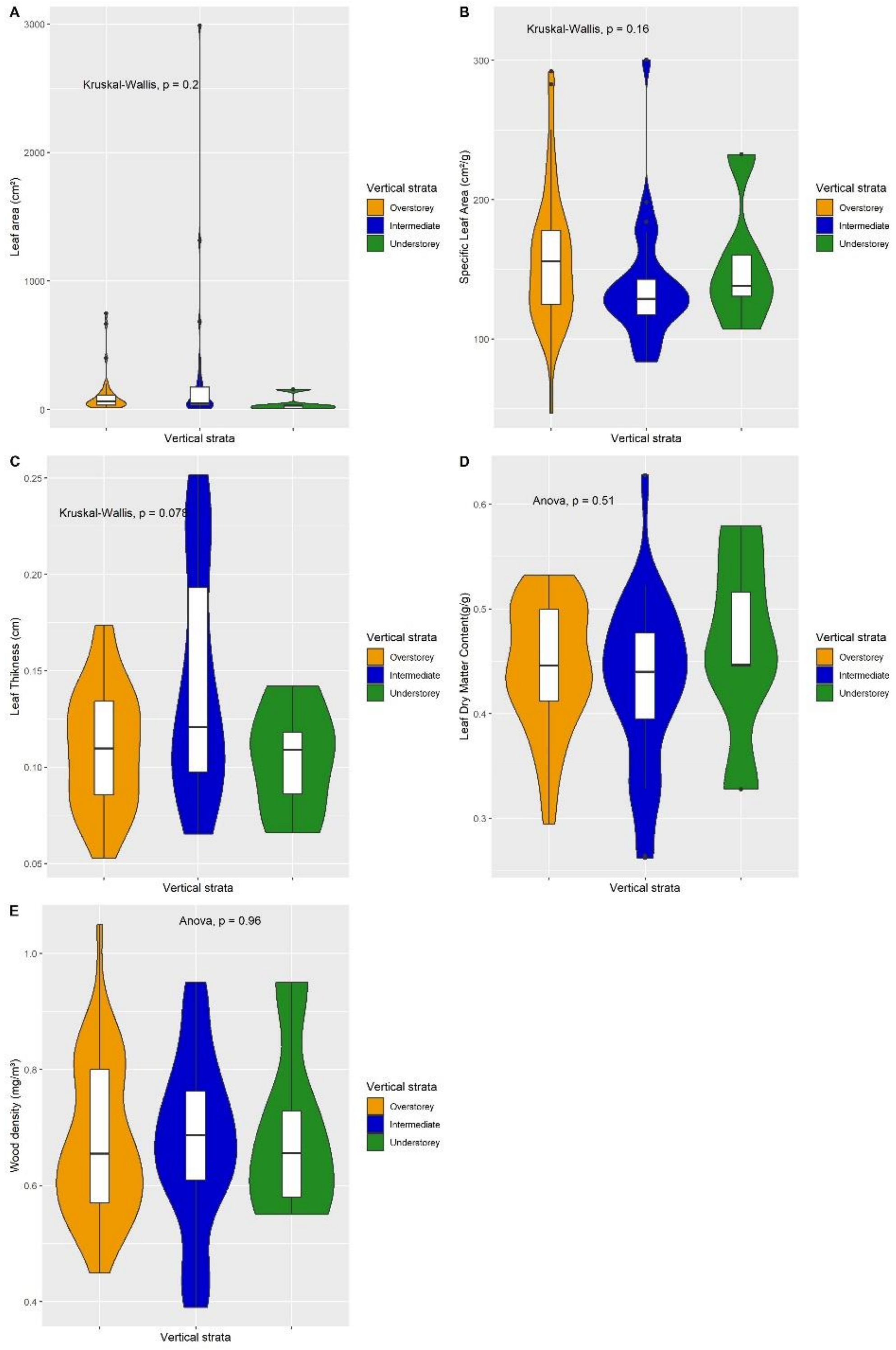

Fig. 7 - Variation in the mean trait's values for vertical stratification. The functional traits are leaf area (A), specific leaf area (B), leaf thickness (C), leaf dry mass content (D), and wood density (E). The evaluated vertical strata were Overstorey strata (yellow); intermediate strata (blue); and understorey (green).

DISCUSSION

The aim of this study was to understand the differences of traits within leaf phenology and dispersal syndrome strategies, and how this differentiation affects the vertical stratification of forests. On a local scale, the functional groups studied here have different traits mean values within the groups, but they do not seem to affect the functional differentiation of the vertical stratum.

Leaf phenology and Vertical Stratification

We found that deciduous species are the leaf phenology strategy that most contributes to the dependence on vertical stratification, especially correlated with the overstory strata. Our results support the first hypothesis that the leaf phenology change along the vertical stratum, showing significant dependency in a Seasonal Forest. The relationship between deciduous species and vertical stratification observed in this study was reported before (Reich 1995; Condit et al. 2000; Lopes et al. 2014; Souza et al. 2014). In tropical forests, the species richness, individuals, and the crown area of deciduousness patterns change along the rainfall gradient (Condit et al. 2000; Fauset et al. 2012; Aguirre-Gutiérrez et al. 2019). Seasonal forests are more related with deciduousness canopy, since the rate of deciduousness tend to increase with the increase of dry periods (Condit et al. 2000). This relationship could be related with the differences in the functional traits, within the leaf phenology group (Alvarez-Yepiz et al. 2014; Aguirre-Gutiérrez et al. 2019).

The deciduous species are taller, have less thick leaf and bigger values of SLA, while evergreen species are smaller than the other strategies and have more thick leaf, and lower values of SLA. This significant differences between functional traits mean results in a resource acquisitive-conservative trade-off (Reich 2014) between the different leaf phenology strategies. Deciduous species have leaves with a short leaf lifespan (Reich 1995), then associated with their functional characteristics, lik higher mean SLA andg higher mean height, allowed a high photosynthetic rate (Reich 1995), even losing the leaves in the driest season. This leaf phenology strategy shows higher investment on photosynthesis (Aguirre-Gutiérrez et al. 2019), structural allocation (Álvarez-Yépiz et al. 2017), and drought-tolerant (Fauset et al. 2012). We found that the evergreen species are positively correlated with the understory and negatively with the overstory. This leaf phenology strategy has a long leaf lifespan (Reich 1995) being associated to a continuous production of leaf along the year (Perina et al. 2019). In addition with other functional traits, like higher WD, low leaf nitrogen and phosphorus content (Aguirre-Gutiérrez et al. 2019) suggest that evergreen species tends to assume a conservative resource usestrategy, allowing evergreen species to occupy the understory (Fauset et al. 2012; Lopes et al. 2014), since the understory species tend to show a lower competition to light and slower growth rates (Laurans et al. 2014). This result supports the hypothesis of a trade-off of resource acquisitive-conservative strategies within the leaf phenology strategies, between conservative evergreen species and acquisitive deciduous species. The leaf traits associated with maximum height allow deciduous species to maximize photosynthesis during the wetter season, while in the dry season photosynthesis is dormant (Fenner 1998).

Dispersal syndrome and Vertical Stratification

The results show that dispersal strategies present clear differences in mean values of the traits. The zoochoric species have thicker leaf, higher LDMC and lower SLA, while the autochoric species are taller, have higher WD and lower thick, showing a resource acquisitive-conservative trade-off (Díaz et al., 2016; Reich, 2014; Wright et al., 2010) between conservative zoochory species and acquisitive non-zoochoric species, anemochory and autochory. The rapid-growth and the stature of non-zoochoric species increase the competitive abilities (Wright et al. 2010), mostly for a better dispersal success. Although positive correlation between autochory and overstorey trees is not always found for Tropical forests (Clark et al. 2018). The correlation between Hmax and non-zoochoric species could be an advantage for seed and fruit dispersal, since the canopy species can achieve long distance dispersal and decreasing the aggregation between species especially for autochoric species (Clark et al. 2018).

The autochoric species are the dispersal syndrome strategy that more contribute to the dependency with vertical stratification, especially with the overstory strata. Our results support the first hypothesis that the dispersal syndrome change along the vertical stratum, showing significant dependency of vertical stratification, as well with leaf phenology in a Seasonal Forest. In Seasonal forests, autochory and anemochory are both related with seasonal patterns during the year, occurring mainly in the dry season (Perina et al. 2019), like the tree deciduousness occurs have the peak of leaflessness in the same season (Reich 1995; Rubim et al. 2010; Perina et al. 2019). This overlap between leaflessness and dispersal syndromes could be associated with dispersal facilitation (Perina et al. 2019), as well as with a better performance for the recruitment of new individuals. The moment when germination occurs is the most important of the plant, the dispersal of seed before the rainy season occurs before the mostly resource season favoring the seeds germination (Rathcke & Lacey 1985; Reich 1995; Fenner 1998).

Patterns of traits along a vertical stratification

We found that, despite of relationship between leaf phenology and dispersal syndrome with vertical stratification and the differences between values traits inside these groups, the results show that there are no significant differences of traits mean values within strata. Although Ali and Yan (2017) showed that overstory and understory layers could present different functional identities in a Subtropical forests. In Seasonal forest, the presence of deciduous species on the overstory layer doesn't affect the species richness and density of the sub-canopy (Souza et al. 2014). The different leaf phenology strategies in the overstory and along the vertical strata provide great variability in luminosity along the vertical structure and throughout the year (Souza et al. 2014), allowing different strategies to occur in the sub-canopy, allows the growth of light-demanding species inside the forests (Souza et al. 2014), together with shade tolerant species can explain the no partition of the functional identity between strata. Light demanding species tend to have more acquisitive traits and shade-tolerant tend to have more conservative traits (Sterck et al. 2011; Rüger et al. 2012; Martínez-Garza et al. 2013), leading to a greater variation in traits values by strata, as our results for Seasonal Tropical Forests.

CONCLUSION

Our results showed that there is a relationship between leaf phenology and dispersal syndrome of species with vertical strata, but despite this dependence observed, the functional traits of vertical strata are not associated with the functional composition of these groups. We observed that deciduous species tend to possess more acquisitive leaf traits and bigger average height, while evergreen species have more conservative leaf traits and lower average height. This result is in line with what we expected, both for the foliar phenology and the dispersion strategy. This result is very important to understand how seasonal tropical forests are structured vertically at the level of functional composition. We can conclude that the correlations between dispersal and vertical stratification, as well as dispersal and foliar phenology strategies, demonstrate how the synchrony of these two phenological phases may be associated with a strategy to increase the success of dispersions and recruitment in Seasonal Tropical Forests. This study highlights the importance of studying the relationships between leaf and fruit phenology of plants, as well as the phenological patterns, for a better understanding of how this relationship can contribute to obtaining resources and the survival of tropical forest trees.

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SUPPLEMENTARY DATA

Figure S1 – The Pearson residual values of categories of leaf phenology (A) and dispersal syndrome (B) to the categories of vertical stratification.

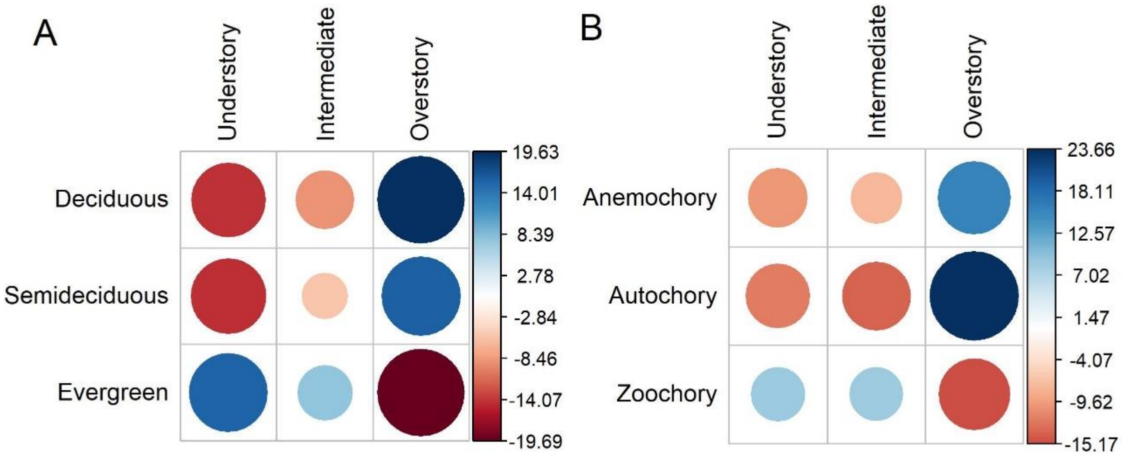


Figure S2 – The Pearson residual values of each category of dispersal syndrome to the categories of leaf phenology.

Figure S3 - Principal correspondence analysis (PCA) of relations between Leaf phenology (A and B), Dispersal syndromes (C and D) and mean species traits values. The functional traits are leaf area (LA; cm²), specific leaf area (SLA; cm²/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m³), leaf thickness (LT; mm) and maximum height (Hmax; m). The evaluated leaf phenology was Deciduous (Browm circles); Evergreen (green triangle); and Semideciduous species (yellow square).

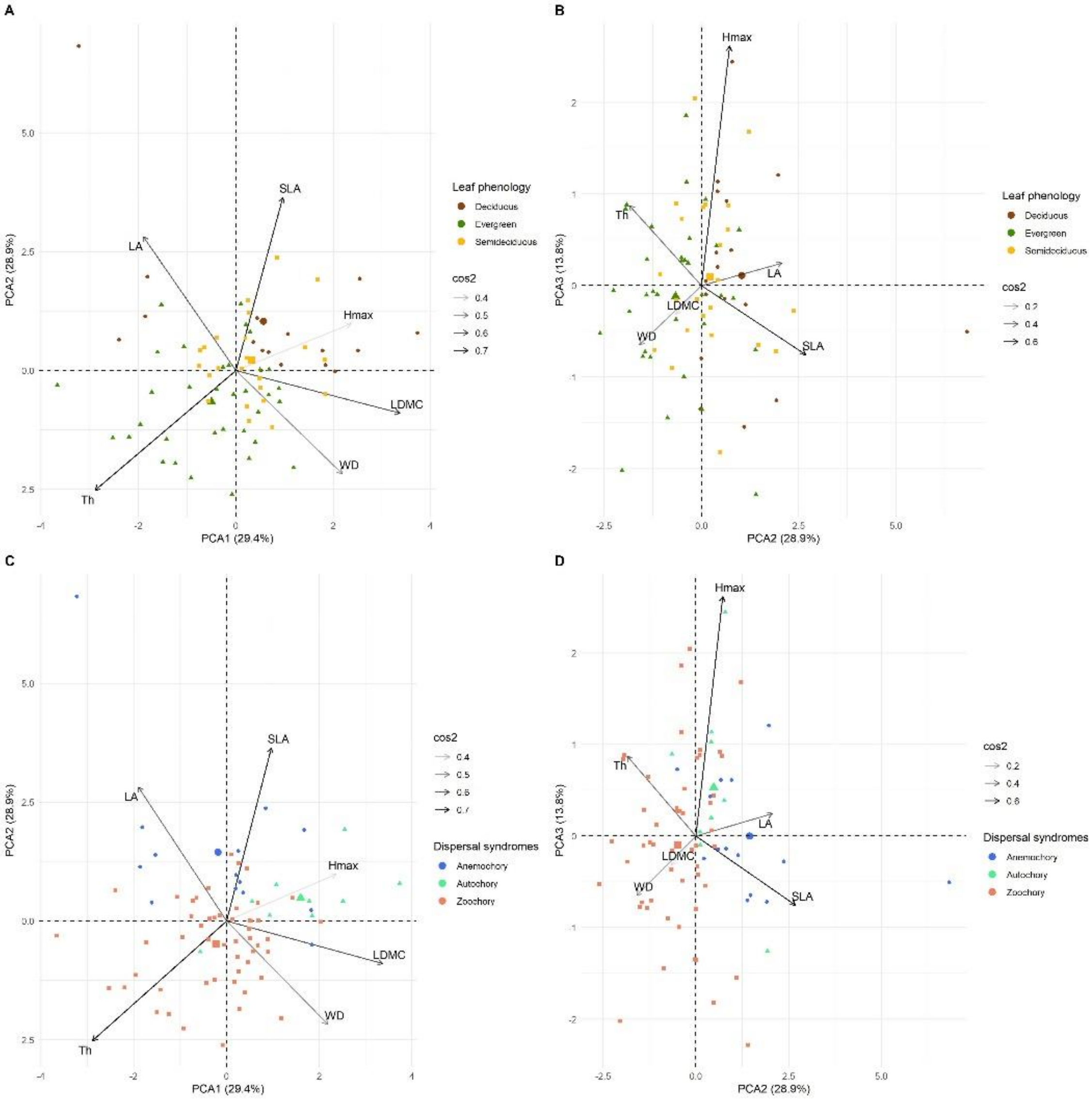


Figure S4 - Principal correspondence analysis (PCA) of relations between the vertical stratification and mean species traits values. The functional traits are leaf area (LA; cm²), specific leaf area (SLA; cm²/g), leaf dry mass content (LDMC; g/g), wood density (WD; mg/m³) and leaf thickness (LT; mm). The evaluated vertical strata were Overstorey strata (yellow circles); intermediate strata (blue triangle); and understorey (green square).

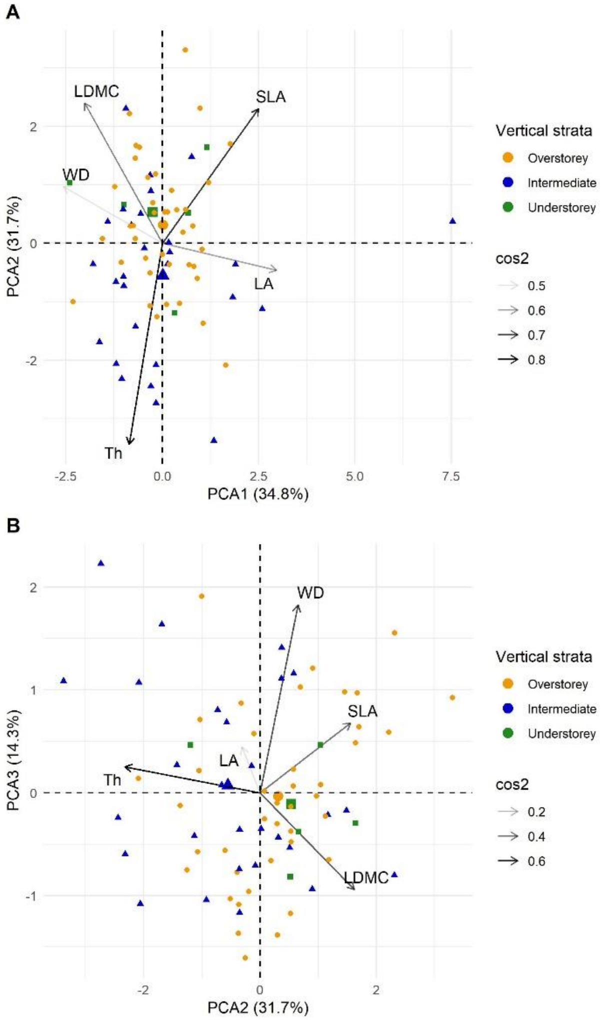
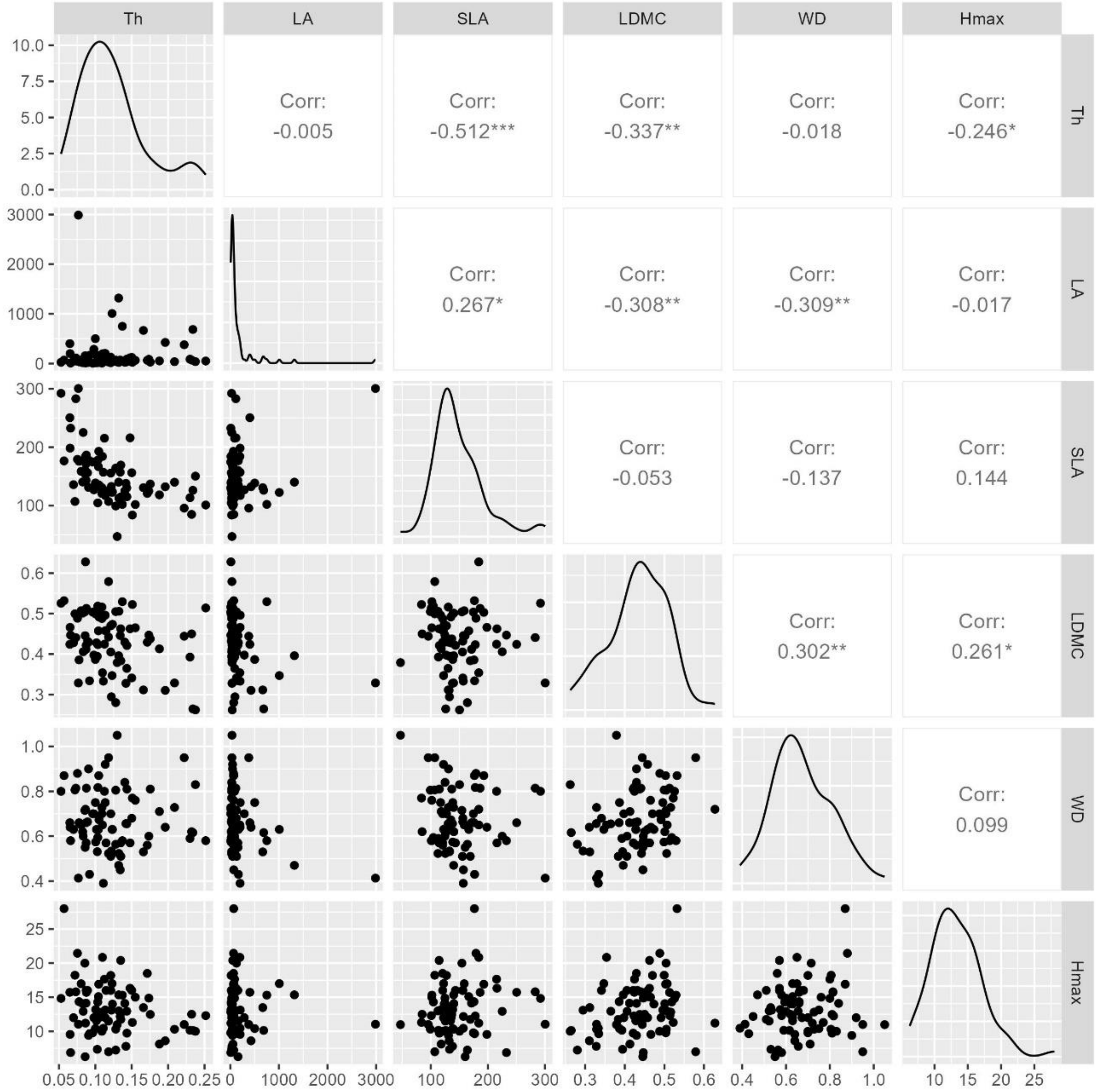


Figure S5 – The correlation between functional traits.



GENERAL CONCLUSION

This study aimed to evaluate how local-scale topography (edaphic-topographic gradient) influences and shapes the diversity (taxonomic, functional, and phylogenetic) and functional traits of the tree community in a secondary fragment of the Atlantic Forest and to verify the patterns of functional composition of the vertical stratification. We can conclude that topography at a local scale can influence the taxonomic, phylogenetic, and functional diversity of the community, with soil variables having the greatest influence on community assembly. Higher areas were characterized by lower diversity, and the closest species were more distant from each other and functionally showed conservative leaf characteristics. The intermediate areas behaved as phylogenetically and functionally intermediate and stood out for their greater species diversity. In the lower areas, the species showed more acquisitive functional characteristics, particularly leaf traits, and less functional divergence. The vertical distribution of functional composition showed that the trees that make up the canopy and sub-canopy were more deciduous and had a higher rate of non-zoochoric dispersal. Within the strategies of leaf deciduousness and dispersal syndrome, the species presented a trade-off of resource acquisition-conservation, the deciduous species and those with autochoric dispersals presenting acquisitive strategies, while the evergreen and zoochoric species presented conservative characteristics. Despite the relationship between deciduousness and dispersal with vertical stratification, the different strata did not show significant differences in average trait values per species, demonstrating a wide dispersal of traits by strata.

In general, we can conclude that on a local topographic scale, soil seems to be the main factor influencing the distribution of species and the functional characteristics of the horizontal distribution. Even on a local scale, edaphic variations promoted by variations in topography (elevation, slope, and convexity) act on the community, with the gradient of water and nutrient availability being the most important for the taxonomic and functional structuring of the tree community. This result stands out because it occurs in seasonal vegetation, which is characterized by a more demarcated dry season. These results showed that small variations in the chemical and physical characteristics of the soil can influence the availability of water, which is directly related to species selection. We must emphasize the need for more studies at a local scale to understand the local environmental factors that influence species distribution, especially in seasonal forests. These results are important for clarifying the relationships between species, functions, and the environment on a local scale, especially in seasonal forests. They can contribute to the understanding, conservation, and restoration of Semi-deciduous Seasonal Forests.