



ANDRÉ MACIEL DA SILVA SENE

**MORTALITY IN TROPICAL FORESTS: INVESTIGATING
SCALES TO UNRAVEL PROCESSES**

LAVRAS–MG

2024

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Botânica Aplicada, área de concentração em Botânica Aplicada, para a obtenção do título de Doutor.

Prof. Dr. Rubens Manoel dos Santos

Orientador

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ANDRÉ MACIEL DA SILVA SENE

**MORTALIDADE EM FLORESTAS TROPICAIS: INVESTIGANDO ESCALAS PARA
DESVENDAR PROCESSOS**

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Aprovada em 27 de março de 2024.

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LAVRAS-MG

2024

Aos meus pais “Bebel” e “Nenzinho”, meu irmão “Guto” e minha esposa Andressa.

Dedico

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“É triste pensar que a natureza fala e que o gênero humano não a ouve.”

(Victor Hugo)

RESUMO

A dinâmica das comunidades arbóreas é diretamente influenciada pelas condições dos ambientes em que se desenvolvem, particularmente em relação às características do solo e ao clima. Esses fatores exercem influência direta na funcionalidade dos organismos, selecionando aqueles capazes de adaptar suas características anatômicas e/ou morfológicas para otimizar a utilização dos recursos disponíveis no ambiente. Nesse contexto, esta tese resulta em dois artigos. O primeiro busca avaliar especificamente a mortalidade das maiores árvores de cada espécie em diferentes áreas florestais do estado de Minas Gerais, em relação aos padrões de precipitação e temperatura. Os resultados permitem elucidar os efeitos dessas variáveis na mortalidade das árvores, identificando as espécies mais afetadas por essas interações em cada tipo de floresta. O segundo artigo aborda de maneira mais detalhada a dinâmica e o funcionamento de uma área de Floresta Estacional Decidual localizada na região Norte do mesmo estado, com o objetivo de compreender como os indivíduos arbóreos de diferentes classes diamétricas respondem funcionalmente às condições do solo, especialmente em relação à fertilidade. Os resultados deste segundo estudo revelam que tanto a dinâmica da comunidade quanto a funcionalidade são diferentes quando avaliadas as classes diamétricas e as diferentes características de solo.

Palavras-chave: Dinâmica Florestal; Características Funcionais; Condições Climáticas; Condições edáficas.

ABSTRACT

The dynamics of arboreal communities are directly influenced by the environmental conditions in which they develop, particularly concerning soil characteristics and climate. These factors exert a direct influence on organism functionality, selecting those capable of adapting their anatomical and/or morphological characteristics to optimize the use of available resources in the environment. In this context, this thesis results in two articles. The first aims to specifically assess the mortality of the largest trees of each species in different forest areas of the state of Minas Gerais, in relation to precipitation and temperature patterns. The results help elucidate the effects of these variables on tree mortality, identifying the species most affected by these interactions in each type of forest. The second article addresses in more detail the dynamics and functioning of an area of Deciduous Seasonal Forest located in the northern region of the same state, aiming to understand how arboreal individuals of different diameter classes respond functionally to soil conditions, especially regarding fertility. The results of this second study reveal that both community dynamics and functionality differ when evaluating diameter classes and different soil characteristics.

Keywords: Forest Dynamics; Functional Traits; Climatic Conditions; Edaphic Conditions.

INDICADORES DE IMPACTO

As florestas são caracterizadas como extensas áreas dominadas por árvores, mas que abrigam uma ampla diversidade de outros seres vivos. Esse ecossistema desempenha um importante papel no equilíbrio ecológico do planeta, principalmente no que diz respeito ao fornecimento de habitats para diversos organismos vivos e também pela prestação de serviços ecossistêmicos à sociedade, como é o caso da regulação do clima, regulação do ciclo da água, regulação de carbono, estabilidade de solo, abrigo a polinizadores, dentre vários outros fatores, que afetam diretamente a vida na Terra. Nesse sentido, estudos como este, que visem compreender o funcionamento das florestas em relação às condições climáticas, como é o caso da dinâmica florestal, em especial quando se trata de mortalidade, são de extrema importância social, econômica e ambiental, principalmente. Com a mortalidade das árvores nas florestas, os serviços ecossistêmicos sofrem modificações substanciais, que podem influenciar diretamente na vida das pessoas, inclusive, financeiramente, pois afetará o sistema de produção agrícola e, conseqüentemente, tornará o processo e os produtos mais caros. Além da questão abordada acima, a floresta se configura como um modelo de estudo em relação às condições climáticas e às mudanças drásticas que tem ocorrido sobre esses fatores, principalmente no que tange a precipitação e a temperatura, mas os resultados influenciados por essas modificações nas florestas ocorrem também em outros ecossistemas terrestres, mostrando a importância deste tipo de estudo na indicação desses efeitos. Nesse sentido, o presente estudo impacta o item 5 (Meio Ambiente) da Política Nacional de Extensão, se relacionando com os seguintes Objetivos de Desenvolvimento Sustentável (ODS) da Organização das Nações Unidas (ONU): 11. Cidades e comunidades sustentáveis, 13. Ação contra a mudança global do clima, 15. Vida terrestre.

IMPACT INDICATORS

Forests are characterized as extensive areas dominated by trees, but which harbor a wide diversity of other living beings. This ecosystem plays an important role in the ecological balance of the planet, primarily concerning the provision of habitats for various living organisms and also by providing ecosystem services to society, such as climate regulation, water cycle regulation, carbon regulation, soil stability, shelter for pollinators, among several other factors, which directly affect life on Earth. In this sense, studies such as this one, aimed at understanding the functioning of forests in relation to climatic conditions, such as forest dynamics, especially when it comes to mortality, are of extreme social, economic, and environmental importance. With the mortality of trees in forests, ecosystem services undergo substantial modifications, which can directly influence people's lives, including financially, as it will affect the agricultural production system and, consequently, make the process and products more expensive. In addition to the issue addressed above, the forest serves as a model for studying climatic conditions and the drastic changes that have occurred in these factors, especially regarding precipitation and temperature, but the results influenced by these modifications in forests also occur in other terrestrial ecosystems, showing the importance of this type of study in indicating these effects. In this sense, the present study impacts item 5 (Environment) of the National Extension Policy, relating to the following Sustainable Development Goals (SDGs) of the United Nations (UN): 11. Sustainable cities and communities, 13. Action against global climate change, 15. Life on land.

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PRIMEIRA PARTE

INTRODUÇÃO GERAL

O funcionamento das florestas tem sido um tema de interesse contínuo na ecologia, principalmente devido à sua complexidade, que é resultante da interação entre diversos fatores, tanto bióticos quanto abióticos. Esses fatores são suscetíveis a variações temporais e espaciais, resultando na formação de florestas distintas, cada uma caracterizada por suas próprias condições ambientais. Essas condições podem incluir aspectos como topografia, clima, ciclo de nutrientes, dentre outros. Como resultado dessas variações, as florestas diferem entre si e esta diversidade influencia diretamente na composição das espécies de árvores presentes. Assim, cada floresta é única em sua composição e funcionamento, refletindo a complexidade e a diversidade dos processos ecológicos que operam em seu interior.

Contudo, devido à sua sensibilidade aos fatores que as compõem, as florestas têm sido substancialmente alteradas não apenas por variações temporais ou espaciais, mas principalmente em decorrência de atividades humanas. Estas têm provocado mudanças significativas em um curto período de tempo. Um exemplo notável é o impacto das mudanças climáticas, que têm alterado rapidamente as condições ambientais das florestas e, por conseguinte, os processos que sustentam a integridade desse ecossistema.

Devido a essas circunstâncias, há uma considerável discussão em torno da influência das mudanças climáticas sobre as florestas. Isso é evidenciado pelas alterações nas condições de crescimento das árvores, uma influência direta sobre seu ciclo de vida devido a restrições de recursos, como a disponibilidade de água no solo; pela perda de habitat e fragmentação, especialmente devido à expansão agrícola e outras atividades humanas; e, por último, mas não menos importante, pela mortalidade de árvores, uma consequência provável e lamentável dos efeitos das alterações climáticas sobre as florestas.

Diante dessas considerações, é crucial conduzir pesquisas que tenham como objetivo a compreensão desses impactos, contribuindo de maneira ativa com informações que possam subsidiar a compreensão dos processos que estão sofrendo alterações nas florestas, bem como o desenvolvimento de estratégias de mitigação para essas mudanças, visando evitar uma catástrofe de proporções ainda maiores.

Entre os temas de pesquisa destinados a entender essas questões, destacam-se os estudos relacionados à dinâmica das comunidades arbóreas e às características funcionais. A primeira abordagem permite investigar a história do ecossistema, analisando o comportamento das

espécies arbóreas no ambiente florestal ao longo do tempo. Isso possibilita compreender a influência da interação de vários fatores bióticos e abióticos, especialmente na mortalidade e no recrutamento de indivíduos arbóreos, os quais contribuem diretamente para a manutenção e estabilidade da floresta. A segunda abordagem, por sua vez, oferece uma compreensão mais detalhada dos processos em resposta às condições ambientais, por meio de características mensuráveis nos indivíduos. Tais características refletem diretamente o sucesso adaptativo das plantas, incluindo melhorias nas trocas gasosas, uso eficiente da água e fotossíntese.

Nesse contexto, por meio de experiências pessoais e colaborativas com outros membros do Laboratório de Fitogeografia e Ecologia Evolutiva, observamos durante nossas atividades de campo uma considerável quantidade de indivíduos arbóreos mortos em diversos tipos de florestas. Essa observação motivou a concepção deste estudo e, conseqüentemente, sua realização, com o objetivo de compreender mais detalhadamente os processos envolvidos nesse fenômeno. Nosso estudo se concentrou em investigar a mortalidade de árvores em florestas localizadas no estado de Minas Gerais, abrangendo uma variedade de ecossistemas, desde florestas ombrófilas até decíduas, ao longo de um gradiente latitudinal que se estende do Sul ao Norte do estado.

Nossos resultados mostram, no geral, os padrões de mortalidade em fragmentos de Florestas Tropicais localizadas no estado de Minas Gerais. O primeiro artigo é mais amplo e mostra que a mortalidade tem afetado os maiores indivíduos arbóreos, independentemente do porte das espécies, em diferentes tipos de florestas (Decíduas, Semidecíduas e Ombrófilas), possuindo relação direta com as condições climáticas de temperatura e precipitação; o artigo também lista as 20 espécies arbóreas com maior risco de mortalidade para cada tipo florestal estudado. O segundo busca explorar de forma mais profunda a mortalidade de plantas em um fragmento de Floresta Estacional Decidual, utilizando de abordagem funcional e de dinâmica de comunidades para compreender melhor como se dá o processo, relacionando com as condições edáficas e os diferentes tamanhos que as árvores podem atingir, por meio dos seus diâmetros.

SEGUNDA PARTE - ARTIGOS

ARTIGO 1 - TREE MORTALITY: UNDERSTANDING PATTERNS BEYOND THE DICHOTOMY OF LARGE AND SMALL SPECIES

Artigo elaborado de acordo com as normas do periódico Nature Communications.

ABSTRACT:

Tree mortality has been extensively reported in forest dynamics studies, where special attention has been given to those exhibiting larger sizes within the forest. However, there are no records of studies that avoid the duality between small and large-sized species, which motivated our study. The main objective of this work is to evaluate mortality rates under the influence of climatic conditions in Tropical Forests, not only from the perspective of the largest trees in the forests but rather from the largest individuals of the species regardless of whether it is a small or large-sized species. Different fragments of Tropical Forests were evaluated, comprising Deciduous, Semideciduous, and Evergreen Forests. To test the effects of climate on mortality patterns, the climatic variables Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), and Mean Annual Climatological Water Deficit (CWD) were used. Generalized Mixed Models (GLMMs) were used for data analysis, comparing climatic (MAT, MAP and CWD) and functional variables (Diameter at Breast Height - DBH and Wood Density - WD) and their effects on mortality patterns. As a result, it was possible to list the 20 species at the highest risk of mortality and the 20 at the lowest risk in each forest type. Additionally, the results also showed that climatic conditions influence the mortality of large trees differently when comparing higher and lower values of DBH and WD. From the results, it was possible to conclude that climate affects mortality patterns in forests, but there is no pattern showing that only the largest individuals of the forests are dying, but rather the largest individuals of each tree size, regardless of the maximum size the species can attain.

Keywords: Climate Change; Tropical Forests; Temperature; Precipitation; Forest Conservation; Community Dynamics; Mortality Patterns.

1 INTRODUCTION

Trees are defined as a group of woody plants with significant ecological and economic importance, exhibiting widespread distribution and occupying various terrestrial ecosystems, including those most susceptible to climate change (Kremer et al., 2012). This distribution pattern is directly related to the adaptive processes of these plant organisms throughout their life history, primarily concerning adaptation to climatic conditions (Woodward and Williams, 1987; Alberto et al., 2013; Aguirre-Gutiérrez et al., 2015; Tshwene-Mauchaza and Aguirre-Gutiérrez, 2019). Different climatic conditions have led to different adaptive strategies and, consequently, species differentiation, forming distinct forest types across the globe (Woodward and Williams, 1987; Allen et al., 2010; Alberto et al., 2013), including Tropical Forests.

Tree mortality related to climate has been the focus of discussions, particularly concerning drought and thermal stress (Allen et al., 2010; Bennet et al., 2015; Stovall, Shugart, & Yang, 2019; Hammond et al., 2022). These variables have undergone modifications in terms of severity, duration, and frequency, leading to a gradual increase in tree mortality rates (Allen et al., 2010; Hartmann et al., 2018). It is noteworthy that there is no forest type or climatic zone that is immune to these factors, emphasizing the need for further studies to determine global trends regarding the topic (Allen et al., 2010).

These statements reflect the current discussion on the influence of climate change on forest ecosystems, particularly regarding the survival of tree species. Climate change, especially concerning temperature and precipitation modifications, has affected Tropical Forests (Garcia et al., 2014; Esquivel-Muelbert et al., 2020). The main effects caused by climate change in these forests include alterations in plant distribution, forest dynamics, structure and composition, and phenology (Deb et al., 2018). Among these effects, mass tree mortality processes have been observed in more extreme cases (Dale et al., 2001; Margrove et al., 2015; Esquivel-Muelbert et al., 2020; Bordin et al., 2021; Lima et al., 2023).

As a means to better understand the influence of climate modifications on tree mortality, studies of forest dynamics have been emphasized. This type of study is characterized by "telling the story" of the studied forest fragment, indicating modifications in forest ecosystem characteristics (composition, biomass, individual growth, among others) as a result of the spatial and temporal interaction of biotic and abiotic factors in this ecosystem (Condit, 1995; Rees et al., 2001; McDowell et al., 2020). Through these studies, it becomes

possible to understand the processes involved in regulating the forest community, by monitoring the modifications occurring in the studied plant community (Condit, 1995; Higuchi et al., 2008), allowing for the assessment of the tree mortality process as well.

In light of the foregoing, this article aims to assess tree mortality in Tropical Forests, relating it to temperature and precipitation climatic conditions. Our hypothesis is that climatic conditions influence mortality patterns of large trees in forests, not only concerning larger species but also among the largest individuals of smaller-sized species.

2 MATERIALS AND METHODS

2.1 Study area and vegetation data collection

Forest dynamics data collected between 1987 and 2020 were utilized, covering 33 plots primarily distributed in the southern and northern regions of the state of Minas Gerais, Brazil (total sampled area of 37.62 ha, 940 permanent subplots, Fig. 1). These data constitute the database of the Phytogeography and Evolutionary Ecology Laboratory (LEAF) at the Federal University of Lavras, Minas Gerais, Brazil.

Due to the vast expanse of the state of Minas Gerais, there exists a significant hydrological gradient among the sampled areas, featuring drier areas characteristic of the Caatinga further north, where Deciduous Seasonal Forests (DSF) are located, and wetter areas associated with the Atlantic Forest further south, where Semideciduous Seasonal Forests (SSF) and Evergreen Forests (EF) are found (Oliveira-Filho and Fontes, 2000; Santos et al., 2012). The sampling areas exhibit varied altitudes. In the DSF, altitudes range from 447 to 675 meters above sea level; in the SSF, from 820 to 1300 meters; in the EF, from 1151 to 1491 meters.

Among the sampled plots, 11 are characterized as DSF, totaling 9.8 ha, 245 permanent subplots; 16 areas of SSF, with 21.70 ha, 542 permanent subplots; 6 areas of EF, with 6.12 ha, 153 permanent subplots (Fig. 1; Sup. 1). The size of the sampled area varied according to environmental characteristics, comprising transects ranging from 0.2 to 5.04 ha (Sup. 1). A total of 255,923 tree individuals were evaluated, belonging to 874 species from 88 botanical families: 30,067 individuals in DSF, 178,542 in SSF, and 47,314 in EF. Species were identified following the APG IV (2016) and standardized names according to REFLORA (Flora do Brasil, 2020).

In each plot, species-level identification was conducted, and measurements (diameter at breast height - DBH - at 1.3 m) of all trees that met the inclusion criteria ($DBH \geq 5$ cm) were assessed. The remeasurement and reassessment of these trees were performed at certain time intervals (Sup. 1), during which those that were alive, recruited new individuals, or died were identified.

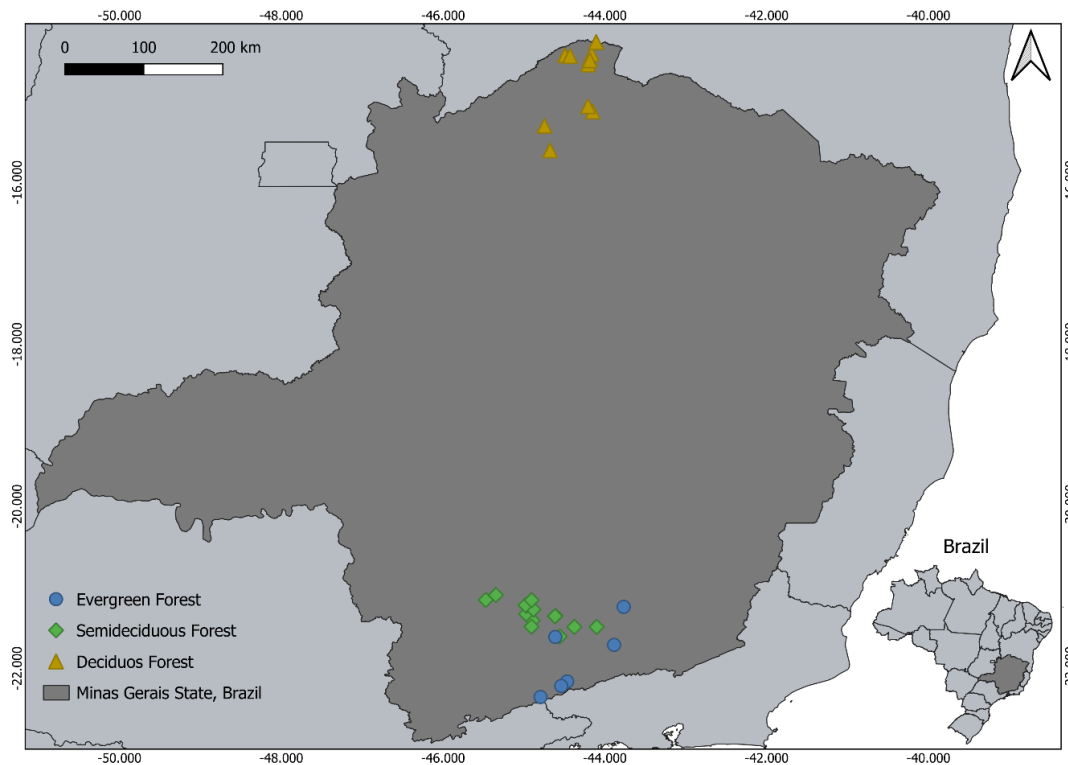


Figure 1: Distribution map of the study areas.

In the case of plants with multiple stems, the “tree inclusion method” was used, obtained through the quadratic mean diameter ($DBHq = \sqrt{d1^2 + d2^2 + d3^2 + d4^2 + \dots + dn^2}$) (Souza et al., 2021). For this purpose, all stems above ground at 1.3 m were considered, provided that the $DBHq$ reached the 5.0 cm inclusion criterion.

In addition to DBH , another functional variable used to understand mortality patterns was wood density (WD). To obtain WD values, species were compared with the global wood density database (Chave et al., 2009), and values were extrapolated. To optimize correspondences, data sets were standardized using The Plant List (2023) and the Taxostand R package (Cayuela et al., 2019). If WD values were not available at the species level, they were extrapolated using the mean WD of the genus or family.

2.2 Obtaining climatic data

Climatic data were obtained from the Climate Research Unit database (CRU TS version 4.04; released on April 24, 2020; <https://crudata.uea.ac.uk/cru/data/hrg>) (Harris et al., 2020). The data used included monthly precipitation (mm), monthly mean temperature (°C), monthly mean daily maximum temperature (°C), and daily evapotranspiration (PETd, mm) with a resolution of 0.5°. The 'downscale' method was used to reduce the data obtained from CRU to a 1 km² resolution; 1 km² data from WorldClim were used (Fick and Hijmans, 2017; Peng et al., 2019). Subsequently, mean values of annual mean temperature (MAT), maximum temperature (Max temp.), and annual mean precipitation (MAP) were calculated over complete years in each monitoring interval of forest dynamics. Another variable used in this study was the maximum annual climatological water deficit (CWD), calculated by summing the differences between reduced monthly precipitation (Pm) and potential monthly evapotranspiration (PET, not reduced) (PET-Pm) only when evapotranspiration exceeded precipitation (water deficit).

Subsequently, through correlation analysis, variables to be used in the tests were selected. For the DSF, only MAP and MAT were used, as Max temp showed a strong correlation with MAT ($r=0.84$) and CWD with MAP ($r=-0.91$); for the SSF and EF, CWD, MAT, and MAP were used, as Max temp demonstrated high correlation with MAT ($r=0.96$ and $r=0.83$, respectively) (Sup.2).

2.3 Data analysis

The analyses were performed in R environment version 4.2.3 (R Core Team, 2023), and the plots were obtained using the ggplot2, corrplot, cowplot, gridExtra, jtools, and interactions packages (Wickham, 2016; Auguie, 2017; Wei and Simko, 2017; Long, 2019b, 2019a; Wilke, 2019).

Initially, information from forest dynamics matrices and climatic data was grouped by forest type studied (DSF, SSF, and EF). Subsequently, climatic variables (MAP, MAT, and CWD), functional variables (DBH and WD), and their effects on mortality rates of large trees were analyzed, along with identifying which tree species were at greater risk of mortality in each forest type.

To understand the probability of mortality of large trees in relation to climatic and functional variables, and the interaction between these variables, Generalized Linear Mixed

Models (GLMMs) were used, with a binomial family and a log-log link function (clog-log) to model the mortality risk. The variable evaluated to understand mortality patterns is the occurrence or non-occurrence of death across intervals. The model used to understand these patterns was: $(\text{lag_Dquad_sca} + \text{WD_sca}) * (\text{map_sca} + \text{cwd_sca} + \text{mat_sca})$. Thus, it was possible to assess how DBH and WD values influence the probability of mortality in relation to climate and vice versa. In this sense, interactions between these variables were tested.

Based on the results of the interactions, the significance of these interactions was evaluated at $p < 0.01$. In the DSF, there was a significant interaction between DBH/MAT and DBH/MAP (Sup 3); in the SSF, significant interactions were observed between DBH/MAP, DBH/CWD, DBH/MAT, WD/MAP, WD/CWD, and WD/MAT (Sup 4); finally, in the EF, interactions were observed between DBH/CWD, DBH/MAT, and WD/CWD (Sup 5).

The second order Akaike Information Criterion (AICc) was used for model selection (Burnham et al., 2011), the lme4 package (Bates et al., 2015) was used to fit the GLMM, and lmerTest was used to calculate the denominator degrees of freedom (Kuznetsova et al., 2017). Subsequently, for model selection, model averaging, and obtaining the marginal R^2 (variance explained by fixed effects) (Nakagawa and Schielzeth, 2013), the MuMIn package was used (Bartón, 2018).

Finally, overdispersion was tested using a simulation-based approach, and the normality and homogeneity of variance were confirmed by inspecting the residuals, using the DHARMA R package (Hartig, 2020).

3 RESULTS

3.1 Relationship between climatic variables and tree mortality risk in each forest type

Based on the results obtained from the analyses, graphs were created for each forest type studied, relating climatic variables (MAT, MAP, and CWD), functional variables (DBH and WD), and plant mortality (Fig. 2). Our initial observation challenges the current findings in research, which suggest that tree mortality is solely linked to the largest tree individuals in forests. But which trees are actually dying? Are they the largest individuals in the forest? Our results indicate that this varies. It can be observed that, in relation to climate and different forest types, the individuals that are dying are, in fact, the largest individuals of the species, regardless of whether they are smaller or larger-sized species, not limited solely to the largest individuals in the forest.

In Deciduous Seasonal Forests (DSF), a relationship with the mortality risk of large trees was observed in the interactions of DBH/MAT and DBH/MAP. In the first case, the analysis results show that the largest trees of small-sized tree species tend to face a higher risk of mortality in warmer DSFs, compared to larger tree species. Conversely, in cooler forests, this risk is elevated for all trees, regardless of whether they are small or large tree species, with the risk increasing slightly as the tree size increases. Overall, it is evident that increasing temperature is directly related to a decrease in the mortality risk of large trees. Regarding the DBH/MAP interaction, small trees were found to be more sensitive to precipitation, whether under high or low rainfall regimes, with higher precipitation rates associated with a higher mortality risk for these species. On the other hand, increased precipitation reduces the mortality risk of larger trees of larger species, but under low precipitation, this risk is high. These results demonstrate that precipitation seasonality has a significant influence on the dynamics of Deciduous Forests.

For Semideciduous Seasonal Forests, relationships were found between mortality risk in the interactions of DBH/MAT, DBH/MAP, DBH/CWD, WD/MAT, WD/MAP, and WD/CWD. In the DBH/MAT interaction, the results show that smaller trees tend to have higher mortality rates in relation to temperature, with higher temperatures associated with increased mortality risk for these plants, meaning that smaller basal area leads to higher risk in cooler temperatures. This general pattern also occurs for species of other sizes, with slightly lower rates for medium and large-sized trees. Thus, it is understood that the larger the tree size, the less influence temperature has in this forest type, and this influence decreases even further as temperatures rise. In the interactions of DBH/MAP and DBH/CWD, the results also show a greater influence of these variables on small-sized trees. For medium and large-sized trees, the mortality rate remains stable with increasing values of these variables.

In relation to the interactions between WD and climatic variables, in SSF, important relationships were observed with MAT, MAP, and CWD. For the WD/MAT interaction, it was noticeable that trees with lower wood density have experienced greater influences on mortality rates in relation to temperature, with this risk tending to decrease as WD increases. However, overall, under low temperatures, the mortality risk in Semideciduous Forests is high regardless of whether the trees have higher or lower density. This risk tends to decrease as temperatures increase. When evaluating the WD/MAP interaction, once again, there is a greater influence on the mortality risk of trees with lower wood density, with higher precipitation rates associated with a higher risk of death for these species. Trees with medium

and high density tend to have greater stability in relation to mortality rate regardless of precipitation values. Finally, in the WD/CWD interaction, the results show that trees with lower wood density tend to have a higher mortality risk regardless of the CWD value. However, this risk tends to increase in forests where CWD is higher. As wood density increases, the mortality risk tends to stabilize at a lower value, regardless of CWD.

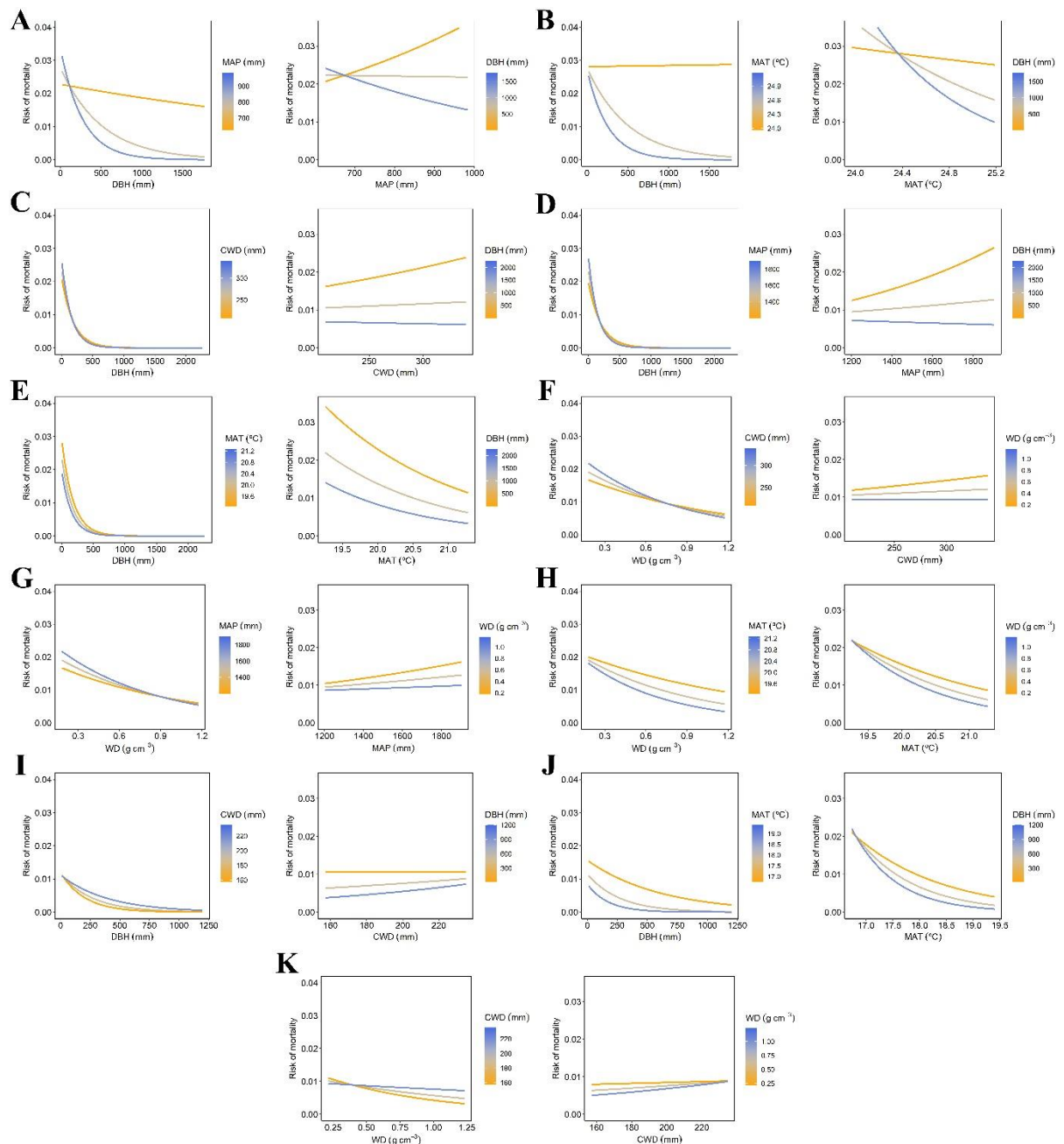


Figure 2: Risk of mortality of the largest trees of each species in each forest type in relation to DBH, WD, and climatic variables. A - B = Deciduous Seasonal Forests; C - H = Semideciduous Seasonal Forests; I - K = Evergreen Forests. WD = Wood Density; DBH = Diameter at Breast

Height; MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation; CWD = Mean Annual Climatological Water Deficit.

In Evergreen Forests, interactions were observed between DBH/MAT, DBH/CWD, and WD/CWD. In the DBH/MAT relationship, it was noticeable that, overall, smaller plants are more influenced by temperature in relation to mortality rates, with rates being higher for plants of this size regardless of temperature, but the effect is more pronounced under lower temperatures. Generally, in colder forests, plants of all sizes tend to have higher mortality rates, and as temperature increases, mortality rates decrease. It is also evident that larger DBH leads to lower mortality rates in relation to temperature. In the DBH/CWD interaction, the results repeat concerning smaller trees, as they exhibit the highest mortality rates under the influence of CWD, remaining constant regardless of the observed value for this variable. In forests with high CWD, trees with larger basal area show the greatest variation in response to this variable, increasing their mortality rate. In the interaction between WD/CWD, it was noticeable that there is a higher risk of mortality for plants with higher wood density as CWD increases. In areas with low CWD, the risk is higher for plants with lower density.

3.2 Tree species with the highest risk of mortality in each forest type

For the three forest types evaluated in this study, a graph was created showing the top 20 species with the highest risk of mortality and the top 20 species with the lowest risk (Fig. 3). In the image, to the right of the red line, the top 20 species are subject to a higher risk of mortality within each forest type, while to the left, those with lower risk are observed.

In Deciduous Seasonal Forests, it was observed that among tree species with a higher risk of mortality, values ranged from approximately 20% to 35%, with the species presenting the highest risk of mortality being *Galipea ciliata*, *Machaerium acutifolium*, and *Goniorrhachis marginata* (Fig. 3-A). Among those with the highest risk, ten species from the Leguminosae family were found, representing 50% of the species at higher risk, three Anacardiaceae (15%), two Malpighiaceae (10%), two Bignoniaceae (10%), one Rutaceae (5%), one Malvaceae (5%), and one Meliaceae (5%) (Fig. 3-A).

In the case of Seasonal Semideciduous Forests, the risk of mortality ranged from approximately 30% to 75% (Fig. 3-B). The species presenting the highest risk of mortality in these forests are: *Magnolia ovata*, *Araucaria angustifolia*, and *Machaerium isadelphum* (Fig. 3-B). Among the species with the highest risk of mortality, four Leguminosae species were found, representing 20% of the species, two Rubiaceae (10%), two Anacardiaceae (10%), and

the families Magnoliaceae, Araucariaceae, Melastomataceae, Apocynaceae, Rutaceae, Connaraceae, Primulaceae, Combretaceae, Myrtaceae, Lauraceae, Cordiaceae, and Malvaceae each had one species, representing 5% of the total each (Fig. 3-B).

Finally, in Evergreen Forests, the risk of mortality ranged approximately from 20% to 45%, and the species with the highest risk are *Huberia nettoana*, *Calypttranthes concinna*, and *Tapirira obtusa* (Fig. 3-C). In these forests, among the species with the highest risk of mortality, four species of Melastomataceae were found, representing 20% of the species at higher risk, four Myrtaceae (20%), two Apocynaceae (10%), two Asteraceae (10%), and the families Anacardiaceae, Arecaceae, Araliaceae, Euphorbiaceae, Ochnaceae, Lauraceae, Salicaceae, and Fabaceae each presented one species (5% of the total for each of these families) (Fig. 3-C).

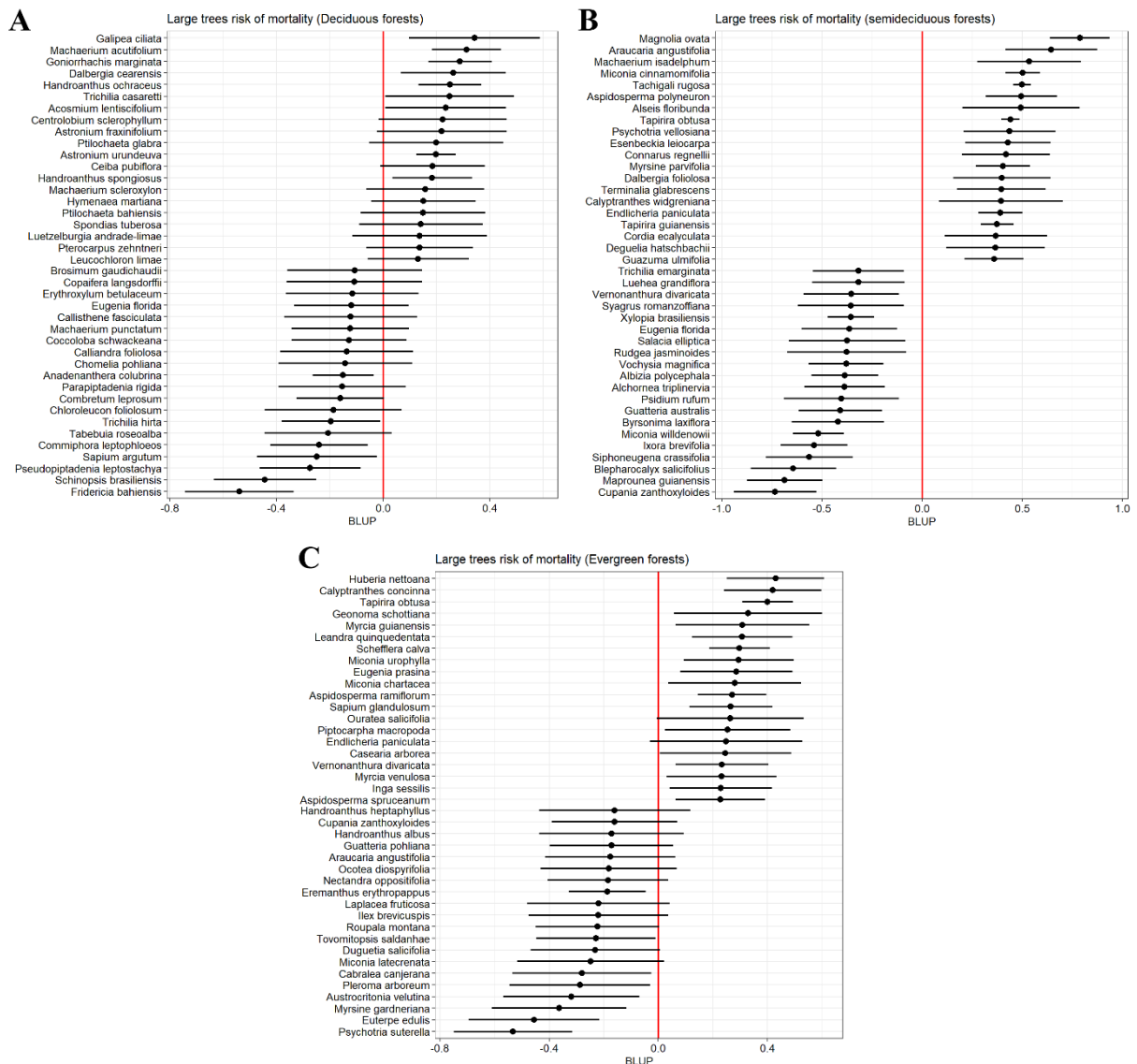


Figure 3: List of the 20 species with the highest and lowest risk of mortality.

DISCUSSION

Previous studies have addressed the mortality of large trees, focusing on the largest individuals present in forests (Bennet et al., 2015; Arcanjo et al., 2020; Esquivel-Muelbert et al., 2020). This study complements these research efforts, as no patterns were identified among species with higher mortality risk in forests regarding diameter at breast height (DBH), suggesting that the largest individuals, regardless of belonging to smaller or larger species, exhibited high mortality rates influenced by climatic conditions. This result is corroborated by the analyses of species at higher risk, where we can observe that there are species of both larger and smaller sizes among the highest mortality rates for all forest types studied.

The only exception regarding mortality patterns among species was the fact that Leguminosae species are highly represented among the 20 species with the highest risk in deciduous forests, reaching 50%. However, the number is also high among the 20 species with the lowest risk (around 33%), indicating that this result is more related to the diversity and widespread distribution of Leguminosae in Deciduous Seasonal Forests. According to Felfili et al. (2007), the Leguminosae family is one of the most representative and characteristic in Deciduous Forest areas, which corroborates with the result found in this study. Regarding the lack of patterns, plant mortality is much more linked to the malfunctioning of its system than to intrinsic factors, for example, the mentioned species, showing that physiological investigation may be a path to identifying tree mortality risk factors (Hartmann et al., 2018).

In this context, this portion of the results assumes greater importance by identifying species at high risk, serving as a primary source of data to support decisions regarding the conservation of these forests. Additionally, it reveals the lack of consistent patterns regarding species succumbing to climatic influence, underscoring the need for a comprehensive approach in studying mortality patterns. Such studies should not be limited to the largest individuals in the forest but rather encompass representatives of species of varying sizes, thereby promoting a more comprehensive understanding of mortality patterns.

In the results regarding species at higher risk of mortality, it is also noteworthy that the 20 species with the highest risk of mortality for each forest were plotted, as well as the 20 species with the lowest risk. In other words, there is a multitude of species located in the region around the red line of the graph that were not plotted at either extreme, indicating that they may not be at risk at the moment, but they may be at risk in the future.

Regarding the influences of climate on forest dynamics, it is known that climatic conditions greatly influence plant adaptive processes and consequently their distribution, as different conditions lead to different adaptation strategies and, consequently, species differentiation (Woodward & Williams, 1987; Allen et al., 2010; Alberto et al., 2013; Aguirre-Gutiérrez et al., 2015; Tshwene-Mauchaza & Aguirre-Gutiérrez, 2019). These climatic factors, especially concerning temperature and precipitation, have a direct impact on tree mortality, including a focus on the largest trees in forests (Bennet et al., 2015; Stovall et al., 2019). However, there is not much discussion about the effect of these variables when evaluating the largest trees of all species found in forests, regardless of whether they are large or small trees, which is the focus of this study.

In general, the growth, development, and functioning of trees are directly related to climatic conditions, which can act as phenological and physiological regulators (Borchert, 1999; Wagner et al., 2016; García-Cervigón et al., 2019, Singh et al., 2023). The quantity and distribution of rainfall and temperature variations have influenced the increase in tree mortality (Allen et al., 2017; McDowell et al., 2018). Both temperature and precipitation directly affect plant functioning, potentially impacting metabolic activity due to deficiencies in carbon supply, water transport, and even stomatal opening and closure mechanisms, which are directly related to plant mortality (Park et al., 2013; Trenberth et al., 2014; McDowell et al., 2018). When considering the largest individuals of tree species in forests, whether they are species with large or small stature, it is expected that, precisely due to differences in size, the optimal functioning conditions also differ among them (Ali & Wang, 2021; Harris et al., 2021). This allows for observing different results in mortality rates considering the DBH in relation to climatic conditions, once again showing that there should not be duality in evaluating large or small individuals in a forest, but rather observing the largest individuals of species with different tree sizes.

Another important point to highlight regarding temperature and precipitation is the influence of rainfall seasonality and temperature variations on the plant's water balance. This balance, measured by the CWD (precipitation-to-evapotranspiration ratio), provides important information about the water deficit of plants in the studied areas. Water deficit is characterized by having a direct relationship with hydraulic failure caused by cavitation and embolism, which also influence plant mortality (McDowell et al., 2018). This occurs because, in addition to the direct influence of water shortage on plant functioning, water deficit can

lead to plant mortality in interaction with other factors existing in forests, such as pests that may attack these trees (Allen et al., 2010).

Regarding wood density, it is known that this variable is mainly associated with adaptation mechanisms to water conditions, which, in turn, are directly influenced by temperature and precipitation (Hacke et al., 2001; Allen et al., 2010; Greenwood et al., 2017; Hammond et al., 2022). In this sense, we can understand the responses obtained in the results of this study regarding the relationship between climatic variables and wood density (WD), as mortality rates vary within the same forest type when comparing trees with higher and lower wood density. In general, trees with higher wood density tend to have greater resistance to climatic factors, especially those related to water conditions (Nogueira et al., 2007; Greenwood et al., 2017), which is consistent with the results found for the studied forests, except for what was observed in the Evergreen Forests.

Finally, it is important to highlight that each studied forest type presents specific climatic characteristics (Oliveira-Filho and Fontes, 2000; Santos et al., 2012). Therefore, it is understood that plants surviving in these distinct locations have undergone different adaptive processes and exhibit different strategies to survive in each of these areas. In this perspective, it is important to emphasize the pressure caused by the current scenario of climate change, in which forest ecosystems have undergone alterations on a short temporal scale, especially concerning temperature and precipitation, whether regarding quality, seasonality, intensity, among other factors, which have influenced plant functioning and, consequently, forest distribution, composition, and ultimately, dynamics, leading to a process of mass tree species mortality (Woodward and Williams, 1987; Dale et al., 2001; Allen et al., 2010; Alberto et al., 2013; Margrove et al., 2015; Garcia et al., 2014; Deb et al., 2018).

CONCLUSIONS

The climatic conditions have been affecting tree mortality in Tropical Forests. Regardless of the size of the evaluated species, the largest tree individuals have shown high mortality rates under the influence of climate. This influence varies according to the intensity of climatic factors, exhibiting different outcomes in smaller and larger species, showing that there is no pattern among species with the highest mortality rates, indicating that there is no duality when studying mortality rates in a forest community, and instead, we should evaluate the whole forest.

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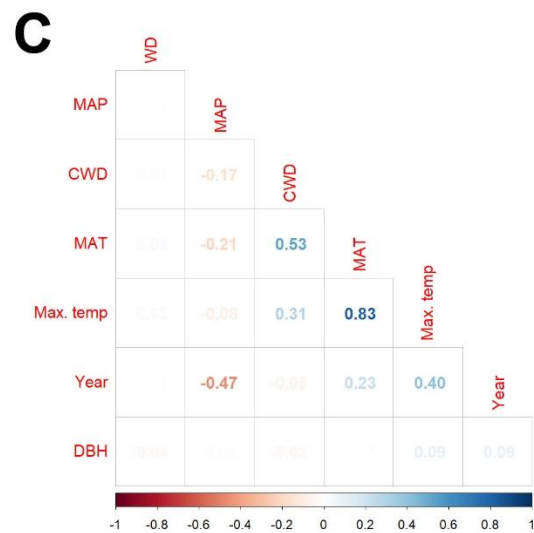
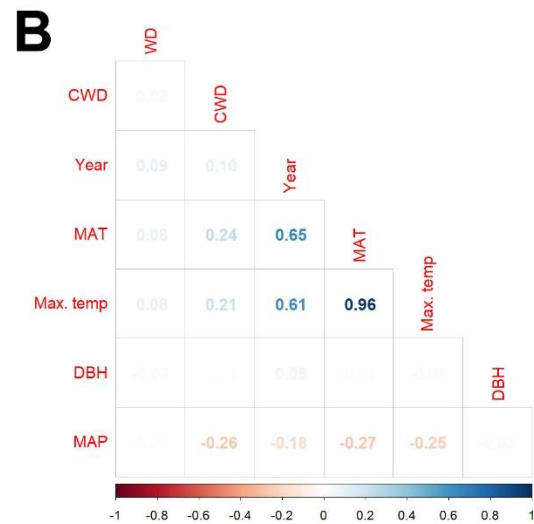
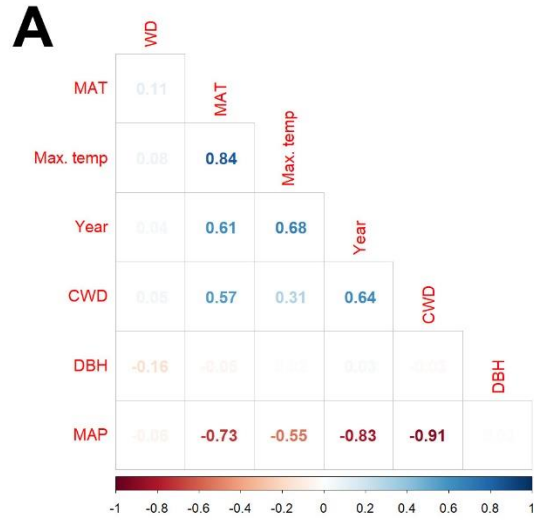
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Supplementary file 1: Characterization of the study areas. DSF = Deciduous Seasonal Forest; SSF = Semideciduous Seasonal Forest; EF = Evergreen Forest.

Area Code	Forest Type	Altitude	Area (ha)	N° of Censuses
BAH-07	DSF	650	2.4	2
BON-01	DSF	500	0.6	3
DEC-01	DSF	513	0.8	5
DEC-02	DSF	507	1.2	3
DEC-03	DSF	630	0.4	4
DEC-04	DSF	447	0.2	2
DEC-05	DSF	541	0.2	5
DEC-06	DSF	530	1.08	5
MON-01	DSF	500	1	2
PNP-01	DSF	675	0.92	2
PNP-02	DSF	480	1	2
COQ-01	SSF	850	0.8	3
COQ-02	SSF	824	1	3
ING-01	SSF	883	1	5
ITT-01	SSF	940	0.945	5
ITT-02	SSF	950	0.84	5
LUM-01	SSF	928	1.28	4
MDD-01	SSF	936	1.5975	7
MTR-01	SSF	1300	1.2	3
PIE-01	SSF	1136	1.2	3
POC-01	SSF	1023	0.78	3
POC-03	SSF	1023	1.14	8
SUB-01	SSF	950	2	4
SUB-02	SSF	920	5.04	8
SUB-03	SSF	930	1.12	6
SUB-04	SSF	870	1.16	4
SUB-05	SSF	820	0.6	5
BCN-01	EF	1200	1.52	2
BOC-01	EF	1151	0.4	2
BOC-02	EF	1285	1.04	4
CRR-01	EF	1491	1.2	4
IBI-01	EF	1403	0.96	5
ITM-01	EF	1460	1	2

Supplementary file 2: Correlation analysis among climatic variables. DSF = Deciduous Seasonal Forest; SSF = Semideciduous Seasonal Forest; EF = Evergreen Forest.



Supplementary file 3: Interactions between climatic and functional variables in tree mortality in Deciduous Seasonal Forests.

Fixed effects	p-value	Significance (p<0.01)
lag_Dquad_sca	9.81e-05	*
WD_sca	0.08134	n.s.
map_sca	0.9261	n.s.
mat_sca	0.0690	n.s.
lag_Dquad_sca:map_sca	0.0001	*
lag_Dquad_sca:mat_sca	2.73e-06	*
WD_sca:map_sca	0.3794	n.s.
WD_sca:mat_sca	0.1488	n.s.

Supplementary file 4: Interactions between climatic and functional variables in tree mortality in Semideciduous Seasonal Forests.

Fixed effects	p-value	Significance (p<0.01)
lag_Dquad_sca	2e-16	*
WD_sca	0.0001	*
map_sca	0.0016	*
cwd_sca	0.0630	n.s.
mat_sca	2e-16	*
lag_Dquad_sca:map_sca	6.72e-12	*
lag_Dquad_sca:cwd_sca	1.83e-05	*
lag_Dquad_sca:mat_sca	0.0049	*
WD_sca:map_sca	0.0068	*
WD_sca:cwd_sca	0.0005	*
WD_sca:mat_sca	1.65e-10	*

Supplementary file 5: Interactions between climatic and functional variables in tree mortality in Evergreen Forests.

Fixed effects	p-value	Significance (p<0.01)
lag_Dquad_sca	2.11e-13	*
WD_sca	0.1082	n.s.
map_sca	0.4643	n.s.
cwd_sca	0.0885	n.s.
mat_sca	2.32e-09	*
lag_Dquad_sca:map_sca	0.5051	n.s.
lag_Dquad_sca:cwd_sca	0.0004	*
lag_Dquad_sca:mat_sca	1.85e-05	*
WD_sca:map_sca	0.6973	n.s.
WD_sca:cwd_sca	0.0207	*
WD_sca:mat_sca	0.7525	n.s.

ARTIGO 2 - COMMUNITY DYNAMICS AND FUNCTIONAL COMPOSITION: AN APPROACH BASED ON THE DISTINCTION BETWEEN DIAMETER CLASSES

Artigo elaborado de acordo com as normas do periódico Flora.

Abstract:

Tree species distributions patterns reflect their adaptations throughout their life history. These patterns result from different adaptive strategies, leading to the formation of specific forest types around the world, as is the case with Deciduous Seasonal Forests. This study aims to evaluate the forest dynamics and functional composition of a fragment of Deciduous Seasonal Forest located in southeastern Brazil, highlighting the influence of soil complexity and diameter variability on the adaptive strategies of the tree individuals within it. To achieve this, in an initial forest census, 20 permanent plots were allocated; all individuals with Diameter at Breast Height (DBH) equal to or greater than 3 cm were identified and measured. In addition to the initial census, four additional censuses were conducted, during which tree individuals were remeasured, and dead and recruited individuals were counted in each census. Soil samples were collected from different plots within the fragment for laboratory analysis, and the individuals were separated into 4 different diameter classes (3 to 5.9 cm; 6 to 11.9 cm; 12 to 23.9 cm; 24 to 47.9 cm). Forest dynamics parameters were calculated concerning both different soil conditions and diameter classes, using abundance and basal area metrics. Functional composition was evaluated through abundance-weighted means, compared between soil types and diameter classes. Our results showed a higher number of tree individuals dying compared to recruits. They also demonstrated the influence of different soil conditions on the functionality and dynamics of the fragment. Finally, they reveal distinct functional and dynamic behaviors concerning different diameter classes, highlighting adaptive specificity for various diameter classes.

Keywords: Forest Inventory; Tree Mortality; Functional Traits; Deciduous Seasonal Forest; Soil Complexity.

Introduction

During the process of tree evolution, different adaptive strategies emerged in response to diverse conditions worldwide, leading to the formation of various forest types containing different tree species (Woodward & Williams, 1987; Allen et al., 2010; Alberto et al., 2013), such as Tropical Forests. This occurs primarily due to interactions with climate and soil conditions, which play a crucial role in shaping the adaptive processes of tree species (Woodward & Williams, 1987; Alberto et al., 2013; Aguirre-Gutiérrez et al., 2015; Tshwene-Mauchaza & Aguirre-Gutiérrez, 2019; Hofhansl et al., 2020). In the current scenario of climate change, there is a clear need for studies aimed at better understanding these distribution patterns, as such climate alterations have resulted in a disruption of the functioning patterns of forest ecosystems (Allen et al., 2010; Alberto et al., 2013; Aguirre-Gutiérrez et al., 2015; Tshwene-Mauchaza & Aguirre-Gutiérrez, 2019; Singh et al., 2023).

Among Tropical Forests, Deciduous Seasonal Forests deserve special attention. These forests are characterized by precipitation seasonality, exhibiting pronounced dry periods for much of the year and a short rainy season during the summer (Oliveira-Filho & Fontes, 2000; Santos et al., 2012). Despite the adversities, these forests harbor unique biological diversity, featuring a variety of plant species that have adapted to the restrictive conditions of these areas, and play important roles in climate regulation, biodiversity conservation, and provision of ecosystem services (Oliveira-Filho & Fontes, 2000; Santos et al., 2012). However, as most areas of Deciduous Seasonal Forests have fertile soils, agricultural practices have become common, leading to fragmentation of these forests and causing direct impacts on the existing trees (Coelho et al., 2016), which increases the interest and need for studies in these areas, especially regarding the understanding of processes occurring within these forests in the current scenario of transformations.

To better understand the functioning patterns of forest ecosystems, studies on forest dynamics and research related to functional traits have been prominent. The former approach allows for a better comprehension of the life cycle of tree individuals concerning their interactions within the forest ecosystem, enabling the elucidation of processes involved in the tree community through monitoring changes occurring in forests (Condit, 1995; Rees et al., 2001; Higuchi et al., 2008; McDowell et al., 2020). The second type of assessment allows for a more direct understanding of forest functioning through individual-level measurements that reveal their strategies in achieving adaptive success and better ecological performance, moving

away from common metrics for assessing tree communities (Violle et al., 2007.; Cernansky, 2017).

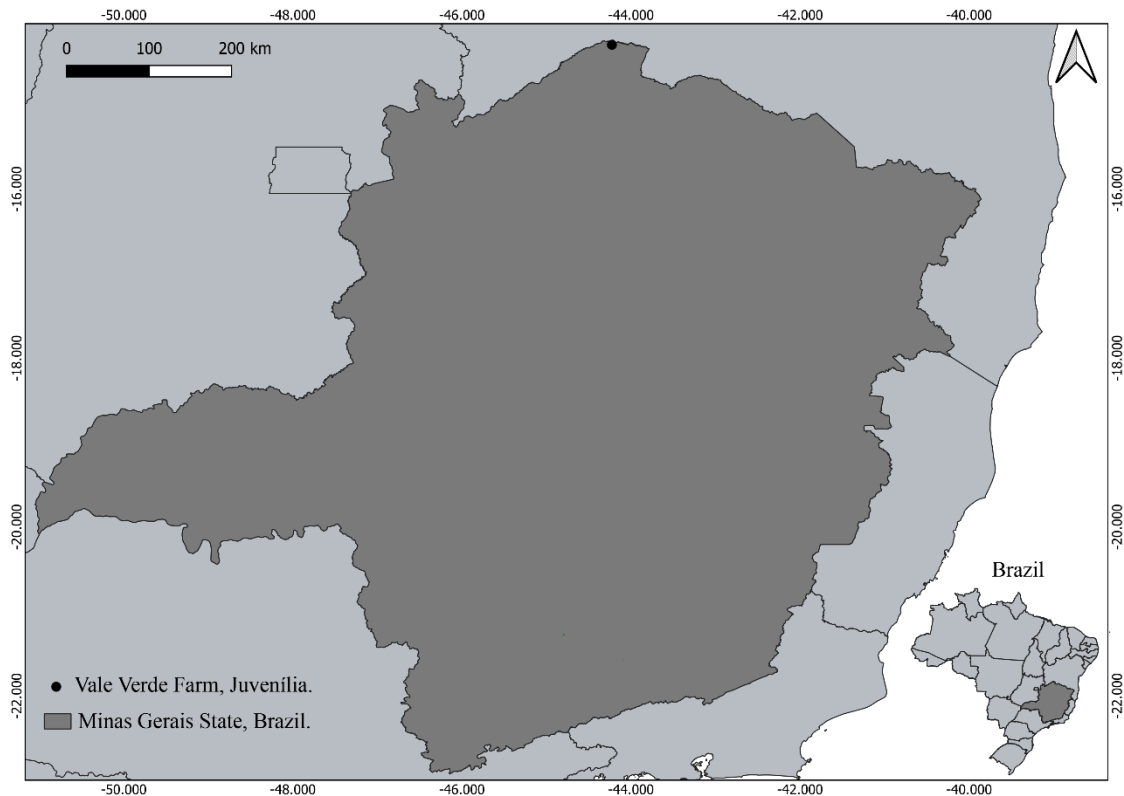
Based on these assumptions, the purpose of this study is to evaluate the forest dynamics and functional diversity of individuals within a Deciduous Seasonal Forest fragment, considering the diameter variability among tree individuals and the soil complexity of the fragment. Our hypothesis is that both functional and dynamic behaviors will be distinct among individuals of different dimensions, and that soil conditions will influence responses according to soil characteristics.

Materials and Methods

Study area and data collection

The sampling was conducted in a fragment of Deciduous Seasonal Forest, located at Vale Verde Farm, municipality of Juvenília, in the state of Minas Gerais, Brazil (Figure 1). The region exhibits precipitation seasonality, with rainfall concentrated during the summer; the average annual temperature is around 20 °C and precipitation is 1000 mm, occurring between November and January (Santos et al., 2011).

Figure 1 - Location of the sampled area.



Source: Author (2024).

The data used in this study belong to the database of the Laboratory of Phytogeography and Evolutionary Ecology (LEAF), Federal University of Lavras, MG (UFLA), and are included in the global tropical forest database, ForestPlots (ForestPlots.net). In the fragment, 20 permanent subplots of 400m² each were allocated, totaling 0.8 ha of studied forest area. The establishment of the subplots, as well as the first survey of the tree community at the site, took place in 2004 (Santos et al., 2011).

In the initial survey, all tree individuals meeting the inclusion criteria of diameter at breast height (DBH at 1.3m) \geq 3 cm were identified at the species level, tagged with metal tags, and measured. In addition to the initial census, four more censuses were conducted on-site (2010, 2015, 2017, 2020). In all these censuses, the DBH of tagged trees was remeasured, and new trees (recruits) that previously did not meet the inclusion criteria but now reached such value were also included. Furthermore, dead trees were counted in the intervals between censuses.

In total, 1641 tree individuals were assessed, corresponding to 68 different species. Species identification was carried out following the APG IV (2016) classification, and standardized names were used using REFLORA (Flora of Brazil, 2020).

For plants with multiple stems, the “tree inclusion method” was used, established by the quadratic diameter ($DBHq = \sqrt{d1^2 + d2^2 + d3^2 + d4^2 + \dots + dn^2}$) (Souza et al., 2021) for inclusion in the database; thus, all stems above the ground were considered, provided that the result of the DBHq meets the 3.0 cm inclusion criterion.

Soil analyses were conducted to understand the soil-vegetation relationship. For this purpose, soil samples of 0.5 liters were collected at a depth of 5-20 cm in each plot. The samples were sent to the Soil Analysis Laboratory at UFLA to obtain the following analyses: texture analysis (proportion of clay, sand, and silt); analysis of potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg), aluminum (Al), and organic matter (OM) contents. The pH in water (pH), base sum (SB), base saturation (V), aluminum saturation (m), cation exchange capacity at pH (T), effective cation exchange capacity (t), remaining phosphorus (P-Rem), and potential acidity (H+Al) were also evaluated in the soil samples, following standard protocols (EMBRAPA, 2006). Based on the soil analysis results, to observe if there would be the formation of groups regarding soil conditions, a principal component analysis was performed (Figure 2), and then the soil variables for each group formed were tested, using R environment version 4.2.3 (R Core Team, 2023); the results were shown in Table 3.

Dynamics of the tree community in the study area

For understanding the population dynamics of the studied fragment, three types of approaches were used: 1) Total number of sampled individuals; 2) Groups formed according to soil analysis (Figure 2); 3) Separation of the community into diameter classes (Table 1).

Table 1 - Diameter classes based on Diameter at Breast Height (DBH).

Diameter Classes	DBH Values
C1	3 a 5.9 cm
C2	6 a 11.9 cm
C3	12 a 23.9 cm
C4	24 a 47.9 cm

Source: Reis et al., 2018 (adapted by the author, 2024).

The determination and direction of the dynamics were determined by annual rates of recruitment, mortality, loss of basal area, gain of basal area, turnover based on abundance and basal area, and net change based on abundance and basal area. These parameters were calculated using mathematical formulas, following standard protocol (Table 2).

Table 2 – Rates of dynamics used in forest dynamics assessments.

Type of rates	Mathematical formula
Mortality	$M = \{1 - [(N_0 - m)/N_0]^{1/t}\} \times 100$
Recruitment	$R = [1 - (1 - r/N_t)^{1/t}] \times 100$
Turnover (abundance)	$TN = (M + R)/2$
Net change (abundance)	$\Delta N = [(N_t / N_0)^{1/t} - 1] \times 100$
Loss of basal area	$L = \{1 - [(BA_0 - (BA_m + BA_d))/BA_0]^{1/t}\} \times 100$
Gain of basal area	$G = \{1 - [1 - (BA_r + BA_g)/BA_t]^{1/t}\} \times 100$
Turnover (basal area)	$TBA = (L + G)/2$
Net change (basal area)	$\Delta BA = [(BA_t / BA_0)^{1/t} - 1] \times 100$

M = mortality rate; R = recruitment rate; TN = turnover rate based on abundance; TBA = turnover rate based on basal area; ΔN = net change based on abundance; ΔBA = net change based on basal area; L = loss rate of basal area; G = gain rate of basal area; t = time interval between censuses; N_0 = initial number of trees; N_t = final number of trees; m = number of trees dead in the current census but alive in

the previous census; r = new recruits; BA_0 = initial value of basal area; BA_t = final value of basal area; B_{Am} = basal area value of dead trees; B_{Ar} = basal area value of recruited trees; B_{Ad} = basal area value of individuals with loss of basal area; B_{Ag} = basal area value of individuals with gain of basal area.

Source: Korning e Balslev, 1994; Sheil e May (1996); Santos et al., 2017 (adapted by the author, 2024).

Functional Traits of Tree Community

The acquisition of functional data was standardized by collecting 1 m long branches, in full sunlight, and under good phytosanitary conditions (Pérez-Harguindeguy, Díaz, Garnier, et al., 2013; Fagundes, Gianasi, & Santos, 2022). This allowed us to obtain functional characteristics of branches and leaves related to efficient water resource utilization, structural investment, and biomass accumulation for all tree individuals sampled in the study area. For branches, the following characteristics were obtained: Total Vessel Area, Sapwood Density, Specific Sapwood Density, Vessel Density, and Vessel Diameter; for leaves, the measured variables were: Specific Leaf Area, Dry Matter Content, and Leaf Mass per Area.

Next, the effects of functional traits on the studied community were quantified using community-weighted mean (CWM), calculated from the mean values of each trait in relation to their abundance (number of individuals). This approach was used in two distinct ways: by observing the previously selected diameter classes (Table 1) and by separating the groups based on soil analysis (Figure 2). The FD package (Laliberté, Legendre, & Shipley, 2014) in R environment version 4.2.3 (R Core Team, 2023) was used to obtain the CWM values.

Data Analysis

Generalized Linear Models (GLMs) were used to compare the soil variables and CWMs (for $p < 0.05$). Initially, comparisons were made between the two groups formed by PCA of the soil variables. Then, CWMs were compared in relation to the intervals of dynamics to understand if there were significant functional differences between the censuses. Next, to observe if there were functional differences related to tree diameter, comparisons were made between the CWMs for each functional trait in relation to the diameter classes established previously. Finally, CWMs were also compared in relation to the groups formed based on soil analysis to observe the functional variation in relation to these groups.

The statistical analyses and graphs were obtained using R environment version 4.2.3 (R Core Team, 2023) utilizing the following packages: ggplot2 (Wickham, 2016); multcompView (Graves et al., 2023); dplyr (Wickham et al., 2023); nlme (Pinheiro & Bates, 2023); multcomp

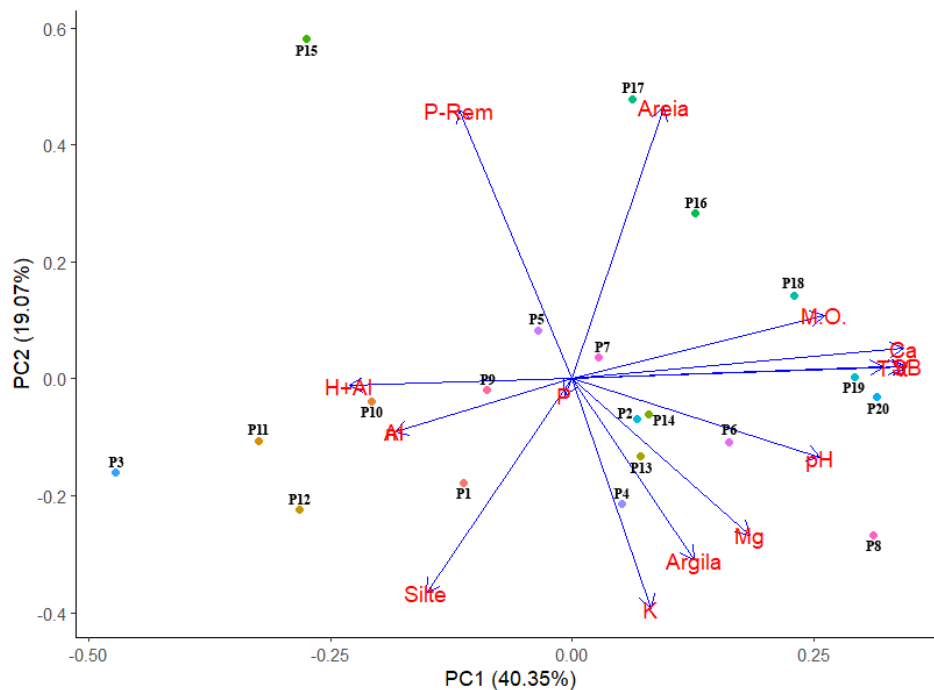
(Hothorn et al., 2008); car (Fox & Weisberg, 2019); emmeans (Lenth, 2024); vegan (Oksanen et al., 2022).

Results

Analysis of Soil Characteristics

In the first result regarding soil conditions, it was possible to observe a separation of the permanent plots distributed in the study area into two groups on the axis 1 of the PCA (Figure 2), with a high percentage of explanation (40.35%). The first group contains eight plots, showing higher values for the variable H+Al, and the second group contains the remaining twelve plots and presents high values for the variable SB. According to Sposito (2008), the H+Al variable indicates poorer, more acidic, and aluminized soils, directly affecting the availability of nutrients for plants, while SB is related to more fertile soils with higher availability of essential nutrients. Thus, the two groups are formed, related to soil fertility.

Figure 2 - Principal Component Analysis (PCA) based on soil conditions.



K = Potassium; P = Phosphorus; Ca = Calcium; Mg = Magnesium; Al = Aluminum; OM = Organic Matter; pH = Water pH; SB = Sum of Bases; V = Base Saturation; m = Aluminum Saturation; T = Cation Exchange Capacity at pH; t = Effective Cation Exchange Capacity; P-Rem = Remnant Phosphorus; H+Al = Potential Acidity.

Source: From author (2024)

When comparing the two groups formed in the PCA using GLMs, the separation of the groups based on soil fertility was confirmed, as observed in Table 3, where all soil variables that were statistically different between the groups for $p < 0.05$ were illustrated. In the figure, it can be observed that, besides the fertility issue illustrated by H+Al and SB, the groups also differ in relation to the variables: Ca, Mg, OM, pH, t, T, V, and Silt.

Table 3 – Comparison of soil variables between the two groups formed by PCA.

Soil Variable	Group 1	Group 2	Significance (p<0.05)
H+Al	2.80	2.36	*
SB	11.03	14.60	*
pH	6.31	6.47	*
K	134.25	140.67	n. s.
P	2.26	2.23	n. s.
Ca	9.12	12.51	*
Mg	1.56	1.73	*
t	11.04	14.60	*
T	13.84	16.97	*
V	79.64	86.04	*
MO	4.12	4.81	*
P-Rem	34.74	33.36	n. s.
Clay	28.87	30.25	n. s.
Silt	46.25	40.92	*
Sand	24.87	28.83	n. s.

Source: From author (2024).

Dynamics of the Tree Community in the Study Area

In the first result of this topic, the overall dynamics of the study area were analyzed based on abundance and basal area (Table 4). It is important to note initially that the number of live individuals gradually decreased over the intervals, indicating that, overall, the number of dead trees (369) was higher than that of recruited trees (352). This result is supported by the values of the mortality rate, recruitment rate, and turnover, as well as the gross number of dead and recruited individuals. From the perspective of basal area, it was noted that the basal area of dead individuals is higher than that of recruited individuals, indicating that the individuals that died are larger than those recruited. Conversely, this was not reflected in the annual loss and

gain rates, which showed an inverse relationship to this result, except for in the case of census 4, as supported by the values of the net change rates, which remained positive in all censuses except the 4th.

Table 4 – Overall dynamics of the studied area across the five surveys.

	2004	2010	2015	2017	2020
Individuals:					
Individuals number	1321	1367	1304	1256	1273
Survivors	-	1244	1255	1206	1174
Deceased	-	77	112	98	82
Recruits	-	123	49	50	99
Mortality (%.year ⁻¹)	-	0.99	1.64	3.46	2.1
Recruitment (%.year ⁻¹)	-	1.50	0.71	1.91	2.50
Turnover (%.year ⁻¹)	-	1.25	1.17	2.68	2.33
Net Change (%.year ⁻¹)	-	1.51	-0.38	-2.25	0.12
Basal Area:					
Total (m ² /ha)	16.16	18.25	18.96	17.54	18.27
Deceased (m ² /ha)	-	0.60	0.92	0.77	0.93
Recruits (m ² /ha)	-	0.26	0.098	0.11	0.2
Loss (%.year ⁻¹)	-	0.87	1.74	4.96	2.21
Gain (%.year ⁻¹)	-	2.93	2.44	1.32	3.49
Turnover (%.year ⁻¹)	-	1.90	2.09	3.14	2.85
Net Change (%.year ⁻¹)	-	2.12	0.71	-3.68	1.32

Source: From author (2024).

Regarding the dynamics of the groups formed by soil analysis, based on abundance (Table 5), it was noted that in Group 1, the number of individuals remained constant, ending with a positive balance. Whereas in Group 2, the number of individuals decreased by 50

individuals in the last census compared to the first. It is also important to note that, in Census 4, there is an intensification of variables related to mortality.

Table 5 – Dynamics of the groups formed by soil analysis, based on abundance.

	2004	2010	2015	2017	2020
G1 – Ind. Number	584	613	579	572	585
G2 – Ind. Number	737	754	725	684	688
G1 – Survivors	-	551	552	544	528
G2 – Survivors	-	693	703	662	646
G1 – Deceased	-	33	61	35	44
G2 – Deceased	-	44	51	63	38
G1 – Recruits	-	62	27	28	57
G2 – Recruits	-	61	22	22	42
G1 – Mortal. (%.year ⁻¹)	-	0.96	1.96	2.77	2.48
G2 – Mortal. (%.year ⁻¹)	-	1.02	1.31	4.14	1.72
G1 – Recruit. (%.year ⁻¹)	-	1.67	0.86	2.33	3.12
G2 – Recruit. (%.year ⁻¹)	-	1.32	0.57	1.48	1.97
G1 – Turnover (%.year ⁻¹)	-	1.32	1.41	2.55	2.80
G2 – Turnover (%.year ⁻¹)	-	1.17	0.94	2.81	1.85
G1 – Net Chan. (%.year ⁻¹)	-	1.70	-0.19	-2.61	1.19
G2 – Net Chan. (%.year ⁻¹)	-	1.33	-0.56	-1.89	-0.94

G1 = Group 1; G2 = Group 2.

Source: From author (2024).

In the analysis of groups based on basal area (Table 6), the same pattern is observed regarding dead individuals and recruits, where greater basal areas are evidenced for dead individuals compared to recruits. Group 2, once again, appears to have suffered more during the years of the study. This result is corroborated by the rates of loss, gain, turnover, and net change when observing the balance of these rates over the study period.

Table 6 – Dynamics of the groups formed by soil analysis, based on basal area.

	2004	2010	2015	2017	2020
G1 – Basal Area (m ² /ha)	6.07	7.00	7.17	6.73	6.96
G2 – Basal Area (m ² /ha)	10.09	11.25	11.79	10.81	11.31
G1 – Deceased (m ² /ha)	-	0.15	0.53	0.26	0.41
G2 – Deceased (m ² /ha)	-	0.45	0.39	0.51	0.52
G1 – Recruits (m ² /ha)	-	0.13	0.057	0.06	0.11
G2 – Recruits (m ² /ha)	-	0.13	0.041	0.05	0.09
G1 – Loss (%.year ⁻¹)	-	0.72	2.10	4.59	2.57
G2 – Loss (%.year ⁻¹)	-	1.03	1.39	5.34	1.86
G1 – Gain (%.year ⁻¹)	-	3.06	2.56	1.53	3.65
G2 – Gain (%.year ⁻¹)	-	2.81	2.33	1.12	3.34
G1 – Turnover (%.year ⁻¹)	-	1.89	2.33	3.06	3.11
G2 – Turnover (%.year ⁻¹)	-	1.92	1.86	3.23	2.60
G1 – Net Chan. (%.year ⁻¹)	-	2.41	0.47	-3.10	1.12
G2 – Net Chan. (%.year ⁻¹)	-	1.83	0.95	-4.26	1.53

G1 = Group 1; G2 = Group 2.

Source: From author (2024).

When evaluating the dynamics by diameter classes (Table 7), we observed that mortality was higher for smaller individuals belonging to class 1, followed by individuals in class 2, 3, and 4, respectively. Recruitment also followed the same pattern. It is worth noting the presence of emigration and immigration of individuals between classes as well. The results show that emigration mainly occurs in class 1, followed by classes 2, 3, and 4, with very low emigration in the last class, indicating an increase in DBH of individuals over the censuses. The result differs when observing Census 4, indicating higher emigration values in classes 2 and 3, suggesting a possible decrease in the DBH of individuals in these classes. Regarding immigration, the highest values are concentrated in class 2, indicating mainly a possible increase in the DBH of individuals in class 1, which is reflected by the previous rate in that class. The same occurs when comparing class 2 and class 3. In class 4, on the other hand, the values are lower compared to the other classes. It is also important to note that while classes 1 and 2 had negative balances when comparing the last and first census, classes 3 and 4 had positive balances.

Table 7 – Dynamics of diameter classes based on abundance.

	2004	2010	2015	2017	2020
C1 – Individual number	409	382	306	340	343
C2 – Individual number	616	635	614	572	562
C3 – Individual number	248	293	326	292	309
C4 – Individual number	48	57	58	52	59
C1 - Deceased	-	34 (1.43)	48 (2.64)	36 (6.06)	30 (2.47)
C2 – Deceased	-	34 (0.94)	49 (1.59)	48 (3.98)	33 (1.61)
C3 – Deceased	-	7 (0.47)	14 (0.97)	13 (2.01)	16 (0.81)
C4 – Deceased	-	2 (0.70)	1 (0.35)	1 (0.35)	3 (0.34)
C1 – Recruits	-	109	47	48	93
C2 – Recruits	-	14	2	2	6
C3 – Recruits	-	0	0	0	0
C4 – Recruits	-	0	0	0	0
C1 – Emigration	-	111	89	21	65
C2 – Emigration	-	73	73	48	52
C3 – Emigration	-	18	15	30	15
C4 – Emigration	-	0	2	5	1
C1 – Immigration	-	9	14	43	5
C2 – Immigration	-	112	99	52	69
C3 – Immigration	-	70	62	9	48
C4 – Immigration	-	11	4	0	11

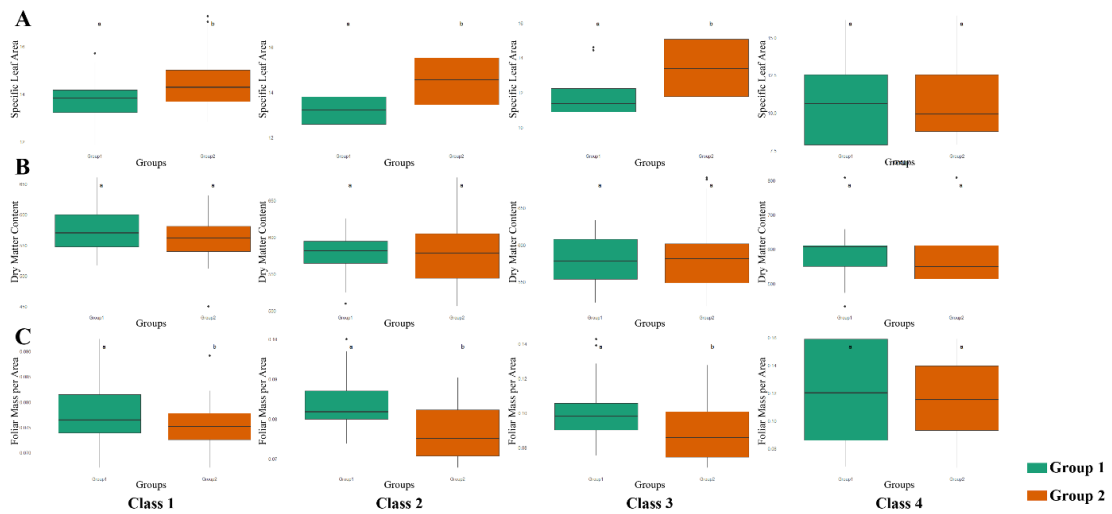
C1 = class 1; C2 = class 2; C3 = class 3; C4 = class 4; In parentheses, in the mortality rows, is the percentage of annual mortality

Source: From author (2024).

Functional Traits of Tree Community

In the functional assessments related among the groups formed by soil analysis, no significant differences were found between individuals in class 4 in the two groups (Figure 3 and Figure 4).

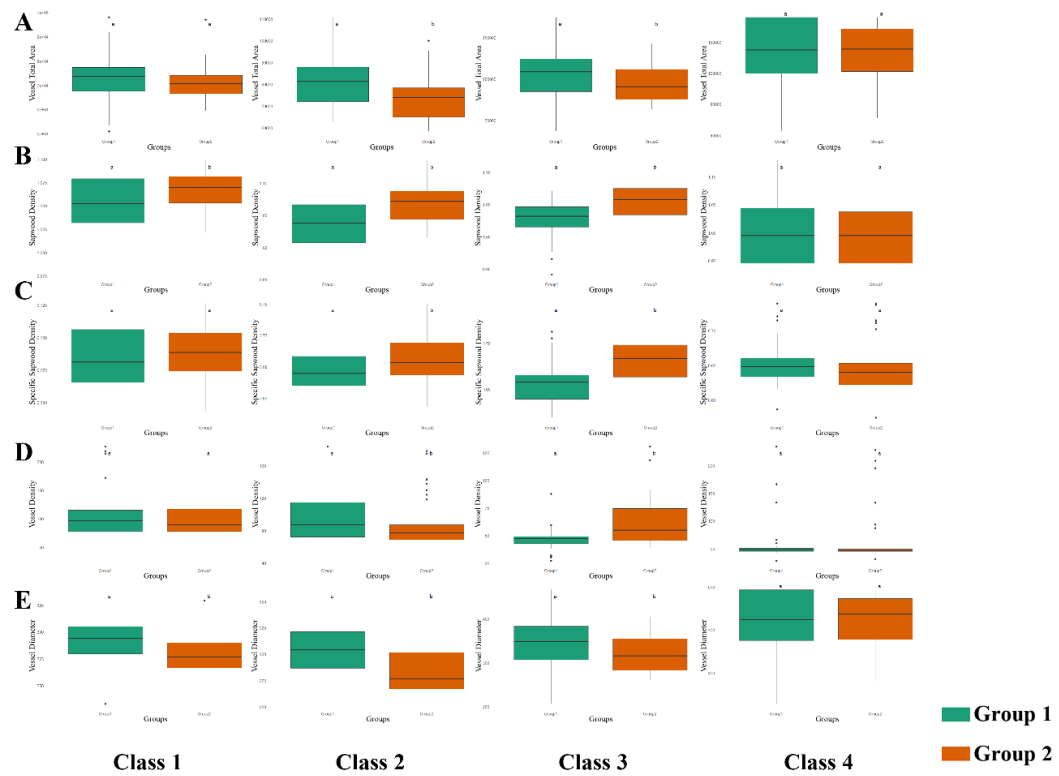
Figure 3 – Comparison of leaf functional traits among the groups formed by soil analysis for each diameter class.



A = Specific Leaf Area(mm².mg⁻¹); B = Dry Matter Content (mg.g⁻¹); C = Leaf Mass per Area (mg.mm⁻²).

Source: From author (2024).

Figure 4 – Comparison of branch functional traits among the groups formed by soil analysis for each diameter class.



A = Vessel Total Area (μm²); B = Sapwood Density (g.cm³); C = Specific Sapwood Density; D = Vessel Density (n° of vessels. mm⁻²); E = Vessel Diameter (μm).

Source: From author (2024).

For class 1, the results showed that Group 1 consists of individuals with larger Vessel Diameter and Leaf Mass per Area, while Group 2 comprises individuals with higher values of Specific Leaf Area and Sapwood Density; the remaining characteristics did not show significant differences.

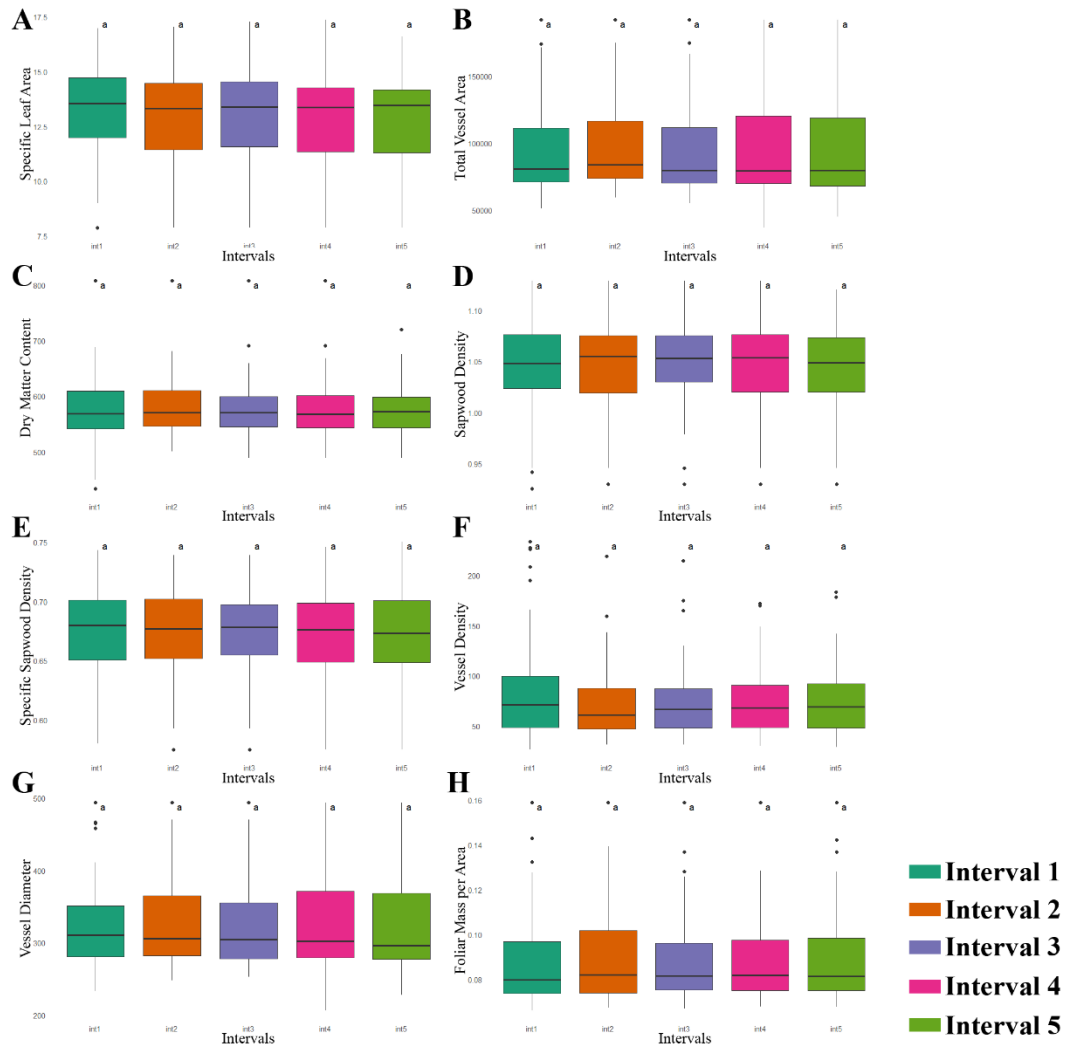
In relation to class 2, it is possible to perceive that Group 1 consists of individuals with higher Total Vessel Area, Vessel Density, Vessel Diameter, and Leaf Mass per Area; on the other hand, Group 2 presents higher values of Specific Leaf Area, Sapwood Density, and Specific Sapwood Density; there were no differences for Dry Matter Content. Class 3 shows a similar pattern to class 2.

When tests of functional traits were conducted across dynamic intervals (Figure 5), no significant differences were found between the values of functional traits in the different intervals. This result is supported by comparisons between classes (Figure 6 and Figure 7), where, when arranging the intervals in parallel, similar patterns are found for the boxplots of the same class.

Classes 1 and 2 are quite similar from a functional standpoint, showing statistically similar values for all studied functional variables. Regarding classes 3 and 4, some differences were observed, both between them and when compared to classes 1 and 2.

In general, regarding classes 1 and 2, the classes comprising individuals with larger diameter exhibit higher values of Total Vessel Area, Vessel Diameter, and Leaf Mass per Area, with the values for the first two variables also differing between the last two classes, being higher in class 4. On the other hand, classes 3 and 4 present lower values of Specific Leaf Area, Sapwood Density, Specific Sapwood Density, and Vessel Density, with the value for the first variable even lower for class 4 compared to class 3.

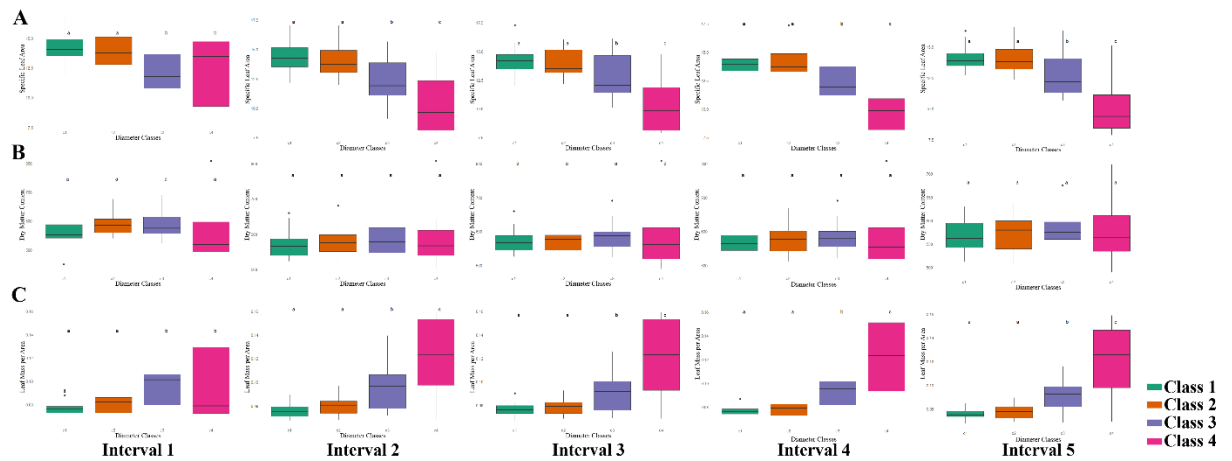
Figure 5 – Comparison of functional traits between dynamic intervals.



A = Specific Leaf Area (mm².mg⁻¹); B = Total Vessel Area (μm²); C = Dry Matter Content (mg.g⁻¹); D = Sapwood Density (g.cm³); E = Specific Sapwood Density (mg.mm⁻³); F = Vessel Density (n° of vessels. mm⁻²); G = Vessel Diameter (μm); H = Leaf Mass per Area (mg.mm⁻²).

Source: From author (2024).

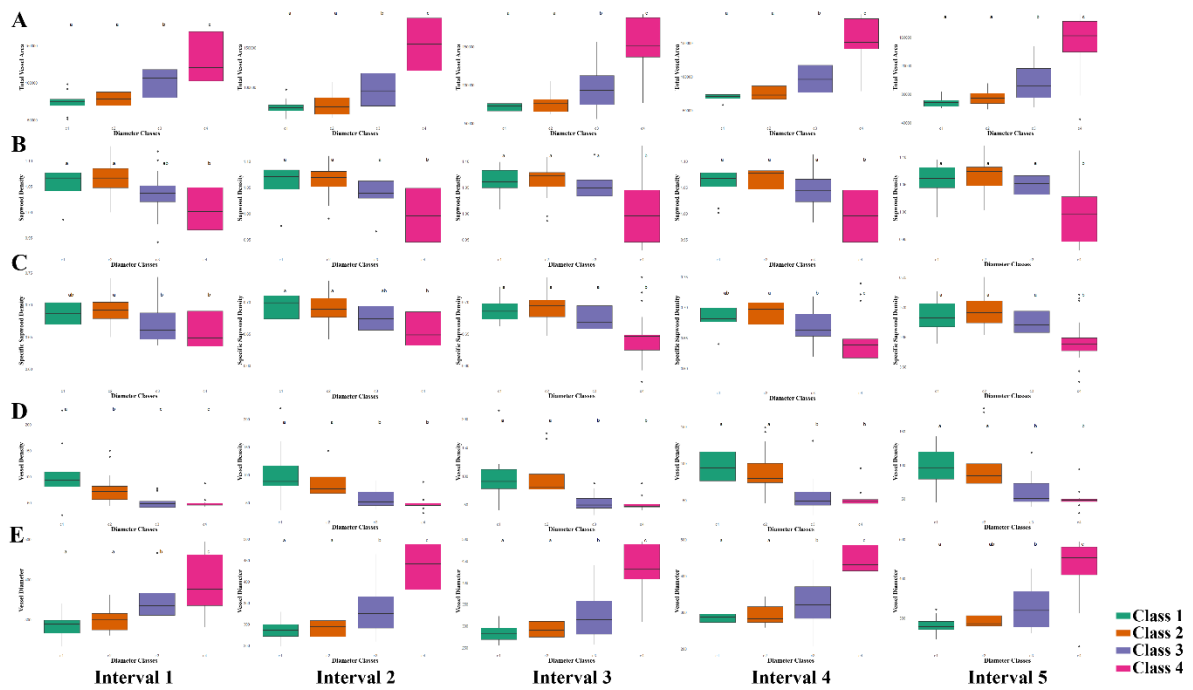
Figure 6 – Comparison of leaf functional traits among diameter classes for each interval.



A = Specific Leaf Area($\text{mm}^2.\text{mg}^{-1}$); B = Dry Matter Content (mg.g^{-1}); C = Leaf Mass per Area (mg.mm^{-2}).

Source: From author (2024).

Figure 7 – Comparison of branch functional traits among diameter classes for each interval.



A = Vessel Total Area (μm^2); B = Sapwood Density (g.cm^3); C = Specific Sapwood Density; D = Vessel Density (n° of vessels. mm^{-2}); E = Vessel Diameter (μm).

Source: From author (2024).

Discussion

Community Dynamics

The first highlighted point in population dynamics concerns the decrease in the number of individuals over the censuses, which is easily observed by comparing the last census with the first, showing a negative balance of the number of sampled individuals. This result is corroborated by the rates of mortality, recruitment, and turnover, even when considering the dynamics in relation to basal area. Studies demonstrate that the main variables influencing forest dynamics are soil and climatic conditions, as these are predominant factors when discussing the establishment, maintenance, and distribution of tree species (Wagner et al., 2016; García-Cervigón et al., 2020; Hofhansl et al., 2020; McDowell et al., 2020; Singh et al., 2023). Currently, in a scenario with evident changes in climatic conditions, this topic has been widely discussed, as the influence of climatic factors on forests has intensified, disrupting the dynamic balance of these ecosystems (Allen et al., 2010; Alberto et al., 2013; Aguirre-Gutiérrez et al., 2015; Tshwene-Mauchaza and Aguirre-Gutiérrez, 2019; Singh et al., 2023). This relationship is strongly connected to the rates of mortality and recruitment of tree individuals, where modifications in mortality and recruitment patterns can be observed (Allen et al., 2017; McDowell et al., 2018; Boisvert-Marsh et al., 2019; Hammond et al., 2022).

However, what really stands out are the abrupt changes observed in census 4, conducted in the year 2017. This census was carried out after the El Niño phenomenon, which occurred from 2015 to 2016, classified as a climatic phenomenon of strong intensity that causes substantial alterations in climatic conditions during its occurrence, and consequently, in forest dynamics (Diem et al., 2018; Leitold et al., 2018; Wigneron et al., 2020). Observing the results of this study, the differences in dynamics after the phenomenon are clearly evident, which are also reflected in the net change rate. Overall, in all approaches used to assess population dynamics, it is noticeable that during census 4, metrics related to mortality were intensified while those related to survival and recruitment were mitigated, indicating a possible influence of the disturbance on forest dynamics.

The present study also shows that in the permanent plots with more fertile soils, there was a greater imbalance in the mortality/recruitment ratio, exhibiting a negative balance in the number of individuals in the final census compared to the initial census. The results for variables related to basal area exhibit the same pattern, corroborating this statement. Soil plays an important role in regulating the functionality of tree species in forest ecosystems, especially

when addressing issues related to fertility and acidity (Ali et al., 2020; Estrada-Villegas et al., 2020; Hofshansl et al., 2020), directly influencing forest dynamics. In addition to soil interaction in forest regulation, climatic interactions occur concomitantly (Ali et al., 2020; Hofshansl et al., 2020), which may explain the ambiguity of the result found for plots with more fertile soils, as apparently, the outcome of census 4 played a significant role in the imbalance in dynamic rates in the study area.

From the obtained results, it is possible to observe a sequence regarding both the mortality and recruitment of individuals. For both cases, more dead individuals and recruits were observed for class 1, followed by classes 2, 3, and 4, consecutively. Regarding mortality, this probably occurs because individuals belonging to the first two classes, especially class 1, are smaller individuals that are still largely developing, not yet having reached the necessary characteristics for their better adaptation. One of the major challenges for survival in Deciduous Seasonal Forests is water scarcity at certain times of the year (Santos et al., 2012; Santos et al., 2017; Reis et al., 2018). In this perspective, the functional attributes of smaller trees may not yet be fully adapted to the local hydrological complexity, especially regarding the root system, limiting access to water and consequently leading to the mortality of young individuals (Fauset et al., 2012; Santos et al., 2017). Regarding emigration and immigration between classes over the censuses, higher values of the former variable are observed in class 1, while immigration is higher in class 2. This result is probably a reflection of the natural growth of trees belonging to class 1 in the area. However, the result is different in census 4, with higher values of emigration for classes 2 and 3, which apparently indicates a decrease in the DBH of these individuals caused, probably, by the climatic pressure exerted by the El Niño that occurred around those years.

Functional Traits

In the functional analysis related to the groups formed by soil analysis, it is observed that, overall, group 1 consists of individuals with higher values of functional characteristics related to water efficiency, both concerning its acquisition, safety in transport, and water use efficiency for the first three diameter classes. The variable that indicates the separation of group 1 (H+Al), according to Sposito (2008), not only indicates poor and acidic soils but also alters the soil configuration, resulting in a decrease in water retention capacity, reducing the amount of water available to the roots. According to the author, the variable encourages soil compaction, hindering the passage of water to deeper layers where the roots are located. Group 2, on the other hand, indicates higher values, mainly for the functional variables related to

sunlight capture. Individuals belonging to this group are located on more fertile soils with greater water retention capacity, which reduces the difficulties of water acquisition. In this sense, the adaptive strategy of group individuals was to optimize functional characteristics of sunlight capture by increasing leaf area at the expense of thickness, presumably due to shading effects from larger individuals, especially in the first two classes.

Regarding class 4, no significant differences were found between the groups formed for any functional variable. Larger individuals tend to be functionally similar, as they have succeeded in facing the environmental challenges of their occurrence area during their development (Snaphre-Villanueva et al., 2016; Rungwatanna & Hietz, 2017;), which in the case of the forest type studied, is precipitation seasonality. The result of functional comparisons between classes supports this theory, as it is possible to observe a greater total vessel area and vessel diameter, variables that, according to Fagundes, Gianasi, and Santos (2022), indicate optimization of hydraulic efficiency, ensuring better water utilization during the short rainy season. Another result that also corroborates this response is the high values of leaf mass per area, a variable indicating investment in individual longevity and growth (Fagundes, Gianasi, & Santos, 2022). This variable indicates higher investment in dry matter in leaves, i.e., structural tissues, which ensure better functioning of the photosynthetic machinery, regulation of gas exchange, and efficient water use, all of which are important for water scarcity tolerance (Shipley et al., 2006; Poorter, 2009).

In comparisons between dynamic intervals, no significant differences were found for any of the functional variables, indicating that, despite the exchanges occurring between classes through emigration and immigration, the selection of functional attributes remains stable across classes.

Regarding the functional comparison between different diameter classes, a similar functional pattern was observed between classes 1 and 2 for all functional variables, while in classes formed by individuals with larger diameters, some differences were found. Smaller diameter classes have higher values of specific leaf area, sapwood density, specific sapwood density, and vessel density. These characteristics are directly related to the optimization of defense and structural support of individuals, hydraulic and photosynthetic efficiency, and consequently, with growth and physical and mechanical resistance of the individual (Fagundes, Gianasi, & Santos, 2022), ensuring their survival and stimulating energy production for their growth and development. Classes 3 and 4, comprising the group of the largest sampled trees, present individuals with functional adaptations related to drought tolerance, one of the main

environmental filters found in Deciduous Seasonal Forests (Oliveira-Filho & Fontes, 2000; Santos et al., 2012). These adaptations explain the lower annual mortality rates observed in these classes compared to individuals with smaller diameters, especially in class 4, indicating their adaptive success. Additionally, larger plants require a greater amount of resources to optimize their biochemical processes (Binkley, 2011; Ali & Wang, 2021; Harris et al., 2021), which corroborates the need for further development of functional traits that optimize water acquisition in a location where this resource is limited.

Conclusions

Overall, it is noticeable that there are more individuals dying than being recruited, resulting in a decrease in the number of individuals over the censuses. The result is alarming, especially concerning census 4, conducted shortly after the occurrence of the El Niño phenomenon, which shows a significant increase in the number of dead individuals compared to other censuses, probably caused by the phenomenon. It is also evident that soil conditions directly influence not only forest dynamics but also the functioning of tree individuals, adjusting their characteristics according to soil specificities. Finally, it is noteworthy that individuals from different diameter classes behave differently both functionally and in terms of dynamics, with survival strategies specific to the classes they belong to.

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TERCEIRA PARTE

CONSIDERAÇÕES FINAIS

O primeiro artigo aborda preocupações substanciais relacionadas aos impactos climáticos na mortalidade de indivíduos arbóreos, demonstrando que, independentemente do porte das espécies avaliadas, as maiores árvores de diferentes espécies exibem taxas de mortalidade elevadas sob a influência climática. Além disso, constata-se que espécies de diferentes tamanhos, em distintas formações florestais, respondem de maneiras variadas às condições climáticas, evidenciando a necessidade de uma abordagem holística ao avaliar a mortalidade nas florestas.

O segundo artigo, por sua vez, enfoca especificamente uma área de Floresta Estacional Decidual. Observa-se um desequilíbrio na dinâmica florestal, evidenciando uma maior taxa de mortalidade do que de recrutamento de indivíduos. O artigo destaca as avaliações da dinâmica florestal realizadas em 2017, após o fenômeno El Niño, que possivelmente teve um impacto direto nesse processo. Além disso, demonstra-se que tanto as características do solo da área quanto o tamanho dos indivíduos arbóreos influenciam tanto na dinâmica quanto na funcionalidade dos mesmos, exibindo padrões distintos de acordo com as classes diamétricas ou diferentes condições edáficas.

Acredito que esses resultados podem servir como um alerta para intensificar a preocupação em relação às Florestas Tropicais, uma vez que têm evidenciado uma forte influência das condições climáticas, agravada pelas mudanças climáticas.