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Community dynamics and carbon storage multifunctionality of an atlantic secondary forest in times of global change

Marina Tack Ramos
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Dissertation submitted to the Botany Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

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Co-adviser: Lhoraynne Pereira Gomes

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ABSTRACT

RAMOS, Marina Tack, M.Sc., Universidade Federal de Viçosa, February, 2025. **Community dynamics and carbon storage multifunctionality of an atlantic secondary forest in times of global change**. Adviser: Andreza Viana Neri. Co-adviser: Lhoraynne Pereira Gomes.

Faced with the current climate crisis, in addition to reducing greenhouse gas (GHG) emissions, conserving and restoring the carbon stocks of tropical forests are seen as nature-based mitigation solutions, but global change is also affecting the dynamics of forest ecosystems. Semi-deciduous seasonal forests, one of the vegetation types of the Brazilian Atlantic Forest domain, provide various ecosystem services, being important for carbon storage and climate regulation. In this way, how climate change is impacting this ecosystem and the multifunctional potential of semi-deciduous forests to mitigate its effects needs to be better understood. Thus, the aim of this work was to analyze how climate variables, especially those related to drought, are affecting the dynamics of the forest community's demographic processes and to evaluate the forest's potential to store carbon in three different compartments. To address this, we asked a few questions: Chapter 01: (i) Are mortality and recruitment rates, growth and biomass, as well as species richness, functional diversity and functional characteristics, changing over time? ii) Considering that changes occur over time, what is the relationship of these changes in forest dynamics with climatic variables? For Chapter 02, we asked: (i) How important is the soil contribution to carbon storage in the Atlantic Forest area studied? (ii) What are the main drivers of carbon storage in above-ground biomass (AGB), soil organic carbon stock (SOCS) and litter carbon stock (LCS)? To do this, we sampled 27 permanent 20m x 20m plots (totaling 1,800 ha) in three different locations in an Atlantic Forest fragment, starting in 1984. Piecewise structural equation models (piecewiseSEM), correlation and multiple regression analyses were carried out to test our hypotheses. We found that the area studied stored around 388 Mg of carbon, 73% of which was stored in the above-ground biomass, 21% in the soil and six percent in the litter. Despite the area's potential for carbon storage, this service has been threatened mainly by the increase in tree mortality following drought events. Our study also showed that both drought and excessive rainfall can be detrimental to forest processes. While drought was responsible for tree mortality, excess rainfall reduced tree growth and recruitment within the community. This work contributes to emphasizing the importance of conserving mature forests and that management and reforestation projects should consider species that are resistant to both drought and excess rainfall.

Keywords: climate change; tropical forest; semideciduous forest; carbon stock; soil carbon; forest dynamics

RESUMO

RAMOS, Marina Tack, M.Sc., Universidade Federal de Viçosa, fevereiro de 2025. **Dinâmica da comunidade de uma floresta tropical sazonal em tempos de alterações climáticas**. Orientadora: Andreza Viana Neri. Coorientadora: Lhoraynne Pereira Gomes.

Diante da atual crise climática, além da redução das emissões de gases de efeito estufa (GEE), a conservação e a restauração dos estoques de carbono das florestas tropicais são vistas como soluções de mitigação baseadas na natureza, mas as mudanças globais também estão afetando a dinâmica dos ecossistemas florestais. As florestas estacionais semidecíduas, um dos tipos de vegetação do domínio da Mata Atlântica brasileira, fornecem vários serviços ecossistêmicos, sendo importantes para o armazenamento de carbono e a regulação do clima. Dessa forma, como as mudanças climáticas estão impactando esse ecossistema e o potencial multifuncional das florestas semidecíduas para mitigar seus efeitos precisa ser melhor compreendido. Assim, o objetivo deste trabalho foi analisar como as variáveis ??climáticas, especialmente aquelas relacionadas à seca, estão afetando a dinâmica dos processos demográficos da comunidade florestal e avaliar o potencial da floresta em armazenar carbono em três compartimentos diferentes. Para abordar isso, fizemos algumas perguntas: Capítulo 01: (i) As taxas de mortalidade e recrutamento, crescimento e biomassa, bem como a riqueza de espécies, diversidade funcional e características funcionais, estão mudando ao longo do tempo? ii) Considerando que mudanças ocorrem ao longo do tempo, qual é a relação dessas mudanças na dinâmica florestal com as variáveis ??climáticas? Para o Capítulo 02, perguntamos: (i) Qual a importância da contribuição do solo para o armazenamento de carbono na área de Mata Atlântica estudada? (ii) Quais são os principais fatores que influenciam o armazenamento de carbono na biomassa acima do solo (BPA), no estoque de carbono orgânico do solo (SOCS) e no estoque de carbono da serapilheira (LCS)? Para isso, amostramos 27 parcelas permanentes de 20 m x 20 m (totalizando 1.800 ha) em três locais diferentes em um fragmento de Mata Atlântica, começando em 1984. Modelos de equações estruturais por partes (piecewiseSEM), análises de correlação e regressão múltipla foram realizados para testar nossas hipóteses. Descobrimos que a área estudada armazenou cerca de 388 Mg de carbono, 73% dos quais foram armazenados na biomassa acima do solo, 21% no solo e 6% na serapilheira. Apesar do potencial da área para armazenamento de carbono, esse serviço tem sido ameaçado principalmente pelo aumento da mortalidade de árvores após eventos de seca. Nosso estudo também mostrou que tanto a seca quanto o excesso de chuvas podem ser prejudiciais aos processos florestais. Enquanto a seca foi responsável pela mortalidade das árvores, o excesso de chuvas reduziu o crescimento e o recrutamento de árvores na comunidade. Este trabalho contribui para enfatizar a importância da conservação de florestas maduras e que projetos de manejo e reflorestamento devem considerar espécies resistentes tanto à seca quanto ao excesso de chuvas.

Palavras-chave: mudança climática; floresta tropical; floresta semidecídua; estoque de carbono; carbono do solo; dinâmica florestal

SUMMARY

GENEREAL INTRODUCTION

After the most recent Intergovernmental Panel on Climate Change (IPCC) report, AR6 (Calvin et al., 2023; IPCC, 2023), it became clear that global warming will exceed 1.5 °C in less than 10 years, even if all countries implement the climate commitments proposed during the Paris Agreement. With the inevitable warming of the planet, changes in the structure of ecosystems like loss of biodiversity and biomass and various socio-economic impacts are currently being witnessed by the world's population, especially those in situations of greater social vulnerability (Weiskopf, 2024; Matthews, Wynes, 2022). In 2019, Brazil ranked 3rd among the countries that emit the most carbon dioxide (CO2) and methane (CH4) through food systems (FAO 2021). About 56.3% of emissions were attributed to the Land Use Change and Forestry sector, which includes deforestation (SEEG, 2023). Cutting down the forest, followed by burning and soil degradation, are the main agents of the great loss of organic carbon protected by forest systems (Don, Schumacher, Freibauer, 2011). As a result, some regions of the country's forests, due to strong anthropogenic pressures, have become sources rather than sinks of carbon (Gatti et al., 2021; Staal et al., 2023). To tackle the current climate crisis, efforts are needed to store and maintain the carbon stored in the forest systems. Thereby, understanding how these ecosystems are being affected by global changes and the patterns related to the sequestration and storage of atmospheric carbon, both in aboveground biomass (AGB) by trees and in the soil sink, is becoming increasingly diligent and emerging (Elbasiouny et al., 2022).

Forest community dynamics mainly studies how the structure and composition of a given community change over time, in relation to demographic processes such as tree growth, recruitment, mortality and survival and what are the main drivers that are related to these changes (Cowles, 1899). However, studies that consider forest dynamics on long-standing permanent plots and its relationship with multiple factors, both biotic and abiotic, as well as an approach based on functional traits are still scarce, especially in Atlantic Forest (Petisco-Souza, 2023). Some of these factors include natural processes and disturbances like ecological succession, forest fires, attacks by herbivores, diseases but also the effects of climate variables (Carroll et al., 2023; Franklin et al., 2016; Pulla et al., 2021). The human-caused impacts have also influenced the dynamics of plant communities over the years. Mainly due to changes in land use, environmental pollution and climate change. These factors are among the most threatening to the conservation and preservation of the world's biodiversity and the loss of fundamental ecosystem services (Steffen et al., 2005). For example, one factor resulting from global change that has a major impact on plant communities are the longer periods of drought that can influence the rates of recruitment, survival, and growth (Rocha et Al., 2020). Analyzing forest dynamics through permanent areas is the best way to understand how climate change is affecting the ecosystems in general and ecological processes both on large and small scales (Zhou et al., 2021).

The sequestration and abundant carbon storage are among the most important ecosystem services tropical forest provides today (Yadav et al., 2022). Estimates of the amounts of carbon stored in different types of tropical forests and how this storage relates to biotic and abiotic factors provide important parameters for improving forest restoration techniques (Holl, 2017). Different forest types and stages of succession exhibit marked contrasts between the carbon content in the above-ground biomass and in the soil (Ma et al., 2015; Rodrigues et al., 2023; Satdichanh et al., 2023). Despite the importance of C in the soil, most studies on carbon storage in tropical forests have focused mainly on the analysis of AGB and litter only. More detailed studies encompassing tropical forests to understand the carbon cycle beyond ABG are needed.

Seasonal semideciduous montane forests in the Zona da Mata of the state of Minas Gerais, Brazil, belong to the Atlantic Forest domain (Veloso, Rangel Filho, Lima, 1991). This domain is responsible for the country's highest soil carbon storage, with around 50 tons of C stored per hectare (MapBiomas, 2023). The semideciduous forest plays an important role as a carbon sink, since deciduous species accumulate more carbon in their biomass than evergreen species, while evergreens contribute to increasing biodiversity (Rodrigues et al., 2023). Thus, analyzing whether there is a trend toward greater mortality of deciduous species and a possible replacement of evergreen species by semideciduous or deciduous ones is an important issue. In addition, studying and understanding these relationships is fundamental to protecting the type of forest, because, despite their fundamental role in mitigating climate change, semideciduous forests are the most threatened ecosystems among those belonging to the Atlantic Forest domain, with only 7.1% of its potential area (537,640.29 km2) occurring within protected areas (Esser, Neves, Jarenkow, 2019).

Based on the above, the objective of this research was to analyze the carbon stock and the dynamics of an Atlantic tropical seasonal semideciduous forest and its relationship with biotic and abiotic variables. We aimed to answer a few questions, Chapter 01: (i) Are mortality and recruitment rates, growth and biomass, as well as species richness, functional diversity and functional traits, changing over time? ii) Considering that does occur change over time, what is the relationship of these changes in forest dynamics with climate variables? For Chapter 02, we asked: (i) how important is the soil contribution to carbon storage in the Atlantic Forest area studied? (ii) What are the main drivers of carbon storage in AGC, soil organic carbon stock (SOCS) and litter carbon stock (LCS)? To answer these questions, 27 (20m x 20m) permanent plots were established and sampled over some years, where we measured and identified all the trees with CBH ≥ 10cm. The growth, recruitment, mortality, survival and AGB increment rates were calculated for each period. Composite samples of soil and litter were collected. We used the TerraClimate database to collect climate data since 1973. Allometric equations to calculate AGB, AGC, SOCS and LCS were used. We calculated the Community Weighted Mean (CWM) for some functional traits, such as wood density and leaf phenology, as well as taxonomic and functional richness. Piecewise structural equation modeling (SEM), correlation and Principal Component and Multiple Regression analyses were performed.

The following hypotheses were tested:

Chapter 01: Climate is affecting tree community succession and ecosystem functioning through demographic processes in semideciduous seasonal forests. In particular, factors related to the availability of water to plants, i.e. increased of Climatic Water Deficit (CWD), Maximum Climatological Water Deficit (MCWD), Vapor Pressure Deficit (VPD), Potential Evapotranspiration (PET), Drought Index (SPEI and PDSI) had a negative effect on forest dynamics. In other words, drought and higher temperatures imply higher rates of tree mortality, reduced survival, growth and recruitment, diversity and therefore, consequently, lower Aboveground Biomass, impacting the capacity of C sequestration.

Chapter 02: The soil in the area studied has as much carbon stored as the aboveground biomass. AGC is being influenced mainly by the CWM of functional traits such as wood density and deciduous trees and by lower slope areas. LCS are being influenced by CWM of deciduous trees, lower slope areas and litter nutrients such as N. (iii) Finally, SOCS has a greater influence of CWM of wood density, clay content, pH, slope and organic matter content.

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CHAPTER 01 - COMMUNITY DYNAMIC OF A TROPICAL SEASONAL FOREST IN TIMES OF CLIMATE CHANGE

Abstract

Global changes are influencing forest demographic processes, directly affecting their capacity to mitigate environmental impacts. However, the effects of climate change on forest dynamics particularly in tropical forests remain poorly understood. This study aimed to analyze how community dynamics in a seasonal semi-deciduous forest have changed over time and how these changes are related to biotic and abiotic factors. We assessed demographic rates, biomass changes, functional diversity, and key functional traits at three sites within a forest fragment monitored since 1984. We calculated community-weighted means (CWM) for wood density, leaf phenology, and maximum height. Climate variables from 1973 to 2023 were obtained from the TerraClimate database, from which we derived the Standardized Precipitation Evapotranspiration Index (SPEI) and the Maximum Climatic Water Deficit (MCWD). We used structural equation modeling (SEM) with linear mixed effects to evaluate relationships among climate variables, demographic processes, species richness, functional diversity, and aboveground forest attributes (AGB). Our results show that net annual growth has declined due to increased tree mortality, particularly following drought events. Piecewise SEM revealed that rising maximum temperatures promote tree recruitment and growth but also increase mortality. High rainfall was associated with reduced growth, AGB, and recruitment, but it also lowered mortality, indicating that excess rainfall can also negatively affect semi-deciduous forests depending on the demographic process being assessed. Trees with low wood density, smaller diameters, late successional status, and evergreen phenology experienced the highest mortality rates. These findings underscore the complexity of forest responses to climate, where the same climatic factor can have both positive and negative effects depending on the demographic process. Our study emphasizes the importance of incorporating species resilient to both drought and excess rainfall into forest management and reforestation strategies.

Keywords: tropical forest, global change, forest dynamics, natural regeneration

1.INTRODUCTION

The effects of global change are becoming more frequent and intense in recent years, causing serious problems for humanity, as happened in the south of Brazil and Valencia, Spain, only in the year 2024 (Meyer, 2023; Pillar & Overbeck, 2024; Wise, 2024). The scientific community has a fundamental role to play in helping to better understand the impacts and proposing actions to mitigate the problem of the century. One of the solutions proposed by environmental researchers is the conservation and restoration of natural ecosystems, especially tropical forests (Verheyen, 2024; Oloo, 2024; Morecroft, 2019; World Bank, 2009). Since they are biodiversity hotspots and provide priceless ecosystem services, such as sequestration and storage of greenhouse gases (Raihan, 2014; Oloo, 2024). But these important ecosystems, key to mitigating climate change, are also being impacted by its effects (Gould, 2024; Deb et al., 2018). Understanding the effects of climatic variables on the dynamics of tropical forests is challenging, due to the great environmental variability and highly diverse and complex systems such as tropical forests (Aguirre-Gutiérrez, 2019). But untangling this knot is fundamental to tackling the climate crisis and advancing the knowledge of forest ecology and proposing forward-thinking restoration and adaptation practices (McDowell et al., 2020).

Different environmental drivers related to global change are having an impact on tropical forests, for instance, rising temperatures affect the water cycle, increasing the likelihood of drought and forest fires, and driving the conversion of humid tropical forests to drier ones (Gould, 2024). In general, these altered climatic factors harm tree survival and growth, which directly affects carbon storage capacity (Bauman et al., 2022; McDowell et al., 2020). Although these effects seem to be well understood, they can change or be less intense depending on the type of forest studied, its location, soil type and specific conditions (IPCC, 2022). Drought, i.e. higher temperatures and lower precipitation, is one of the main factors responsible for the increased rate of tree mortality in tropical forests (McDowell et al., 2020). Bauman et al. (2022), in a study of 49 years of dynamics in the humid tropics of Australia, found that the risk of tree death has doubled in the last 35 years. One of the effects of drought on tree mortality in tropical forests is related to hydraulics, i.e. cavitation of the driving elements (Rowland, 2015). Variables such as Vapor Pressure Deficit (VPD), a measure of air dryness, is related with carbon starvation and hydraulic failure (Hollunder et al., 2024; Bauman et al., 2022), which leads plants to close their stomata in order to reduce the rate of transpiration, particularly, this affects photosynthetic rates and the supply of photoassimilates to the trees (Sancho-Knapik, 2022).

The role of effects related to water stress has long been studied, mainly due to economic and food security issues, as it has a direct impact on agricultural crops (Wilhite, 2017). However, in recent years, a phenomenon that has also become more intense and frequent and that affects forest ecosystems just as much as water deficit is the sudden increase in storms (Hall et al., 2020). Intense and high amounts of rainfall, often bringing with them strong winds, floodings and typhoons have proven to be an important factor that endangers the survival of trees, especially large trees in tropical forests (Uriarte; Thompson; Zimmerman, 2019; Negrón-Juárez, et al., 2018). Therefore, the effects of climatic variables can be intriguing, for example, a study in the rainforests of French Guiana found that drought reduced annual growth and mortality rates, while high rainfall increased mortality rates and high temperature decreased growth (Aubry-Kientz et al., 2015).

Demographic processes such as growth, survival, recruitment and mortality are fundamental for structuring the forest Community (Muscarella et al., 2017; Rüger et al., 2023). However, the dynamics of these processes have been altered by anthropogenic factors, such as fragmentation, forest fires and climate change (McColl-Gausden, Bennett, Penman, 2022; Zhou, 2023). In Brazil, especially in the Atlantic Forest domain, forest fragmentation exerts strong pressure on the resilience of communities, increasing the threat of these forests in the face of a changing world (Dias, Silveira, Francisco, 2023; Torres et al., 2023). With climate change, the semideciduous forest is expected to be the most affected of the Atlantic Forest habitats, losing 64% of its current potential distribution in the worst-case scenario (Esser, Neves, Jarenkow, 2019; Barbosa et al., 2021; Bergamin et al., 2017). Unfortunately it is over-fragmented and neglected in the creation of conservation areas (Bergamin et al., 2017) and moreover, around 20% - 50% of its species lose their leaves during the dry season (IBGE, 2012; Veloso, Rangel Filho, Lima, 1991), thus, they become more susceptible to wildfire during drought periods (Astuti et al., 2022; Oliveira et al., 2023; Piao et al., 2022; Yin et al., 2024).

Based on this, we aimed to understand how climatic variables impact key demographic processes, tree biomass, species richness and functional richness in an Atlantic semideciduous forest. We raised a few key questions: (i) Are mortality and recruitment rates, tree growth, biomass, species richness, functional richness and functional traits, changing over time? ii) Given that changes occur over time, what is the relationship between these changes in forest dynamics and climate variables? We hypothesize that climate influences tree community succession and ecosystem functioning through demographic processes in semideciduous seasonal forests. Specifically, factors related to water availability for plants – such as increased

Climatic Water Deficit (CWD), Maximum Climatological Water Deficit (MCWD), Vapor Pressure Deficit (VPD), Potential Evapotranspiration (PET), and drought intensity, evidenced by Drought Index (SPEI and PDSI) – negatively affect forest dynamics. In other words, drought and higher temperatures lead to higher rates of tree mortality, reduced survival, growth and recruitment, diversity and therefore, consequently, lower Aboveground Biomass, impacting the capacity of carbon sequestration. Based on this, we developed conceptual models to illustrate our hypothesis (Figure 01).

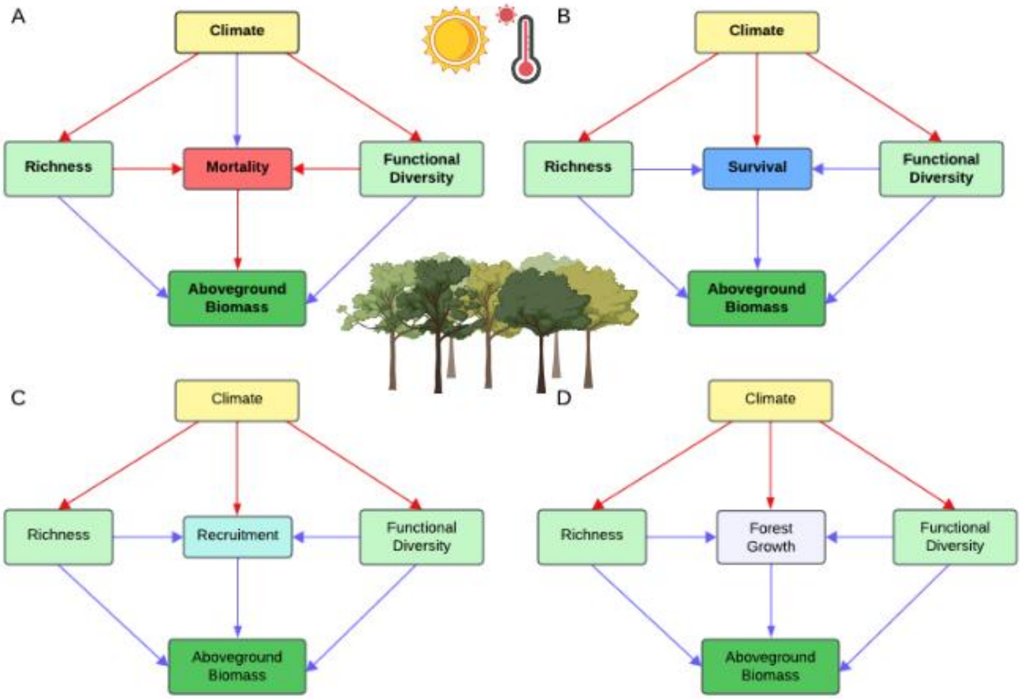

Figure 01. Conceptual models for testing the effects of climatic variables on community succession and ecosystem functioning through demographic processes. Red arrows indicate negative effects while blue arrows indicate positive effects. In A) effect of climatic variables mainly related to drought on the tree mortality rate, survival rate in B, recruitment rate in C and in the forest growth in D.

2. MATERIALS AND METHODS

2.1 Study Area

The study area is located in the Zona da Mata region of Minas Gerais, Brazil. The region underwent major transformations, mainly due to the significant loss of Atlantic forest cover.

The study area is among the regions in the state that have been most deforested for the implementation of coffee, sugar cane, and pasture crops (Meira-Neto, et al., 1997).

The studied area, a 75-hectare of a Montane Seasonal Semideciduous Forest (Veloso, Rangel Filho, Lima, 1991), is located in the municipality of Viçosa – Minas Gerais (20°45'22.3"S 42°51'47.3"W) (Figure 02). The fragment belongs to the Federal University of Viçosa and has been undergoing natural regeneration since the abandonment of the coffee plantations in 1926, when the University was founded. Therefore, the fragment has been undergoing a process of natural regeneration since then, almost 100 years. Each sampled plot is located in specific places within the fragment, which have their own local characteristics (Rodrigues et al.,2019; Peloso, 2012). The climate is a humid mesothermal climate with rainy summers and dry winters, Cwa according to the Köppen classification (Alvares et al., 2013). The average annual rainfall is around 1,300 mm, with a relative humidity of around 80%, and an average annual temperature of 19 °C (Fialho, Santos, 2022). The elevation of the area is around 700m. The predominant soil types are Dystrophic Red-Yellow and Acrisols and Red-Yellow Cambisols (Ferreira-Júnior et al. 2007).

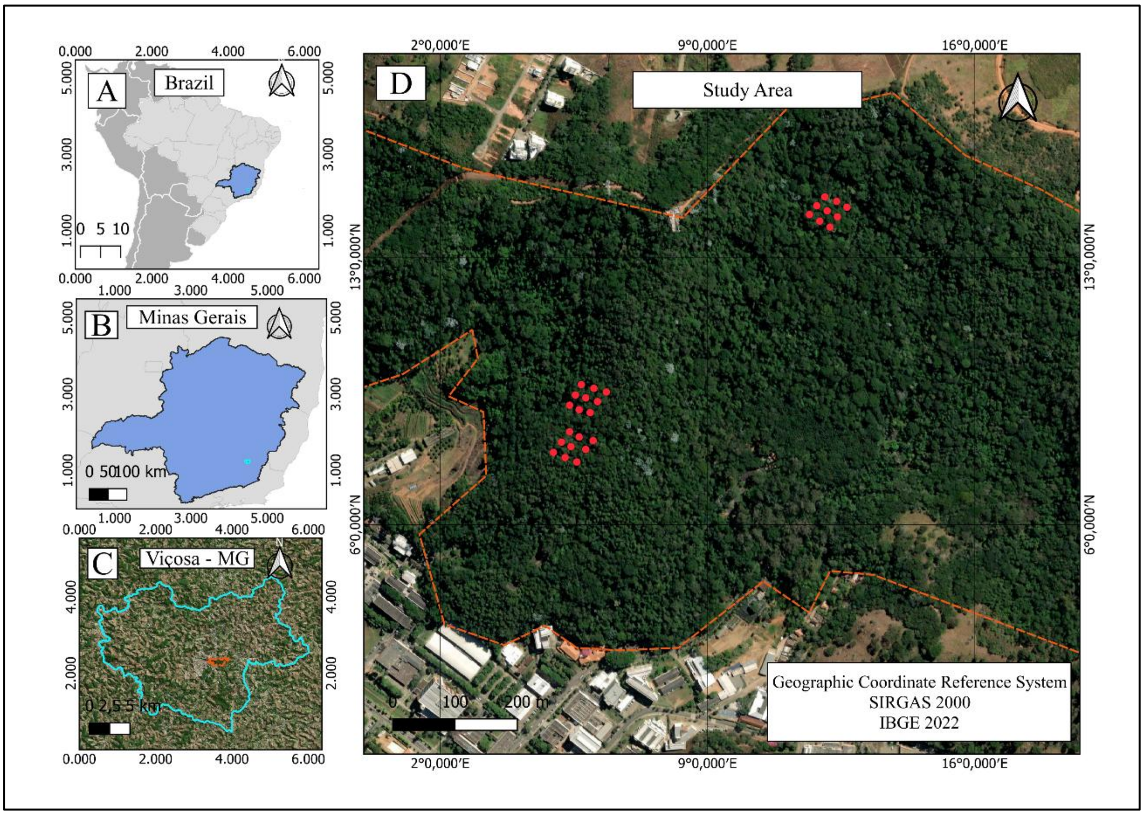

Figure 02. Location of the study area. A) Brazil. B) Minas Gerais state. C) Municipality of Viçosa. D) Location of the forest fragment studied.

2. 2 Data collection

2.2.1 Vegetation data

We sampled 27 permanent plots, each measuring 20 m x 20 m (400 m^2), totaling one hectare and 800m^2, distributed over three different sites in the forest area. Nine plots were established at each site: Southeast 1 (S1), Southeast 2 (S2) and Northeast (N). The monitoring of the study area began in 1984, but each area was monitored in different years. The Southeast Area 1 (S1) was sampled in 1984, 1998, 2003, 2011, 2017, and 2024, totaling six measurements, over a period of 40 years. The Northeast Area (N) was sampled in 1993, 2004, 2011, 2017, and 2024, with five measurements, over 31 years. Southeast Area 2 (S2) was the last to be sampled, starting in 2005, then in 2012 and 2021, over a period of 16 years. In each plot, all trees with a circumference at breast height (CBH) ≥ 10 cm were recorded and all individuals were identified at species level, according to the Angiosperm Phylogeny Group (APG IV, 2016).

2.2.3 Climatic variables

We used monthly climatic variables from 1973 until 2023, from the TerraClimate dataset (Abatzoglou & Ficklin, 2017), at a spatial resolution of 4 x 4 km. From the database, we selected Climatic Water Deficit (CWD), Vapor Pressure Deficit (VPD), Precipitation, Potential Evapotranspiration (PET), Minimum temperature (Tmin), Mean temperature (Tmed), Maximum temperature (Tmax), Soil Moisture (Soilm) and Palmer Drought Severity Index (PDSI). From this data, we also calculated the maximum Climatological Water Deficit (MCWD), water balance (WB) and Standardized Precipitation-Evapotranspiration Index (SPEI).

CWD, given in millimeters (mm), is a measure used to quantify the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET) in a given area over a period of time. It is used to assess drought severity, vegetation stress and predict ecosystem productivity (Stephenson, 1998). Higher CWD values indicate a greater water deficit, i.e. drier conditions or water stress for the vegetation. MCWD is a metric used to assess the severity of drought (Silva Junior et al, 2021), it represents the most negative mean monthly value of climatological water deficit (CWD) (Zelazowski et al., 2011). It is essential for studies that seek to understand the impacts of water stress on forest ecosystems, especially in the context of global change.

VPD is given in kilopascals (kPa), it is a measure of atmospheric demand for water. It's the difference between the amount of moisture in the air and the amount of moisture the air can hold when it is saturated (Grossiord et al., 2020). It is an accurate metric of the atmosphere's ability to extract moisture from the Earth's surface (Seager et al, 2015).

PET, Precipitation, and Soil Moisture are given in millimeters (mm). The Maximum (Tmax), Mean (Tm), and Minimum Temperatures (Tmin) are given in Celsius degrees (°C).

PDSI ranges from -4.3 to 3.4, where, briefly, values above +2 indicate extremely wet conditions; +1 to +2 indicate moderately wet conditions; 0 indicates near-normal conditions; -1 to -2 indicate moderate drought; -2 to -3 indicate severe drought; and -3 to -4 or below indicates extreme drought (Palmer, 1965). The Standardized Precipitation-Evapotranspiration Index (SPEI) is a drought index that measures water balance anomalies, incorporating precipitation and potential evapotranspiration (PET). SPEI is a standardized and cumulative index, and is therefore more efficient than the PSDI. The SPEI is used for drought monitoring studies and climate change impacts and is the most frequently used indicator in studies that seek to understand the relationship between climate and tree mortality (Vicente-Serrano et al. 2010; Eliades et al., 2024). We calculate SPEI for the Timescales of one, three, 6- and 12-months using precipitation and PET data collected from the TerraClimate database for the study area. SPEI values indicate: SPEI > 0: Indicates positive water balance, meaning conditions are wetter than normal. Higher values suggest a surplus of water. SPEI < 0: Indicates negative water balance, meaning conditions are drier than normal. Lower values suggest drought. SPEI between -1 and -1.5: Mild drought conditions. SPEI between -1.5 and -2: Moderate drought conditions. SPEI < -2: Severe drought conditions. To calculate the SPEI, we used “spei” function of SPEI package (Beguería, Vicente-Serrano, 2023).

For each variable we calculated the average for one year prior to each sampling year, two years prior, three, four and five years prior. The aim was to understand which previous time had the strongest effect on forest dynamics.

2.2.4 - Dynamic rates

For each period (years between sampling) and plot, we calculate the tree Mortality rates, Survival, Recruitment, Annual Gross and Net Growth, Basal Area, the Aboveground Biomass (AGB) and the increment of AGB. The Recruitment and Mortality rate (% year^{-1}) was calculated following the formula proposed by Sheil & May (1996) & Sheil; Jennings & Savill (2000):

Mortality (% year^{-1}) = $\{1\text{-}[\text{N0-Nm/N0}]^{1/t}\}$ x 100;

Recruitment (% year^{-1}) = $[1\text{-}(1\text{-r/Nt})^{1/t}]$ x 100.

Survival (%)=$(\text{Ti/Ts})^{1/t}\times 100$

Where t is the time interval between inventories; N0 is the initial number of trees and Nt is the final number; Nm is the number of deaths, r is the number of recruits; Ti is the initial number of trees, and Ts is the number of survivors. The 1/t is to calculate the annual rate, where t is the period of time between samplings.

Gross growth was calculated by adding the increase in basal area of living trees to the basal area of incoming trees. Net growth considers gross growth plus loss of basal area due to tree mortality.

To estimate aboveground biomass (AGB), we followed the general allometric model developed by Chave et al. (2014) for tropical forests, when the height is not available (our case for the first years of sampling). AGB is estimated in terms of DBH (in cm), wood density (WD, in g/cm3), and a measure of environmental stress (E):

$$\text{AGBest}=\exp(-1.803-0.976E+0.976\ln(\rho)+2.673\ln(D)-0.0299[\ln(D)]2)$$

Where ρ is the wood density given in g cm^{-3}, D is the DBH given in cm. E is defined as:

E = (0.178 x TS - 0.938 x CWD - 6.61 x PS) x 10^{-3} (Chave et al. 2014).

Where, TS is the temperature seasonality, CWD is the climatic water deficit and PS is precipitation seasonality (Chave et al. 2014).

2.2.5 Taxonomic and Functional Diversity

We calculated the Shannon-Wiener and Simpson's diversity indices for each period and plot (Kent, 2011). For each species we collected functional traits: Wood Density (WD; mg/m^3) and leaf phenology (evergreen, semi-deciduous and deciduous). Wood Density was obtained from the Global Wood Density Database (Zanne et al. 2009; Chave et al. 2014). We accessed leaf phenology and the successional groups by searching articles, books and plant databases.

For each plot, the Community-Weighted Mean (CWM) for the functional traits (Garnier et al. 2004; Lavorel et al. 2007) was calculated. For this, we utilized the "functcomp" function from the “FD” package (Laliberté & Legendre 2010; Laliberté & Legendre 2014). We also calculated functional richness (FRic), a metric that represents the amount of functional space occupied by a set of species, functional divergence (FDiv), which defines how much species abundance diverges from the center of the functional space, functional uniformity (FEve), which represents the uniformity of the distribution of species abundance in the functional space (Mouchet et al. 2010), and functional dispersion (FDis), which defines the weighted average distance of individual species from the center of the functional space for all species, while the weights correspond to the relative abundances of the species (Laliberté & Legendre 2010), we used the package “fundiversity” (Gruson & Grenié, 2023).

2.2.6 Topographic data

Topographic variables (elevation, slope and convexity) were measured for each plot using a total station with the help of a surveyor (see Rodrigues et al.,2019). Elevation was calculated using the average elevation value of each of the four corners of the plots. The slope (°) was obtained by calculating 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 center of the plot from the average elevation of the eight surrounding plots (Wang et al., 2017 and Rodrigues et al., 2019).

2.3 Statistical analysis

2.3.1 Changes in the local climate over the years

We carried out time-series analyses of climatic variables to identify trends of increase or decrease in the values of temperature, precipitation, vapor pressure deficit, soil moisture, and drought index over the years in the study area.

2.3.2 Forest dynamics over time

To analyze the differences in forest dynamics metrics (mortality, recruitment, gross and net growth etc.) and biotic variables between years in each area, first we tested the normality of the data using the Shapiro–Wilk test. The parametric data were tested with the ANOVA-dependent and the non-parametric data were tested using the Friedman test for significant differences between more than two years and t-test and Wilcoxon test between two years. When the results were significant for more than two years we used t-test for parametric data and

Wilcox test for non-parametric data to calculate the pairwise mean comparison. The graphics were built using the “ggplot2” package (Wickham, 2016).

2.3.3 Selection of variables

We performed Pearson's correlation analysis for parametric data and Spearman's correlation for non-parametric data (Rodgers & Nicewander, 1988) for climate and dynamics variables in order to avoid multicollinearity, which reduces explanatory power due to strong correlations between predictors. Highly correlated variables ($| r | \geq 0.7$) were removed. Based on this correlation analysis, we also selected the variables that were used in the Structural Equation Models (SEM) to test our hypothesis.

2.3.4 Structural equation modeling (SEM)

Based on our conceptual model (Figure 01), we used piecewiseSEM (pSEM) to evaluate the relationship between climatic variables, demographic processes, richness, functional diversity and AGB for the forest community, considering both fixed and random (year|plot) effects (Lefcheck, 2016 , Ali et al., 2020). We perform pSEM with linear mixed-effects models and assess the model fit using Fisher's C statistic, P-value and AIC, where a p-value > 0.05 and lower AIC indicate good models. We evaluated the conditional R^2 (R^2 c) and marginal R^2 (R^2 m) to quantify the variances explained by fixed and random effects (Lefcheck, 2016 , Ali et al., 2020). All analyses were conducted in r 4.4.1 (R Development CoreTeam, 2024).

3. RESULTS

3.1 Weather extremes over time

The Standardized Precipitation-Evapotranspiration Index results indicate both drought and high precipitation peaks. However, there is a clear trend of increasing frequency of drought events in the region, especially from 2001 onwards (Figure 03).

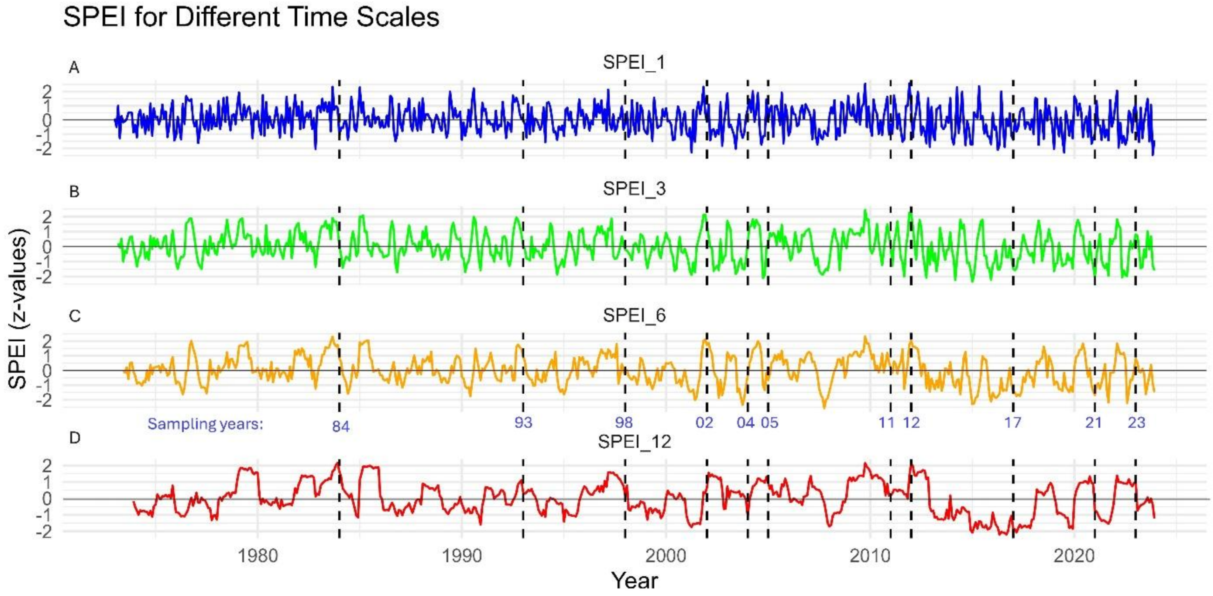

Figure 03. Standardized Precipitation-Evapotranspiration Index (SPEI) for one (A), three (B), 6 (C) and 12-month scale (D), for the study area from 1973 until 2023. Negative values indicate dry periods and positive values indicate periods of greater humidity.

3.2 Forest dynamics over the years of succession

Over the years of monitoring of the secondary forest, 182 species were sampled, belonging to 116 genera and 40 botanical families. Our results showed that there has been a reduction in the growth of the forest community (Figure 04 and Table S 01). Especially when analyzing annual net growth, which refers to the growth of living trees, recruits that have entered the community and the loss of biomass due to tree mortality. In both area N (Anova, $p=1.85^{-06}$) and area S1 (Friedman, $p=4.997^{-06}$) it is possible to notice a drastic decrease in net growth in the year 2011. While the S1 seems to be recovering growth in the last years of sampling (2017 and 2024), the N recovered growth to some extent in 2017 but regressed again in 2024. While in the most recent area, S2, there was a sharp reduction in community growth over the years (t-Test, $p<2.2^{-16}$). With special attention to 2024, where we noticed a negative balance in growth, indicating that there were more dead trees than trees growing and entering the community.

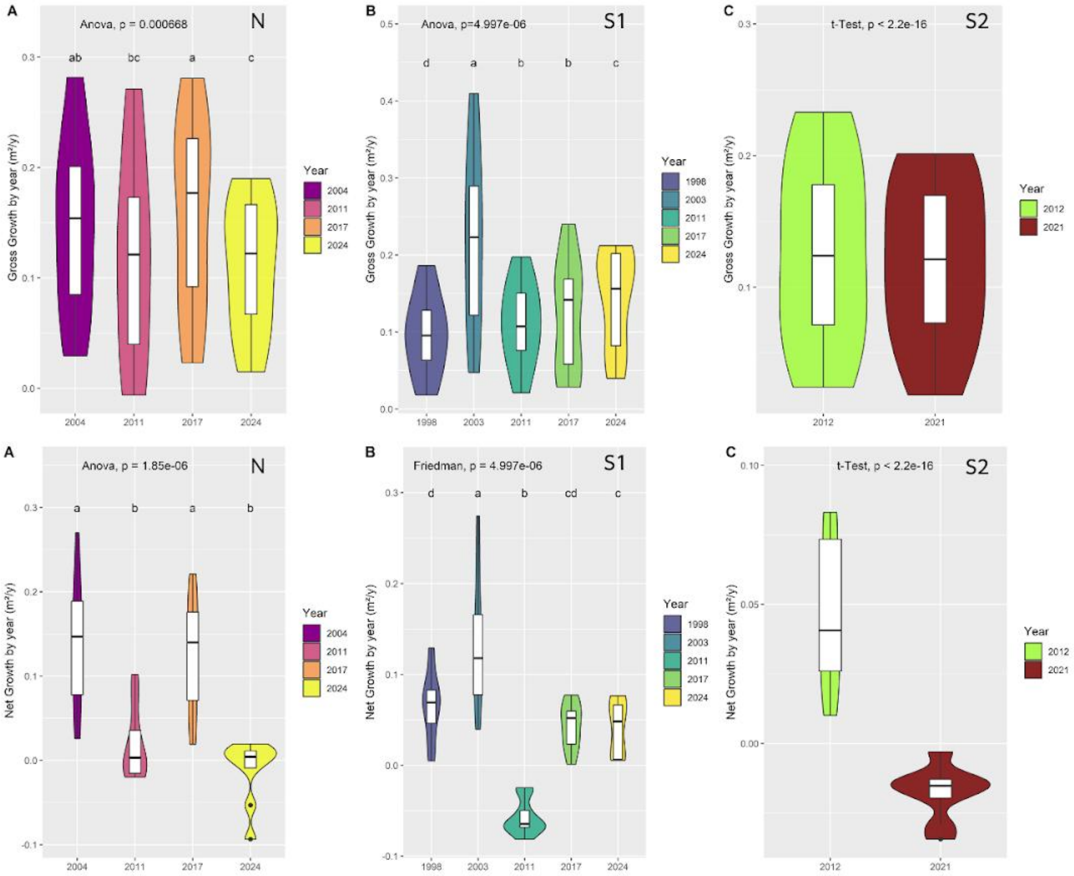

Figure 04. Gross annual growth of areas N (A), S1 (B) and S2 (C) and net annual growth of areas N (A), S1 (B) and S2 (C).

Concerning the tree mortality rate, in general we noticed an increase in mortality over time (Figure 05), with a pronounced increase in the years 2011 and 2024 in the areas N (Friedman, p=0.00066) and S1 (Friedman, p=0.0133), while in the area S2 there was a sharp increase (t-Test, o=0.0099) in the mortality rate during the sampling period. At the same time, recruitment follows the same trend, with the lowest recruitment rates in 2011 in area S1 (Friedman, p=8.94^{-06}) and N (Friedman, p=0.00035). Despite the increase in the number of recruits in 2017, in area N the number decreases again in 2024 in particular. In area S2, there was a low number of recruits in 2012, but the community saw an increase in new trees in 2021 (t-Test, p=0.0015).

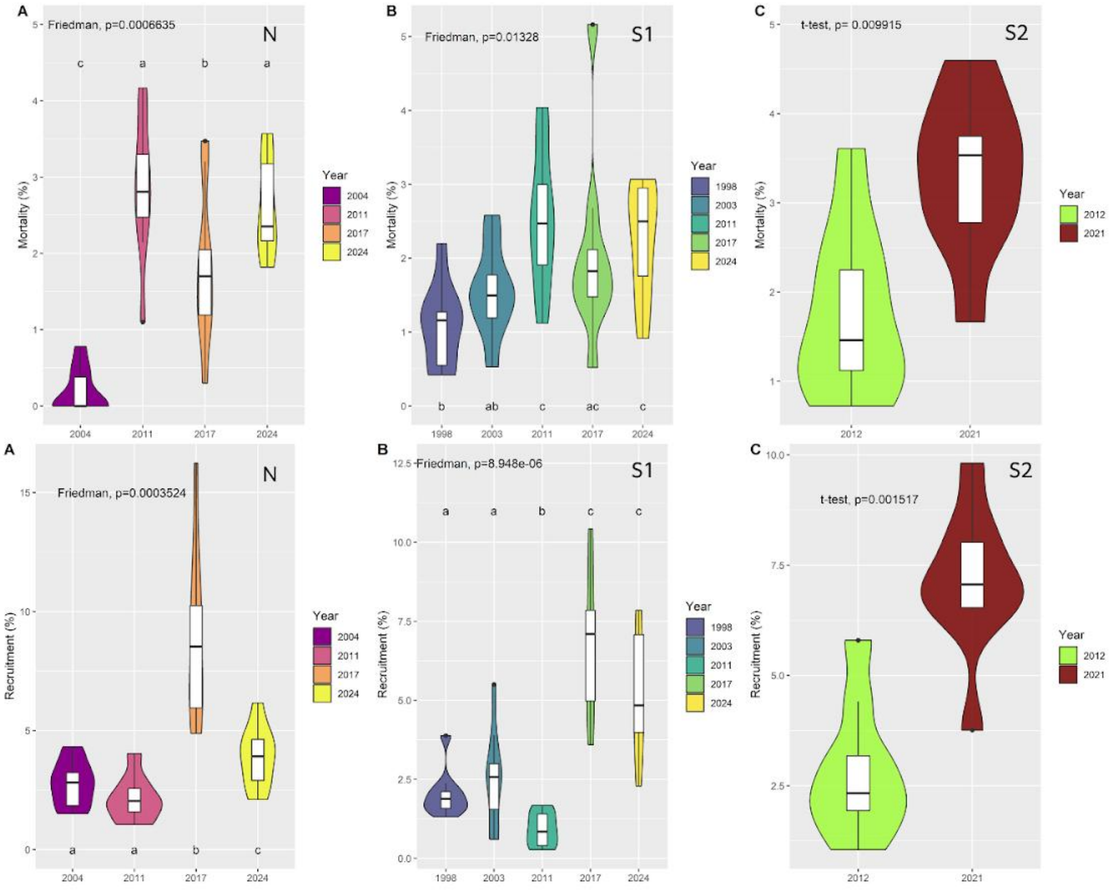

Figure 05. Mortality and recruitment rates (% year^{-1}) observed during the succession period of a semi-deciduous Atlantic forest. N, S1 and S2 indicate the northeast and southwest areas 1 and 2, respectively.

Over the years, we observed a gradual increase in aboveground biomass (AGB) (Figure 06), although this increase has not occurred at a fast rate. Compared to the initial sampling years, biomass has nearly doubled in areas N (Friedman, p= 0.00016) and S1 (Friedman, p= 7.32 x 10^{-6}), while remaining stable in area S2 (ANOVA, p=0.242). Among the studied areas, S1 exhibited the highest biomass accumulation in the final sampling year (Table S 02). Additionally, in 2011, there was a slight reduction in AGB and a significant decrease in AGB increment in areas N (Friedman, p = 3.78 x 10^{-5}) and S1 (ANOVA, p=0.00983).

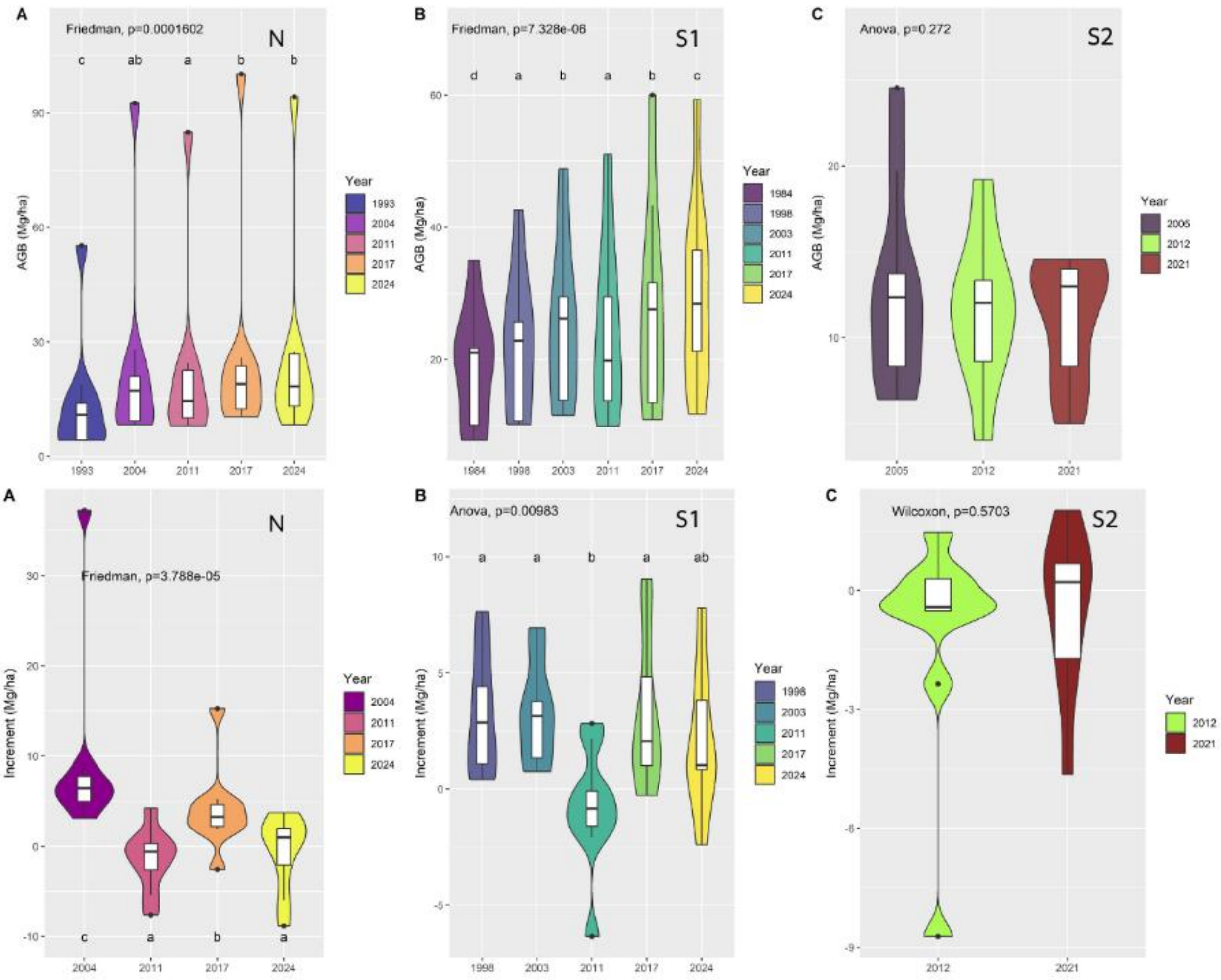

Figure 06. Above-ground biomass (AGB) and AGB increment in the Northeast (A), Southeast 1 (B) and Southeast 2 (C) areas.

We also analyzed the dynamics of taxonomic diversity and functional richness over the years (Figure 07). In area N there is a general trend of increasing taxonomic diversity (ANOVA, p = 0.0177) and functional richness (Friedman, p = 0.019). In contrast, in area S1, taxonomic diversity is decreasing (Friedman, p=0.015) while functional richness appears to be increasing, though not significantly (Friedman, p=0.1185). In area S2, taxonomic diversity has remained stable over the years (ANOVA, p= 0.254) whereas functional richness has increased (ANOVA, p=0.0207).

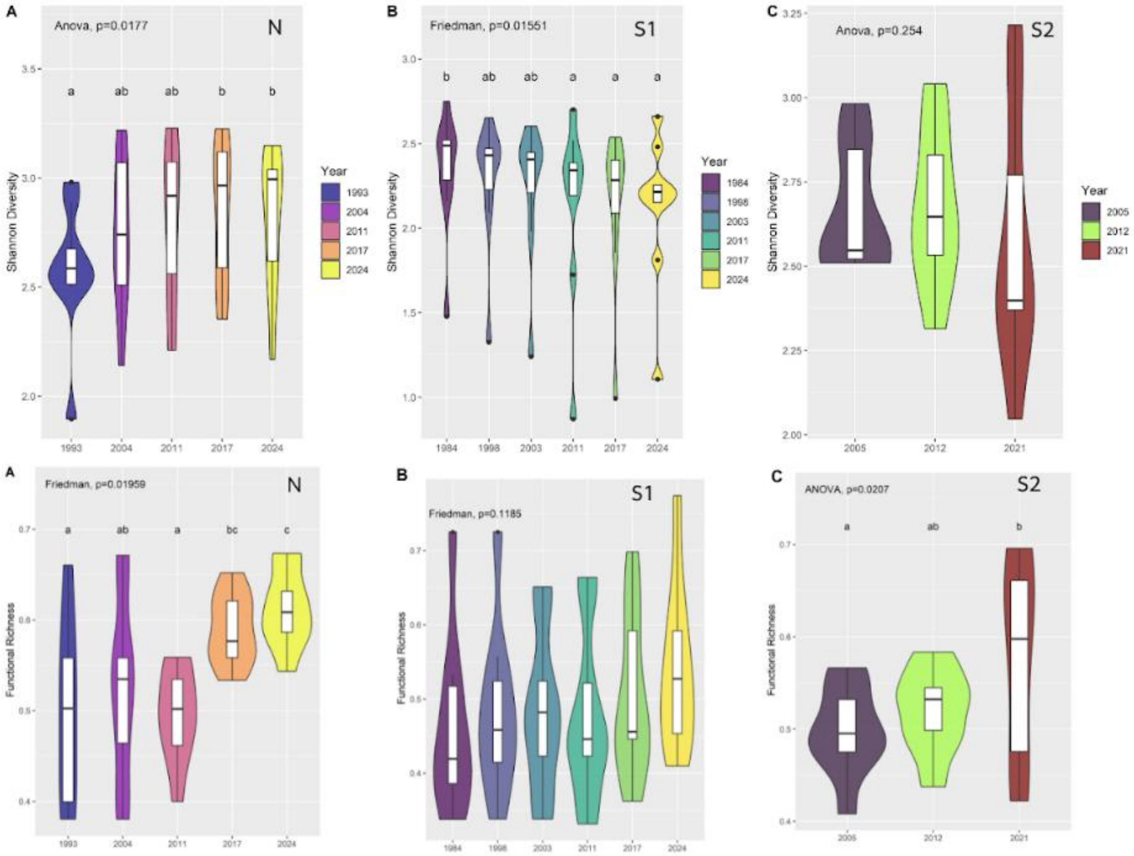

Figure 07. Boxplots showing the Shannon Diversity Index and Functional Richness for the three areas, N (A), S1(B) and S2(C).

The CWM analysis indicates that functional trait composition is changing over the course of succession. In area N, wood density has remained stable (ANOVA, p = 0.422), meaning that species with higher wood densities are not increasing in the community (Figure 08). A similar pattern is observed in area S1, where small fluctuations occurred in certain years (ANOVA, p = 0.0397), but values eventually returned to levels similar to those of the first sampling year. In area S2, wood density also remained stable (Friedman, p = 0.6412).

Leaf phenology is also changing throughout the succession (Figures 09, 10 and 11), characterized by a notable reduction in deciduous species and an increase in evergreen species. Additionally, there is a trend towards a decrease in the presence of semi-deciduous species.

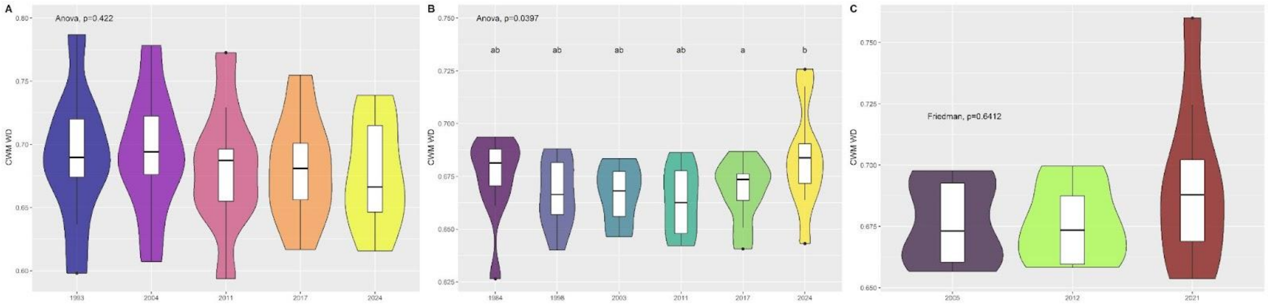

Figure 08. CWM of Wood Density (WD) for areas N (A), S1 (B) and S2 (C).

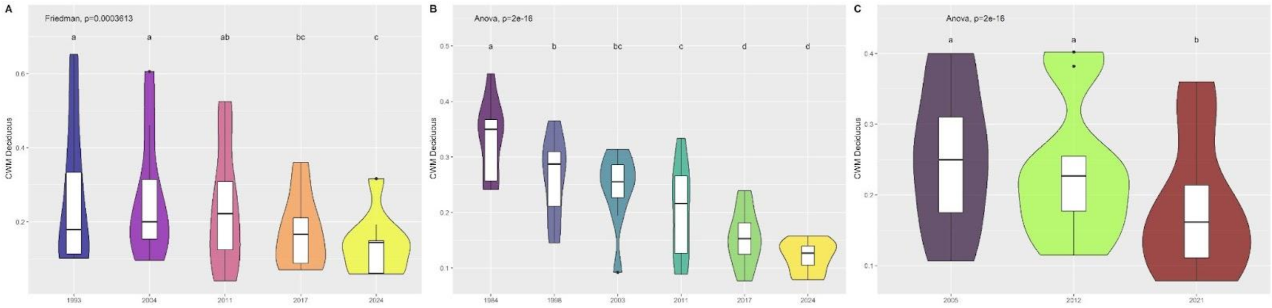

Figure 09. CWM of Deciduous species for areas N (A), S1 (B) and S2 (C).

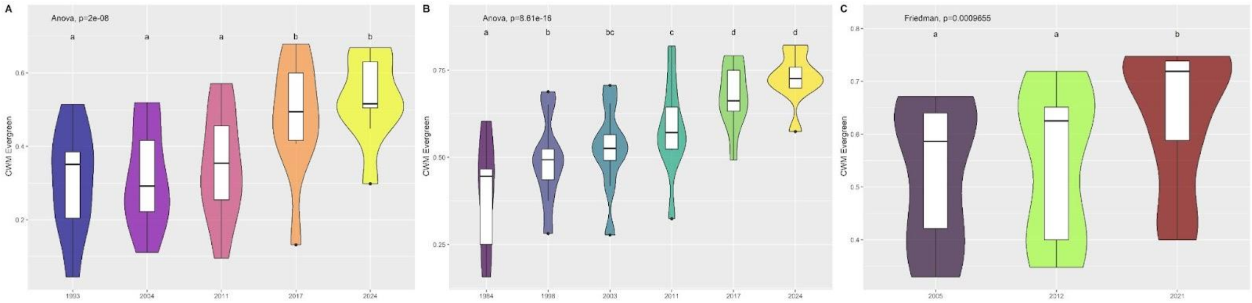

Figure 10. CWM of Evergreen species for areas N (A), S1 (B) and S2 (C).

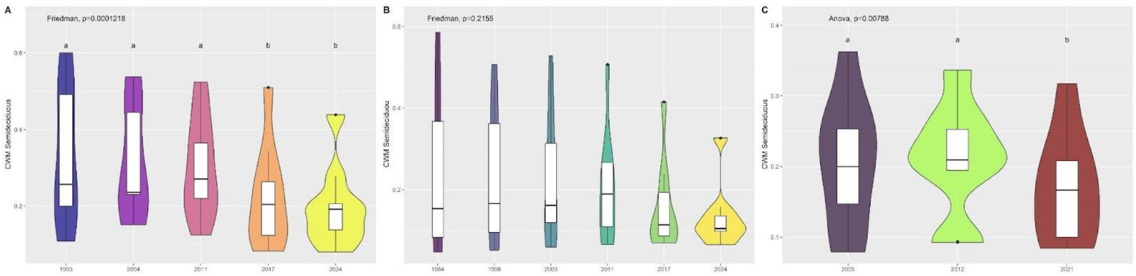

Figure 11. CWM of Semi-deciduous species for areas N (A), S1 (B) and S2 (C).

3.3 Correlation between climate variables and forest dynamics

Correlation analysis ($| r | \geq 0.7$) between community dynamics and climate variables showed interesting results, that were somewhat contrary to expectations, with CWD and MCWD showing a positive relationship with forest growth (Figure S01, S02 and S03). During periods of greater water stress, i.e. during the dry season, there was an increase in growth in the community. This was corroborated when we analyzed the relationship between growth and soil moisture, PDSI and precipitation, where soil moisture, PDSI (positive values indication higher humidity) and precipitation were negatively correlated with annual growth (Figure S04, S05 and S06).

We found similar results for the recruitment rate. When analyzing the recruitment of new trees in the forest community, a positive relationship was found with PET, VPD and Tmax (Figure S07, S08 and S09) and a negative correlation with precipitation, WB and SPEI (Figure S10, S11 and S12). This suggests that tree recruitment, defined as trees reaching a circumference greater than or equal to 10 cm at 1.30 m from the ground, is higher during drier periods, than during the wetter ones.

When we investigated the correlation between climatic variables and tree survival rate of trees, we found a negative relationship with mean temperature (Figure S13). We also found a positive correlation between Tmax and tree mortality (Figure S14), and a negative correlation between SPEI and mortality (Figure S15). In other words, an increase in temperature reduces survival and increases tree mortality, while higher humidity decreases tree mortality.

3.4 Piecewise structural equation modelling (piecewiseSEM)

We performed piecewiseSEM analyses to test our hypothesis, based on our conceptual models (Figure 01). The test of climate variables in relation to growth and AGB based on pSEMs (Figure 12) showed that Tmax had a significant and positive effect on forest growth rate ($R^2m = 0.13$, $R^2c=0.13$), as well as on AGB ($R^2m = 0.03$, $R^2c=0.92$) and functional richness ($R^2m = 0.05$, $R^2c=0.59$). The same goes for PET, that had a positive and significant effect on both forest growth ($R^2m = 0.30$, $R^2c=0.60$) and AGB ($R^2m = 0.05$, $R^2c=0.93$), functional ($R^2m = 0.08$, $R^2c=0.64$) and taxonomic richness ($R^2m = 0.03$, $R^2c=0.41$). In contrast, precipitation showed a negative effect on growth ($R^2m = 0.25$, $R^2c=0.55$), AGB ($R^2m = 0.05$, $R^2c=0.93$), functional ($R^2m = 0.08$, $R^2c=0.63$) and taxonomic richness ($R^2m = 0.04$, $R^2c=0.42$). Despite the negative effect of precipitation on growth, growth continued to contribute to AGB.

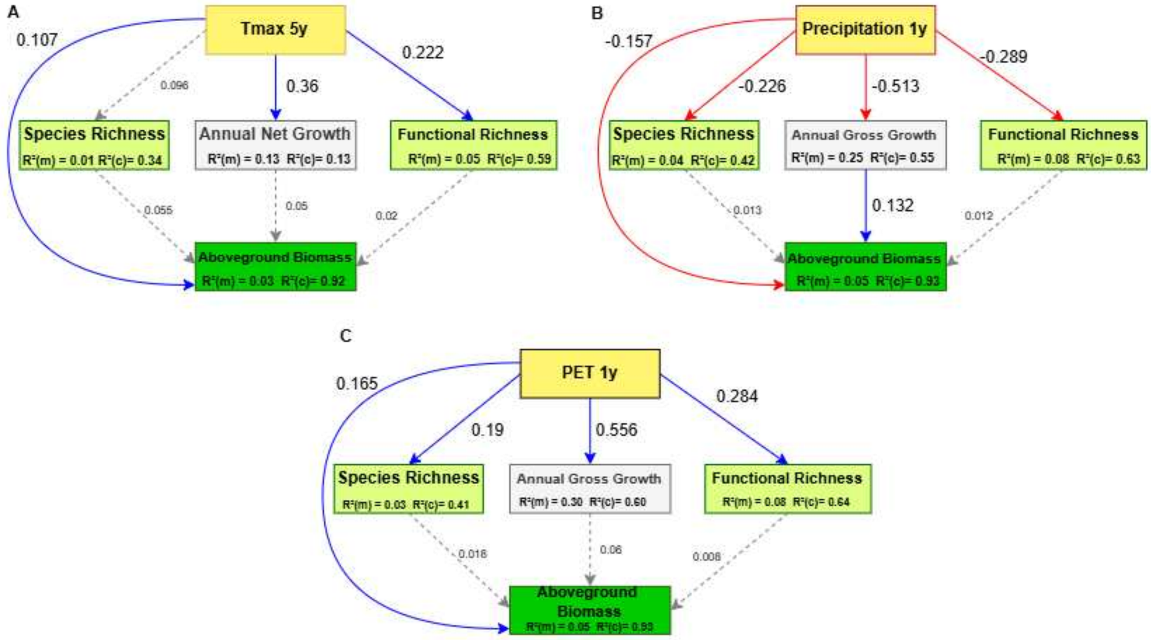

Figure12. Results of the piecewiseSEM models, showing the main climatic variables that influenced the forest growth rate and AGB. A) Influence of Tmax of five years on annual net growth and AGB.; B) Influence of precipitation on annual gross growth and AGB; C) Relationships of one-year PET on annual gross growth and AGB. Blue arrows indicates a positive effect, red arrows indicates a negative effect, dotted gray arrows indicate non-significant paths. R²(m) represents the marginal R² value and R²(c) represents the conditional R² value.

In relation to the recruitment rate (Figure 13), pSEM showed a positive effect of Tmax ($R^2m = 0.50$, $R^2c=0.50$), VPD ($R^2m = 0.44$, $R^2c=0.55$) and MCWD ($R^2m = 0.39$, $R^2c=0.40$) on recruitment of new trees and a small effect on AGB. Whereas, SPEI had a negative impact on the recruitment rate ($R^2m = 0.50$, $R^2c=0.50$) and AGB ($R^2m = 0.02$, $R^2c=0.92$), as well as in functional ($R^2m = 0.11$, $R^2c=0.65$) and taxonomic richness ($R^2m = 0.03$, $R^2c=0.36$).

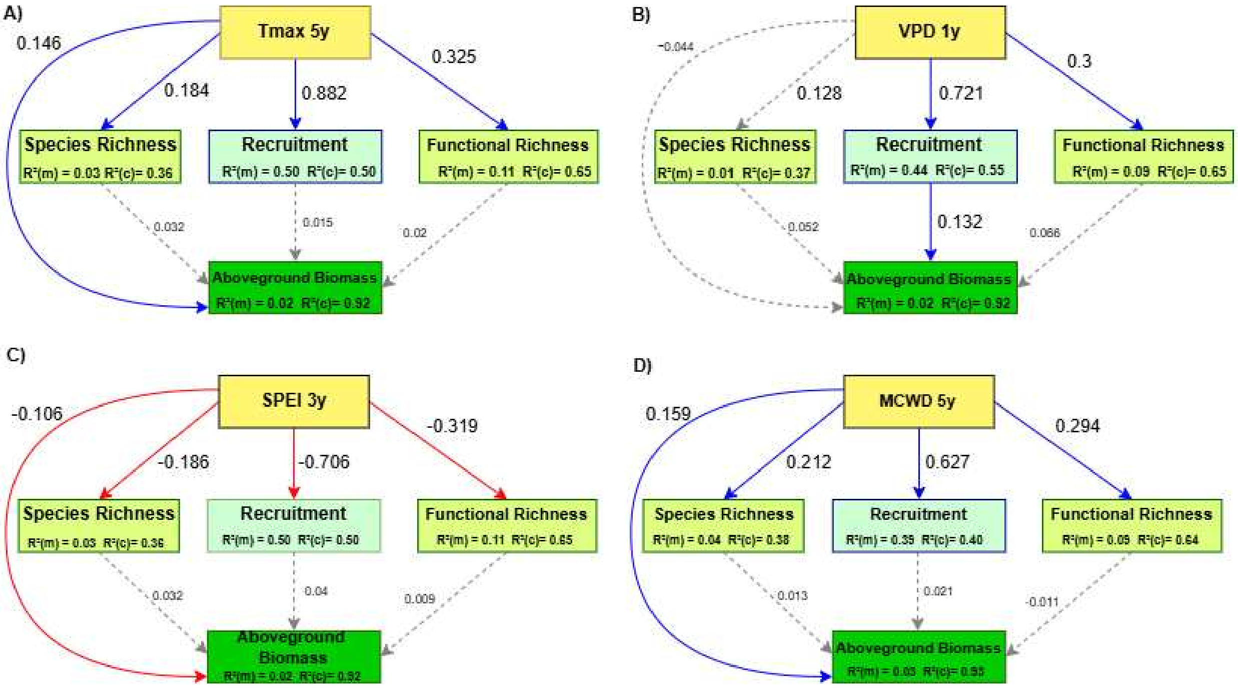

Figure 13. PiecewiseSEM models, showing the main climatic variables influenced recruitment rate and AGB. A) Influence of Tmax on recruitment, functional and species richness and AGB; B) Relationships considering VPD; C) Relationships considering SPEI; D) Relationships considering MCWD. Blue arrows indicate positive effects, red arrows indicate negative effects, dotted gray arrows indicate non-significant paths. R^2(m) represents the marginal R^2 value and R^2(c) represents the conditional R^2 value.

When considering the demographic process of mortality (Figure 14), we found that PET and maximum temperature have a positive influence on mortality. The model shows that PET has an influence on AGB through mortality ($R^2m = 0.34$, $R^2c=0.48$) and that PET also has a direct positive influence, although small, on AGB ($R^2m=0.02$, $R^2c=0.34$). Our results also indicate that SPEI ($R^2m = 0.21$, $R^2c=0.23$), one of the main drought indices, and WB ($R^2m = 0.25$, $R^2c=0.39$) had a negative effect on mortality rates, species richness and functional richness, as well as having a direct negative small effect on AGB.

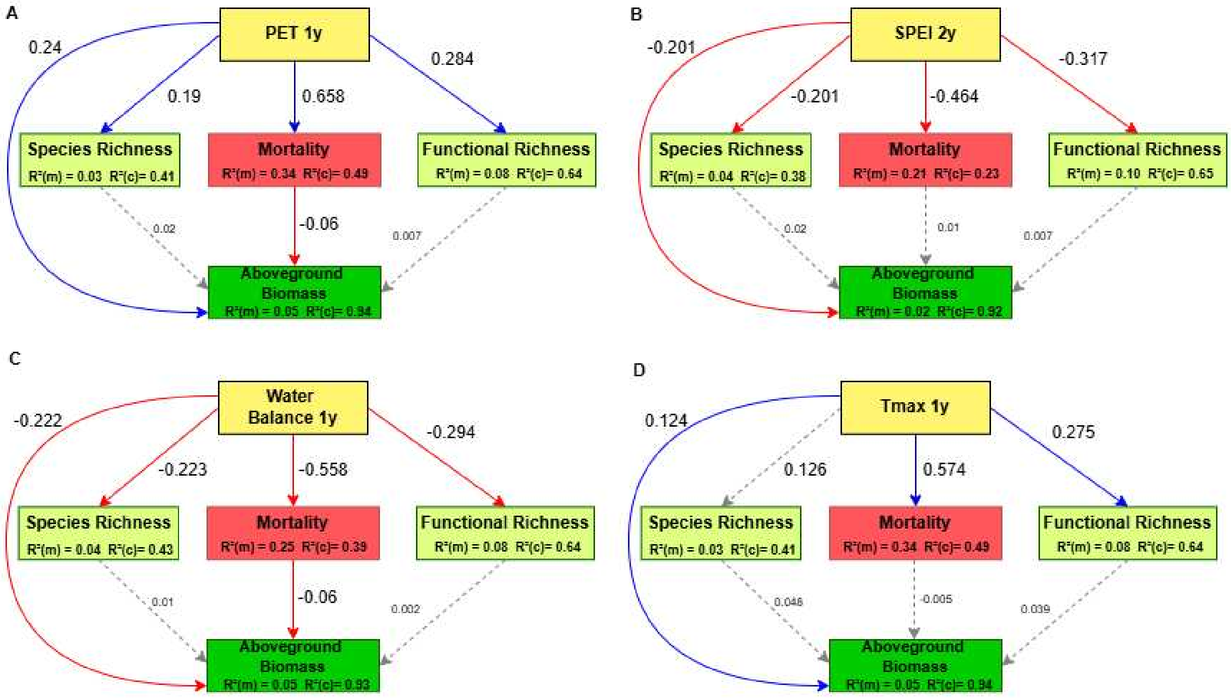

Figure 14. Results of the piecewiseSEM models, showing the main climatic variables that influenced the mortality rate and AGB. A) Influence of PET on mortality, functional and species richness and AGB.; B) Relationships considering SPEI; C) Relationships considering the WB; D) Relationships considering the Tmax. Blue arrows indicate positive effects, red arrows indicate negative effects, dotted gray arrows indicate non-significant paths. R^2(m) represents the marginal R^2 value and R^2(c) represents the conditional R^2 value.

With regard to the survival rate, our results indicate that Tmax ($R^2m = 0.35$, $R^2c=0.35$) and PET ($R^2m = 0.27$, $R^2c=0.46$) had a negative effect on survival, while having a direct positive small influence on AGB (Figure 15). In addition, SPEI ($R^2m = 0.12$, $R^2c=0.18$) and WB ($R^2m = 0.16$, $R^2c=0.31$) had a positive effect on survival rate, while having a small negative effect on AGB, species richness, and functional richness.

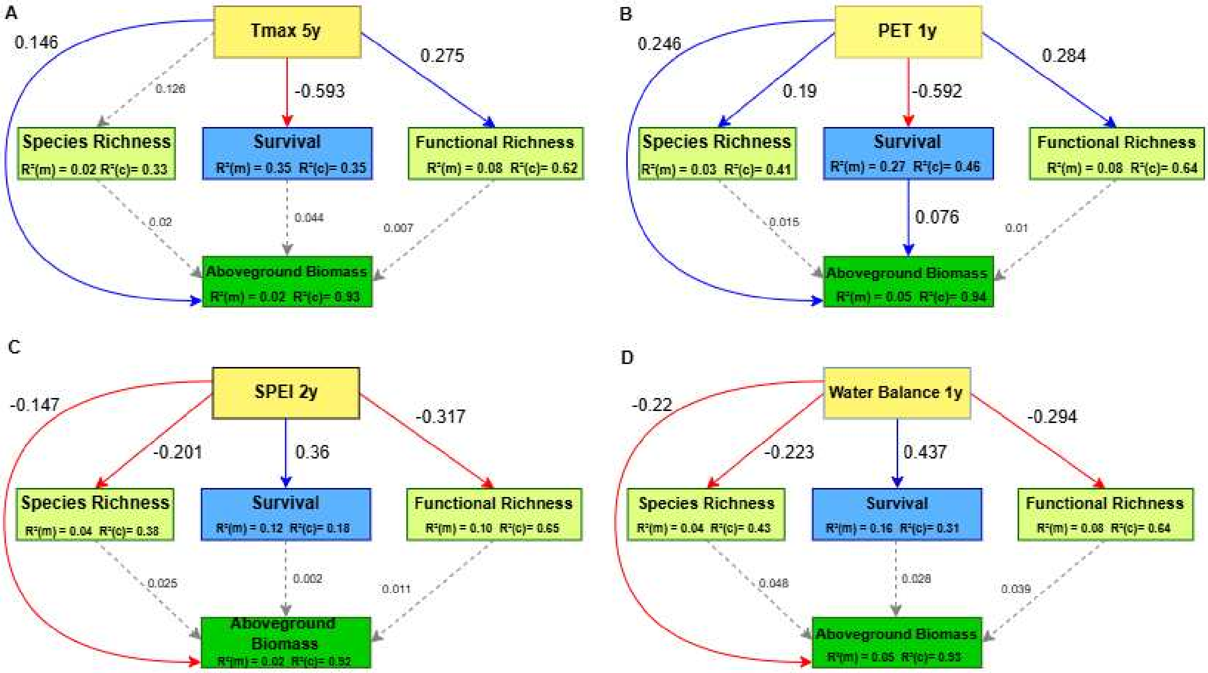

Figure 15. PiecewiseSEM models showing the main climatic variables that influenced survival rate and AGB. A) Influence of Tmax on survival, functional and species richness and AGB; B) Relationships considering PET; C) Relationships considering SPEI; D) Relationships considering WB. Blue arrows indicate positive effects, red arrows indicate negative effects, dotted gray arrows indicate non-significant paths. $R^2(m)$ represents the marginal R^2 value and $R^2(c)$ represents the conditional R^2 value.

In order to better understand tree mortality, we analyzed the percentage of dead trees according to leaf phenology (deciduous, semideciduous and evergreens), successional group (pioneers, early secondary(ES) and late secondary(LS)), small trees (CAP < 50 cm) or large trees (CAP ≥ 50 cm) and low wood density (wd < 0.7 g cm-3) or high wood density (wd ≥ 0.7 g cm-3). When we analyzed which phenological and successional groups had the highest mortality percentages, we found that in area N, semi-deciduous trees, followed by deciduous trees, accounted for the highest percentage of dead trees (Figure S18 and Table S3). While ES, followed by pioneers, had the highest percentages (Figure S19).

A similar pattern was found in area S1, with the highest mortality of deciduous and semi-deciduous trees in the first years of sampling, but in the last sampling period, evergreen mortality reached 66% (Figure S20). The early secondary group had the highest number of dead trees in all periods (Figure S21).

Interestingly, in area S2, evergreens followed by deciduous had the highest number of dead trees, as well as early secondary (Figure S22). When counting all areas and all sampling periods, the smallest trees, trees with low wood density, early secondary and evergreen trees had the highest percentage of dead trees (Table S3).

4. DISCUSSION

Our results indicate that climatic variables play a significant role in forest succession dynamics and ecosystem functioning by influencing key demographic processes of tree communities. As hypothesized, increased water stress, represented by variables such as Potential Evapotranspiration (PET) and negative values of Standardised Precipitation-Evapotranspiration Index (SPEI), were expected to negatively impact tree survival. However, we found unexpected relationships, where periods of higher water deficit were associated with increased growth and recruitment rates, suggesting that certain species may be better adapted to seasonal dry conditions or that water excess limitation may be a stronger determinant than water scarcity. On the other hand, we confirmed that higher temperatures (Tmax) reduced survival rates and increased mortality, supporting the negative influence of rising temperatures on forest biomass maintenance. Additionally, we observed that periods of high precipitation were correlated with lower growth, possibly due to soil saturation and oxygen uptake limitations by roots, as highlighted in previous studies. These findings reinforce the need to consider multiple interactions between climatic variables and ecosystem processes when projecting future scenarios for seasonal tropical forests, especially in the context of climate change.

Assessing the main climatic factors influencing the demographic processes of tropical forests is crucial to understanding how these ecosystems are responding to current climate changes. Furthermore, understanding forest dynamics over years of succession allows us to determine whether the forest is losing or gaining biomass, whether mortality and recruitment rates are increasing or decreasing, and how this changes directly impacts the carbon storage capacity and the resilience of tropical forests.

4.1 Forest dynamics over the years of succession and the correlation with climatic variables

In our study area, a montane seasonal semideciduous forest, there has been a decrease in growth in the most recent years of sampling, especially when we analyzed net annual growth, considers the biomass lost due to tree mortality. This reduction in growth is possibly related to different drivers, as evidenced by our results. Water excess due to heavy rains showed a negative correlation with tree growth, while drought-related variables seem to benefit it. A similar finding for forest growth was suggested by the study by O'Donnell et al. (2021) where increased rainfall events could have a negative effect on tree growth in the tropical Australia region. O'Brien et al. (2024) also found that increased rainfall can have a stronger negative effect than drought in growth in a seasonal tropical forest. The results of the study showed that growth decreased in 48% of species during periods with higher rainfall, while only 4% of species showed a reduction in growth with drought (O'Brien et al.,2024). Excessive rainfall can lead to water saturation of the soil, which is the main reason for anoxia, i.e. a lack of available oxygen in the soil, that result in reduced growth, as demonstrated by various studies of tropical species (Parolin, 2001; Mielke et al., 2005; Neatrour, Jones, Golladay, 2007; Kreuzwieser & Gessler, 2010). This, coupled with soil waterlogging, can also alter the microbial community, which reacts quickly to these changes, thus affecting the availability of nutrients and symbiotic relationships between trees and microorganisms (Kreuzwieser & Gessler, 2010).

The relation between forest growth and Tmax and PET can be explained because higher temperatures promote tree growth by increasing photosynthetic efficiency (Collalti et al., 2020; Wang et al., 2008). Furthermore, if mortality is increased during drought, there is a reduction in basal area, that leads to an opening of niche space, reducing competition and increasing resource availability (Bradford & Bell, 2017), therefore allowing for greater growth and recruitment during the dry season.

Increasing maximum temperature, VPD and MCWD increase new tree recruitment, while increasing SPEI (more humid) leads to decreases in the recruitment rate. This result indicates that periods with less precipitation, but higher temperatures favor the growth in diameter of new individuals with CBH > than 10 cm. This result agrees with the observed by Herrera-Bevan & Ibáñez (2024), in which there was a reduction of between 66% and 88% in the abundance of native tree seedlings in areas where there were floods. In addition, during drier seasons there is a greater amount of light entering the forest understory, as around 50% of the trees in the seasonal semideciduous forest lose their leaves, thus reducing competition for light, and by other resources, due to tree mortality, which increased during this period (Bradford & Bell, 2017; Chen et al.,2019). Studies such as the one carried out by Palma & Stevenson

(2022) emphasize the importance of light as a limiting factor for seedling growth in tropical forests (Montgomery & Chazdon, 2002).

4.2 Drought and high temperatures as predictors of tree mortality

There is a clear relationship between drought and mortality of trees in forests at a global level (Bradford & Bell, 2017; Hammond et al., 2022). Higher temperatures combined with lower water availability (just like our results), imply atmospheric water stress, and can bring trees to a physiological limit, which can be lethal, thus being among the primary causes of tree death in tropical forests (Bauman et al., 2022). In addition, prolonged periods of drought can affect the renewal of fine tree roots and hinder the absorption of nutrients and can have effects long time after the drought event (Kreuzwieser & Gessler, 2010). The effects of drought may not be immediate, some studies have reported that the effects appeared four years after the date of the event (Da Rocha et al., 2020). Some studies even indicate that the results of drought can persist for approximately two years after the event (Phillips et al., 2010; van Nieuwstadt & Sheil, 2005). Our SPEI results showed both peaks of severe drought and excess humidity. However, a few years before the year in which there was a major mortality, we could notice prolonged peaks of severe drought, around three/four years before the mortality event. Therefore, how a community reacts to drought events may also depend on its resilience at the species level (Marchin et al., 2016).

Drought affects each species differently, with larger trees and those with lower wood density being more susceptible to the risk of death (Esquivel-Muelbert et al. 2020; van Nieuwstadt & Sheil, 2005;). Our results are in line with the higher risk of death for trees with lower wood density, but not for larger trees, as smaller trees (CBH < 50 cm) had a higher percentage of mortality in the forest studied. Phillips et al. (2010) in a study on a pantropical and regional scale shows that although larger trees present a greater risk in some locations, trees with low wood density are at greater risk, regardless of size. There is still a lack of studies on leaf phenology and its relationship with the risk of mortality due to drought (Song et al., 2024). We noticed that in area N, semideciduous trees accounted for the largest number of dead trees throughout the sampling period, but in areas S1 and S2, evergreen trees accounted for the largest number of dead trees. This result could probably be related to the fact that deciduous species lose their leaves during the dry season and thus rapidly reduce their transpiration, reducing water loss, while evergreen species maintain high transpiration during the dry season and can increase it even more with increasing VPD (Song et al., 2024). Marod et al., (2025) found similar patterns, with drought strongly correlated with tree mortality and higher mortality rates for evergreen species, indicating that they are more sensitive to the microclimate than deciduous species.

The global trend towards a hotter, drier climate (IPCC, 2023) may trigger the loss of some species and genera of trees that are less resistant to drought and have a poor ability to colonize during the dry season (Da Costa et al. 2010). Our results indicate that the mortality of trees, especially smaller, early secondaries and those with low wood density, has increased significantly in recent years. This increase in mortality may have consequences for the structure, composition and carbon dynamics of the forest (Andrus et al., 2021; McMahon, Arellano & Davies, 2019).

4.3 Changes in tree biomass over the years

Despite the negative net growth in some years, in general the fragment has been increasing AGB throughout the succession and is therefore an important carbon sink for the region (Rodrigues et al., 2023 et al.; Villanova et al., 2019). The greater amount of AGB in area S1 is probably related to the greater proportion of deciduous trees, which contribute more significantly to carbon stock than evergreen species in this area (Rodrigues et al., 2023). Although AGB tends to increase in areas N and S1, when we analyze the increment in AGB, it is possible to notice its reduction with a practically negative balance in 2011 in areas N and S1 and a reduction in 2024 in both areas. In area S2, AGB has not increased over the years, on the contrary, it has decreased. This relationship between AGB and variables related to drier or wetter periods reflects the same relationships with growth, recruitment and mortality. Studies indicate that mortality is the main driver of changes in above-ground biomass dynamics in natural forests (Yuan et al., 2019; Poorter et al., 2017). AGB decreases a lot in 2024 in area S2, mainly due to high tree mortality this year. Despite the pSEM result indicating an influence of some climatic variables on AGB, their explanatory power and that of demographic processes on AGB was almost insignificant. Our correlation analyses showed that AGB has a strong relationship with basal area only. This result agrees with other studies that have shown that stand structure characteristics influence AGB more strongly than environmental variables (Ma et al., 2023).

This study highlights the complex relationship between climate and demographic processes in forests. Making it necessary to be studied in a way that considers this complexity in greater detail. One of the challenges of working with forest dynamics is the sampling of vegetation in permanent plots for frequent and certain periods of time, especially in tropical forests with high density and biodiversity. In order to carry out analyses that capture finer details, ideally it would be necessary to sampling the vegetation each year, during the dry and rainy seasons. Including analysis at the level of species, functional groups, forest structure and strategies of the trees. Since some species may be more resistant to floods and others to drought, some species are also able to acclimatize more easily (Marchin et al., 2016). Studies with seed bank and seedling would also be important to refine this knowledge. Our samplings took place over relatively long periods of time, which may have made it difficult to capture these relationships in more detail. Since between the five-year period or more, tree individuals could have died due to various factors, that perhaps couldn't be captured at the time they occurred. In addition, predicting drought mortality is a challenge, given the complexity of ecological interactions, physiological relationships, species characteristics and biotic agents that can confound mortality predictions (Trugman et al., 2021; Baraloto et al., 2011).

5. CONCLUSION

Our study shows that even though semideciduous seasonal forests are adapted to different conditions, long periods of drought can result in high mortality, while the mortality of these trees and the increase in light during the dry season opens space for growth and recruitment of new individuals. Increased mortality of small trees, trees with low wood density, early secondary and evergreens can lead to changes in the structure and composition of the forest community and have consequences for carbon storage. Furthermore, the work highlights the importance of understanding that global change does not only imply drought for forests, but that water excess can also become a problem. Therefore, studies aimed at understanding the physiology of species and how resistant they are to both drought and excess water are fundamental for promoting better conservation practices in times of global change. Furthermore, only through scientific dissemination, critical environmental education and multidisciplinary research, working directly with society, will it be possible to truly adapt to the adverse and complex effects of climate change that is already present and yet to come.

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Supplementary Material

Table S 01. Dynamics rates of demographic processes over the sampling periods.

Period	Area	GG	NG	nDT	M	R	S	iAGB
1993 - 2004	N	0.146	0.138	8	0.181	2.764	97.99	9.554
2004 - 2011	N	0.119	0.019	107	2.879	2.134	79.84	-1.445
2011 - 2017	N	0.156	0.123	51	1.809	8.982	89.14	4.0784
2017 - 2024	N	0.1104	-0.011	140	2.623	3.91	81.916	-0.6026
1984 - 1998	S1	0.0977	0.0661	84	1.093	2.0412	84.686	3.2771
1998 - 2003	S1	0.2207	0.1376	60	1.549	2.5499	90.701	3.2836
2003 - 2011	S1	0.1112	-0.057	142	2.544	0.9228	79.646	-0.8267
2011 - 2017	S1	0.1205	0.0433	72	2.056	6.8306	87.817	3.2875
2017 - 2024	S1	0.1441	0.0408	132	2.249	5.0373	84.251	2.0471
2005 - 2012	S2	0.1264	0.0467	98	1.772	2.8218	87.585	-1.1908
2012 - 2021	S2	0.1174	-0.017	250	3.322	7.1088	70.406	-0.4918

GG: gross annual growth; NG: net annual growth; nDT: number of dead trees in the period; M: annual mortality rate; R: annual recruitment rate; S: survival rate; iAGB: AGB increment. All values are the average per plot, except for the number of dead trees, which is the sum of dead individuals in the period between samplings.

Table S 02. Total AGB and AGC for each area in the different sampling years

Area	**Year**	**Total AGB (Mg ha^{-1})**	**AGC (Mg ha-1)**
N	1993	130.33	61.2551
N	2004	216.32	101.6704
N	2011	203.31	95.5557
N	2017	240.02	112.8094
N	2024	234.59	110.2573
S1	1984	170.42	80.0974
S1	1998	199.92	93.9624
S1	2003	229.47	107.8509
S1	2011	222.03	104.3541
S1	2017	251.62	118.2614
S1	2024	270.04	126.9188
S2	2005	115.50	54.285
S2	2012	104.79	49.2513
S2	2021	100.36	47.1692

Table S 03. Percentage of tree mortality according to: functional groups of leaf phenology, succession, wood density, circumference and family Fabaceae.

T	**A**	**D**	**SD**	**E**	**P**	**ES**	**LS**	**C< 50**	**C ≥ 50**	**wd < 0.7**	**wd ≥ 0.7**	**Fabaceae**
93-04	N	12.5	50	25	0	37.5	37.5	75	25	62.5	37.5	12.5
04-11	N	31.7	39.2	23.3	28.0	50.4	18.7	82.2	17.7	46.7	53.3	26.1

11-17	N	35.2	39.2	15.6	31.3	35.3	27.4	92.1	7.8	54.9	45.1	21.5
17-24	N	20.7	30	40.7	22.8	47.1	26.4	84.3	15.7	51.4	47.1	22.1
Total	**N**	**26.7**	**35.3**	**30.1**	**25.5**	**46.1**	**24.2**	**84.6**	**15.3**	**50.6**	**48.7**	**23.2**
84-98	S1	40.4	29.7	27.4	21.4	52.4	26.2	91.6	8.3	42.8	57.1	33.3
98-03	S1	36.6	28.3	33.3	16.6	63.3	20	86.6	13.3	50	51.67	26.6
03-11	S1	35.2	25.3	38.0	16.2	67.6	16.2	83.8	16.2	59.8	40.1	24.6
11-17	S1	20.8	40.2	36.1	9.7	68.0	22.2	84.7	15.3	69.4	30.5	11.1
17-24	S1	18.1	14.3	65.9	2.2	75	22.7	87.1	12.8	76.5	23.5	9.1
Total	**S1**	**29.6**	**25.7**	**42.8**	**12**	**66.5**	**21**	**86.5**	**13.4**	**61.6**	**38.6**	**20.2**
05-12	S2	37.7	18.3	42.8	16.3	72.4	9.2	82.6	17.3	65.3	34.7	24.5
12-21	S2	20.4	18.4	58.4	16	72	8.8	91.2	8.8	65.6	34.4	12.8
Total	**S2**	**25.3**	**18.4**	**54**	**16.1**	**72.1**	**8.9**	**88.8**	**11.2**	**65.5**	**34.5**	**16.1**

T= sampling period; A= area; D= deciduous; SD = semi-deciduous; E= evergreen; P= pioneers; ES= early secondary; LS= late secondary; C= circumference at breast height less in cm; wd= wood density in g cm-3.

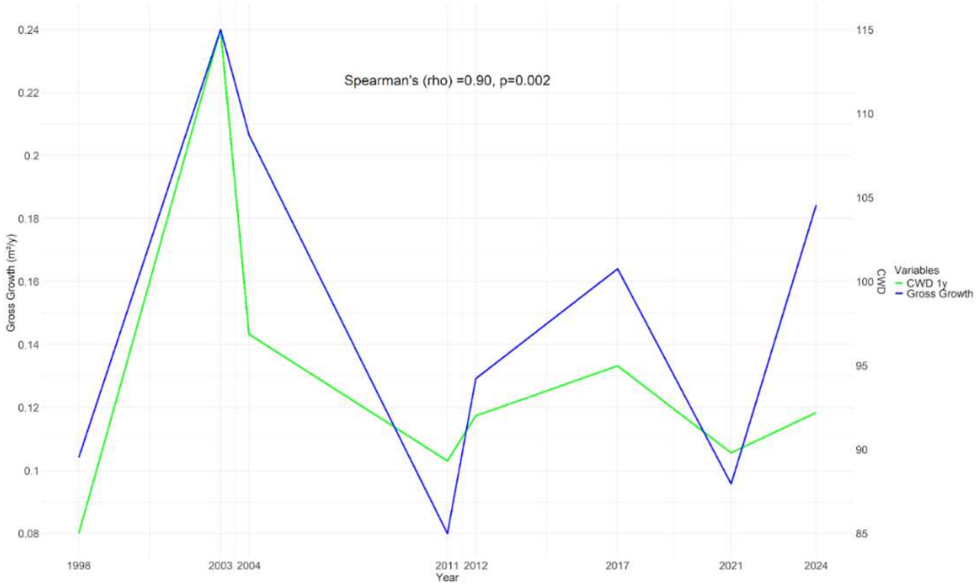


Figure S01 - Correlation between CWD and Gross Growth.

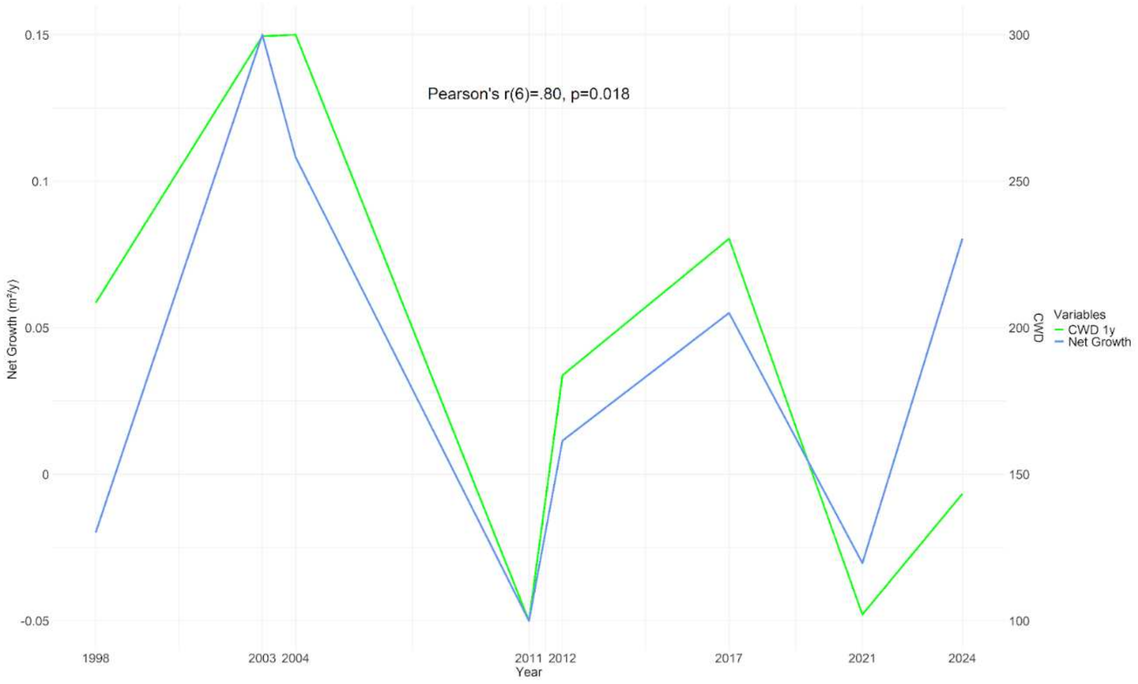


Figure S02 - Correlation between CWD and Net Growth.

Figure S03 - Correlation between MCWD and Gross Growth.

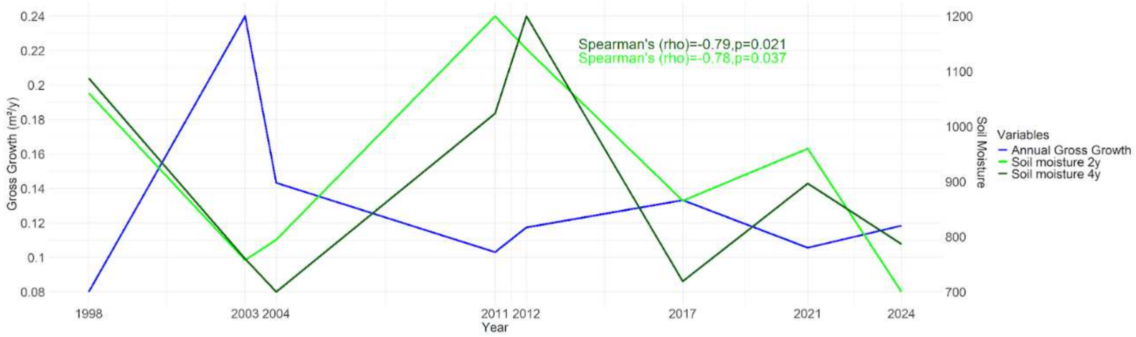


Figure S04 - Correlation between soil moisture and gross growth.

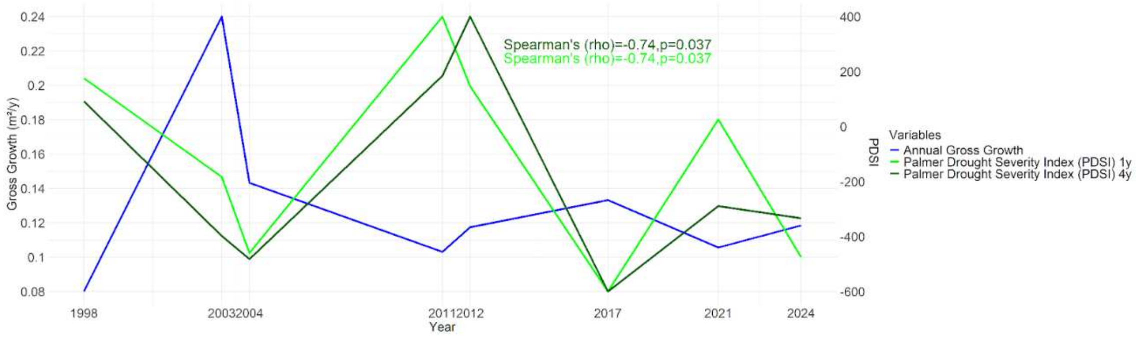


Figure S05 - Correlation between PDSI and gross growth.

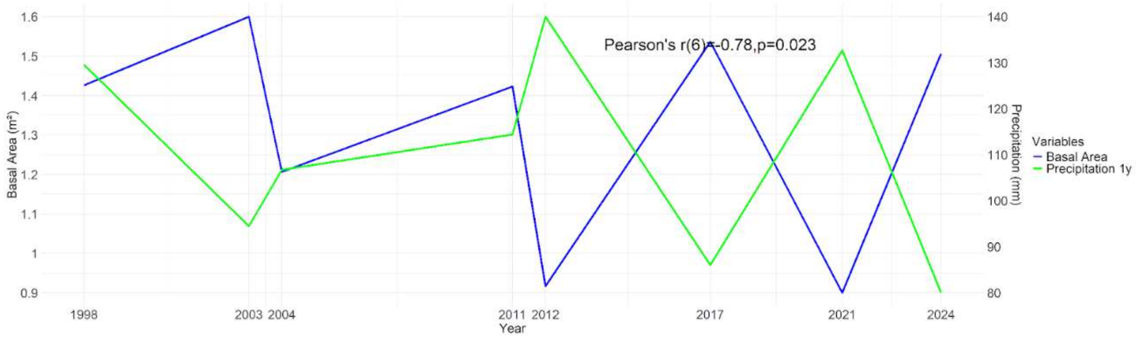


Figure S06 - Correlation between precipitation and basal area.

Figure S07 - Correlation between PET and recruitment.

Figure S08 - Correlation between VPD and recruitment.

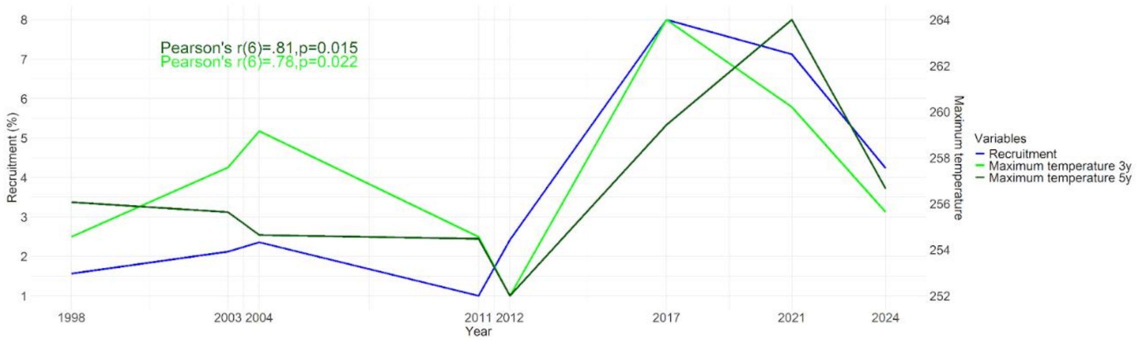


Figure S09 - Correlation between Tmax and recruitment.

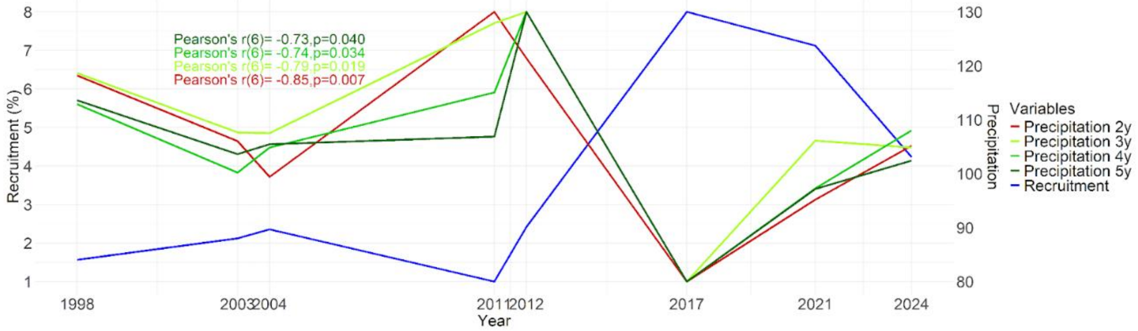


Figure S10 - Correlation between precipitation and recruitment.

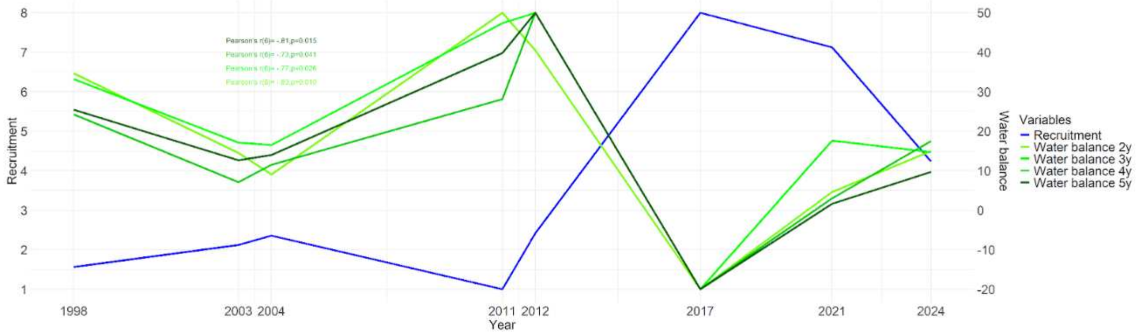


Figure S11 - Correlation between WB and recruitment.

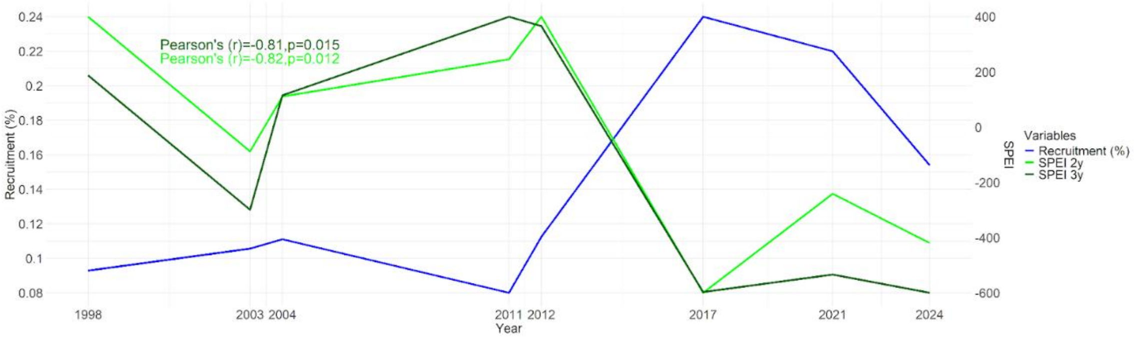


Figure S12 - Correlation between SPEI and recruitment.

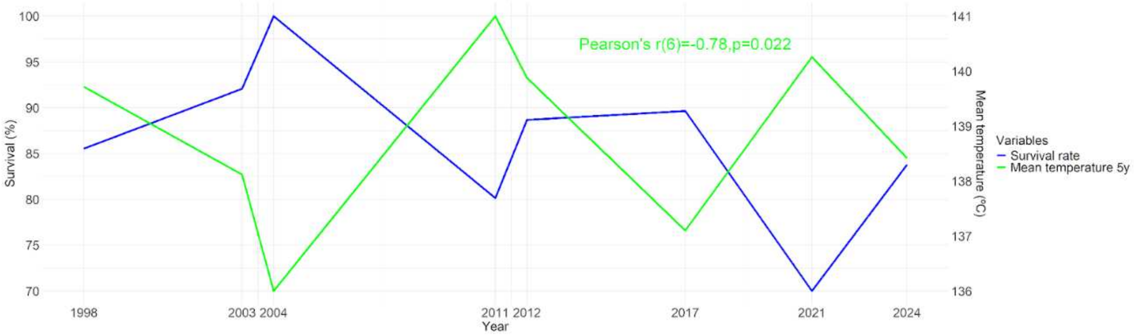


Figure S13 - Correlation between mean temperature and survival.

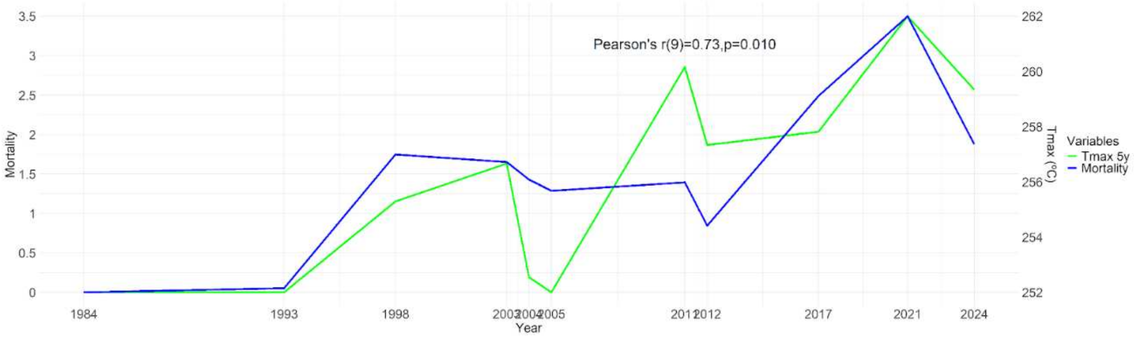


Figure S14 - Correlation between Tmax and mortality.

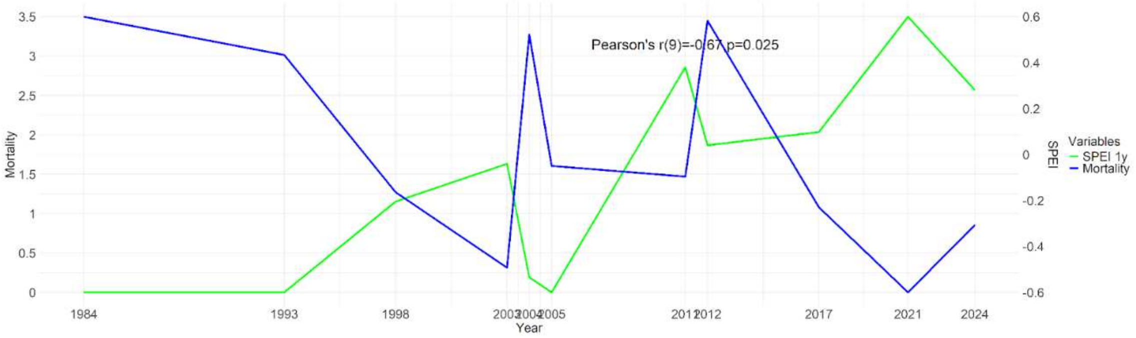


Figure S15 - Correlation between SPEI and mortality.

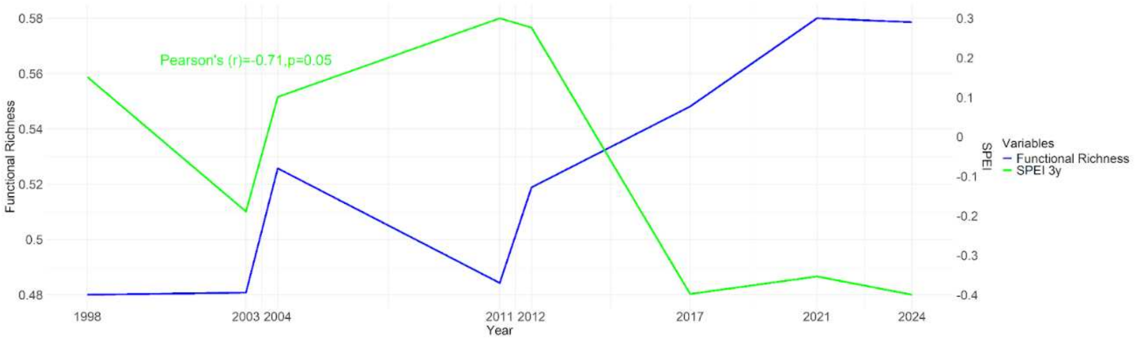


Figure S16 - Correlation between SPEI and functional richness.

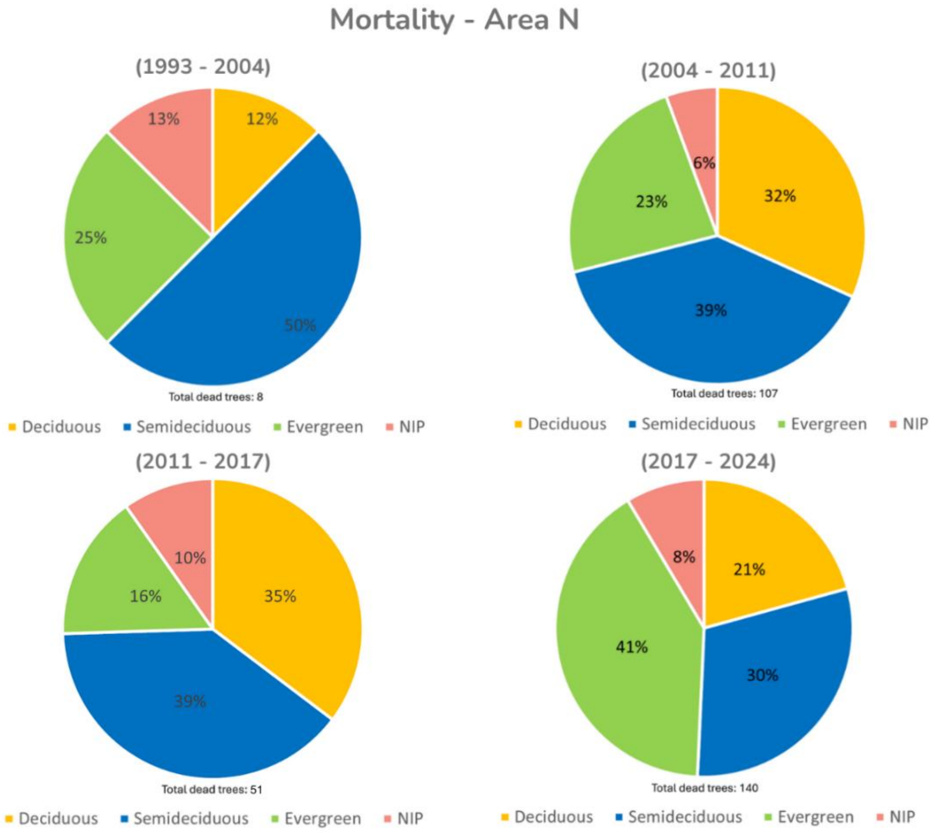


Figure S18. Percentages of dead trees in area N according to leaf phenological group. NIP = Non-identified leaf phenology

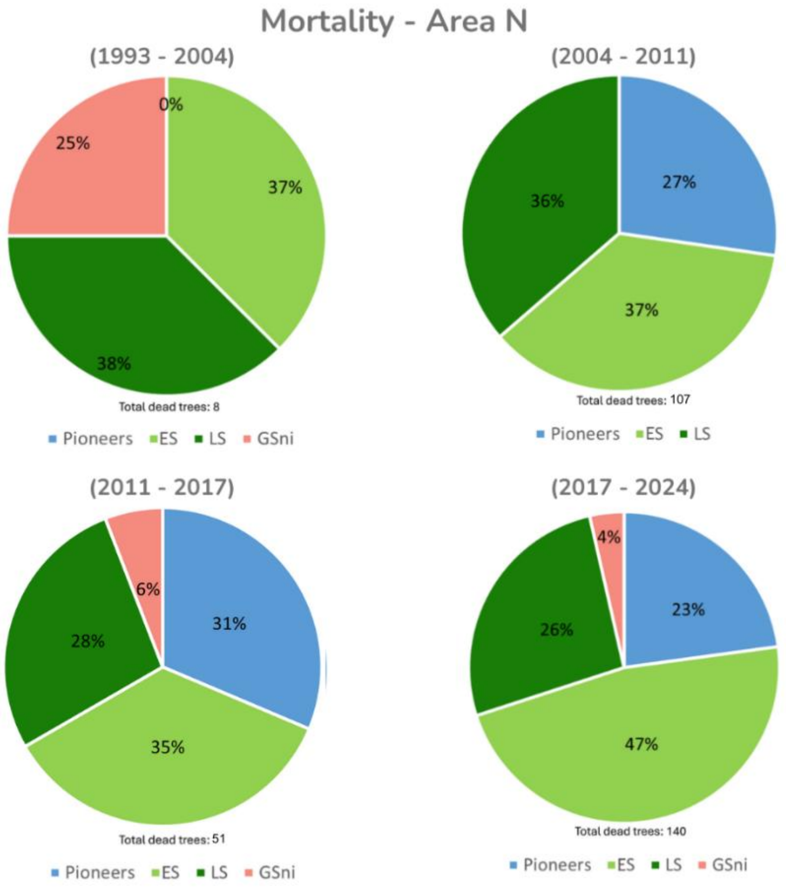


Figure S19. Percentages of dead trees in area N according to succession group: Pioneers, Early Secondary (ES), Late Secondary (LS), GSni = Succession group not identified.

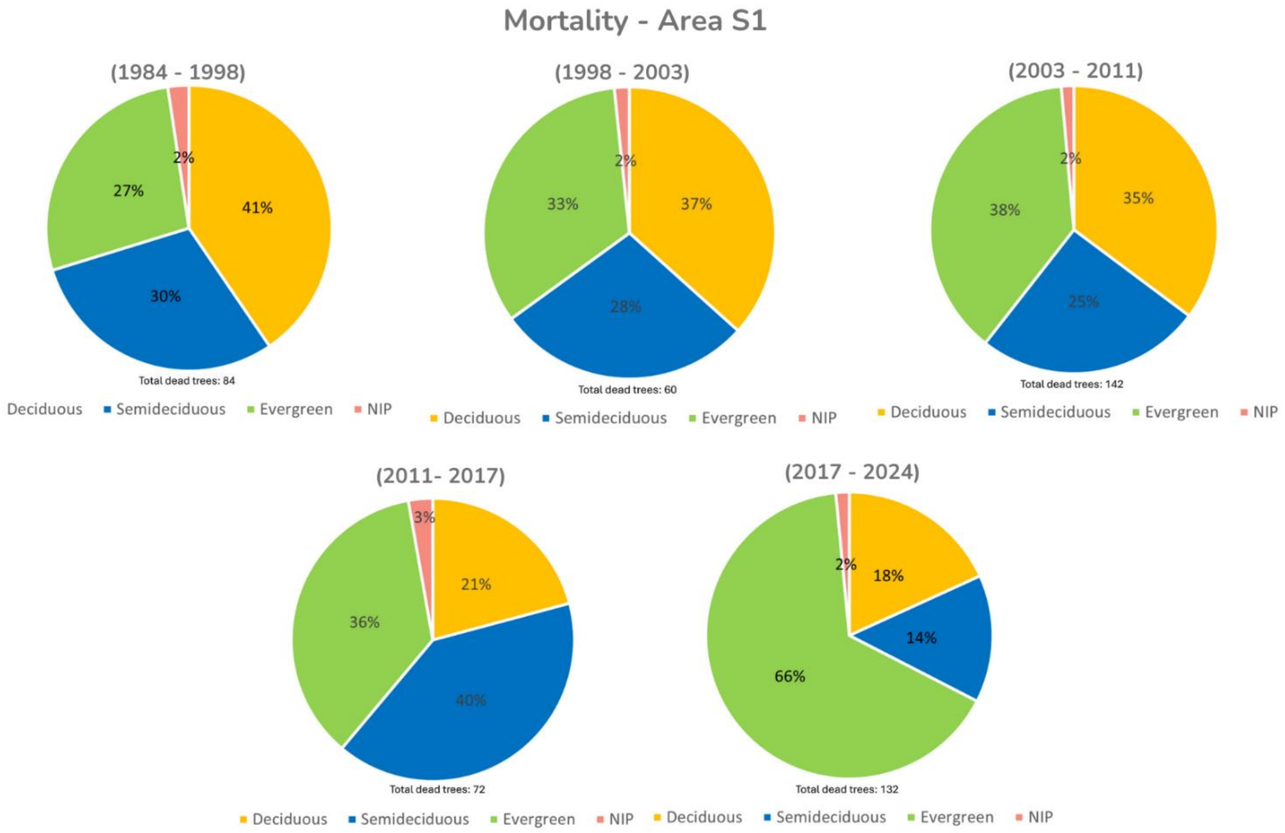


Figure S20. Percentages of dead trees in area S1 according to leaf phenological group. NIP = non-identified leaf phenology.

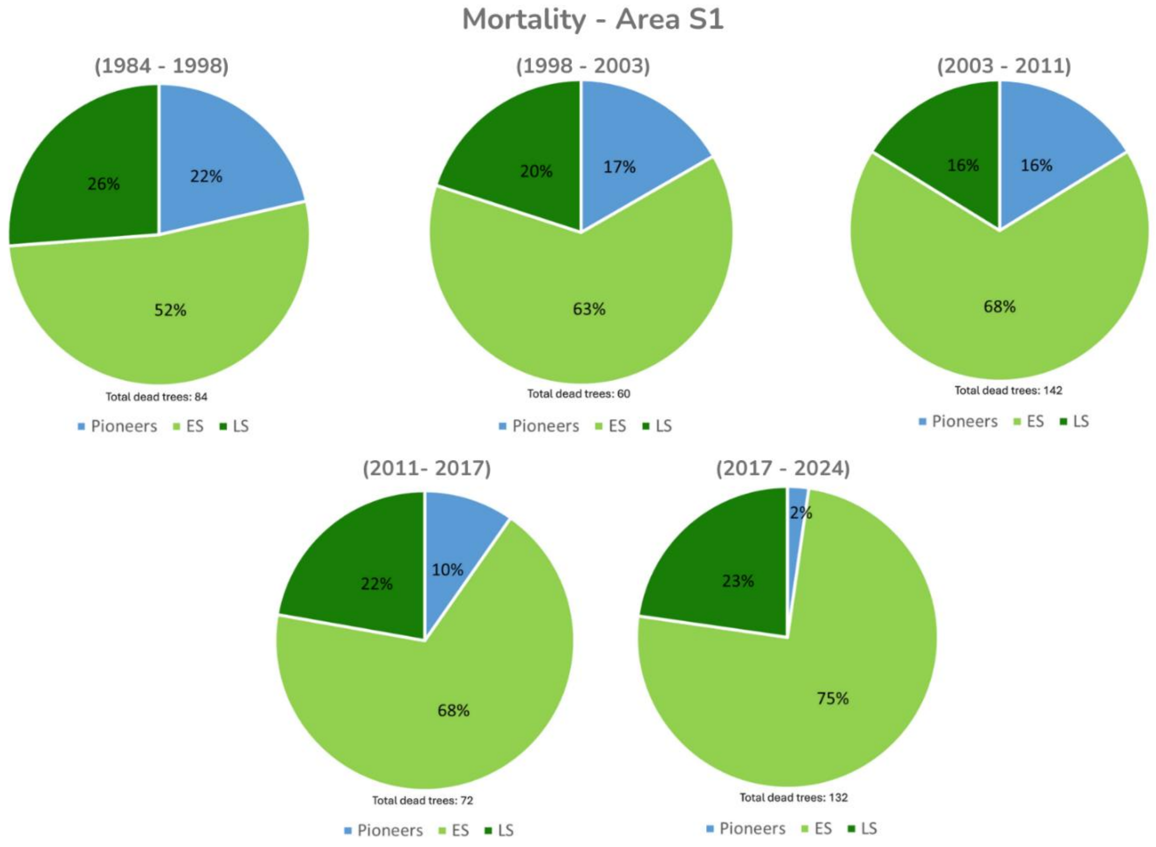
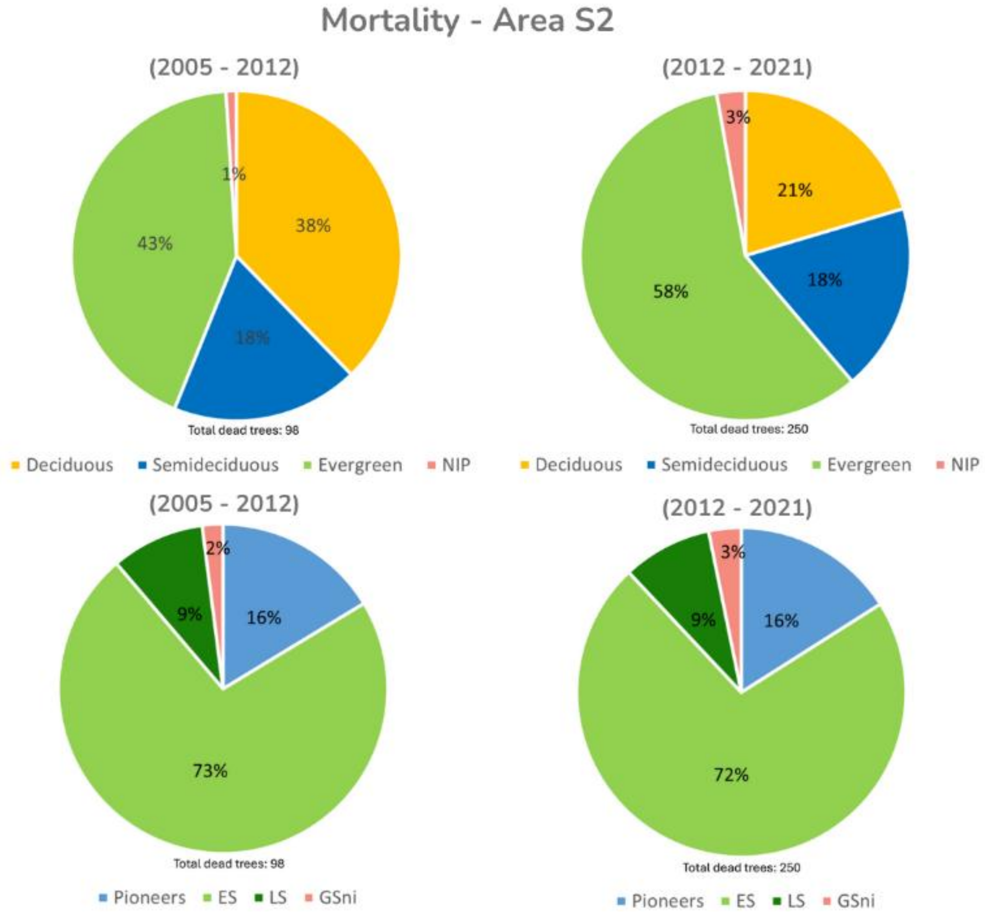


Figure S21. Percentages of dead trees in area S1 according to succession group.



FigureS22. Percentages of dead trees in area S2 according to leaf phenological group and succession group. NIP = non-identified leaf phenology; GSni = succession group not identified.

CHAPTER 02

MULTIFUNCTIONALITY OF CARBON STORAGE IN A SECONDARY ATLANTIC FOREST: IMPLICATION OF ALMOST 100 YEARS OF NATURAL REGENERATION

ABSTRACT

Brazil emits a large proportion of greenhouse gases through land use changes, mainly due to deforestation of forests areas. Secondary Atlantic forests have great potential for carbon storage in different compartments. In view of this, our goal was to analyze the multifunctionality in carbon storage of an Atlantic seasonal forest that was naturally regenerated with almost 100 years. A secondary Atlantic Forest fragment was sampled, where we analyzed the carbon stock in aboveground biomass, soil and litter. We considered richness, diversity, CWM of functional traits, topography, soil properties and litter as predictors of C stock. To analyze the differences between three sites with different ages in the fragment, we carried out correlation analyses, principal component analyses and multiple linear regressions. The results showed that carbon in aboveground biomass was mainly influenced by stand age and basal area. In addition, soil moisture, clay and soil density had a negative effect on carbon storage. Wood density and calcium content in litter had a positive effect on litter carbon storage. Soil carbon was correlated only with organic matter content and not with richness. Our results indicate that stand and species characteristics were more important than species richness and diversity for carbon stocks in the studied area. Furthermore, we emphasize that throughout succession, aboveground carbon increases, but not necessarily soil carbon, which was more related to the properties of the soil itself. We argue that projects and public policy focused on the recovery and restoration of degraded areas should consider the approach of functional characteristics and the role of soil as a nature-based solution for climate change mitigation.

Keywords: Atlantic forest, natural regeneration, global change mitigation, carbon stock, soil carbon stock, semideciduous forest.

1. INTRODUCTION

Natural regeneration is often assumed to be one of the best forest reforestation techniques, as it is efficient, low-cost and promotes many environmental and social benefits services to local communities (Chazdon et al., 2016; Crouzeilles et al., 2020; Houghton, Byers, Nassikas, 2015). After a few years, regenerated areas can accumulate substantial amounts of carbon within a few decades (Chazdon et al., 2016; Matos et al., 2020). Therefore, tropical secondary forests play a crucial role in mitigating climate change, by sequestering and storing gases related to global warming (Bieluczyk et al., 2023). Many studies when analyzing the carbon storage of these naturally regenerated forests often do not consider the multifunctionality of the forest in storing carbon in different compartments, such as the carbon stored in the soil and in litterfall (Ali & Yan, 2017). Furthermore, in order to increase the level of scientific knowledge about the relationship between different drivers on Carbon stock, it is essential to include an approach based on functional traits, and not just taxonomic species richness and stand structure, to promote a more complete understanding of carbon storage capacity and its relationship with biotic and abiotic factors (Ali & Yan, 2017). The multifunctionality in Carbon stock approach is fundamental to promote the maintenance and management of ecosystems in a sustainable way, as well as to highlight the relevance of even small conserved areas as important environments which play a role in microclimate regulation and other services (Matos et al., 2020). In this way, secondary tropical forest areas function as biodiversity refuges, are habitats for numerous species, play a role in flood prevention, store water and carbon in multiple compartments, i.e., essential services for human well-being in times of climate insecurity (Strassburg et al., 2016).

Due to the multiple factors that influence aboveground biomass (AGB) storage in tropical forests, these ecosystems can exhibit variations in the amount of plant biomass stored in each forest community (Ayer, 2023; Paembonan et al., 2019). Stand age, community composition and structure, soil properties, topographic heterogeneity, and climatic variables are the main factors influencing the capacity to store AGB in secondary forests (Capellesso, Bayer, Sausen, 2024; Pinto et al., 2023; Santiago-García, Finegan, Bosque-Pérez, 2019). In addition, studies investigating the relationship between functional traits and above-ground Carbon storage have found interesting results, such as the link between the community's weighted mean traits (CWM) like DBH, leaf phenology and specific leaf area, that have a positive relationship with AGB, and also that functional composition increases the carbon stock during succession

(Poorter et al., 2017; Rodrigues et al., 2023a, 2023b, 2021; van der Sande et al., 2017). Therefore, considering functional diversity in the assessment of AGB in tropical forests is a necessary approach, but determining precisely which functional traits are most relevant to Carbon storage remains a question that requires deeper investigation (Ali & Yan, 2017). Furthermore, in tropical ecosystems, due to their immense diversity and complexity, research into functional biology can be a major challenge, especially due to the difficulty in collecting functional traits, which have great diversity and variability between species and individuals (Swenson & Rubio, 2025; Worthy & Swenson, 2019).

Soil plays a crucial role in the functioning of ecosystems, containing a great diversity of life forms, such as fungi, bacteria, microorganisms and others, thus contributing to nutrient cycling and plant growth (Wiesmeier et al., 2019). Soil should be considered indispensable in nature-based solutions to mitigate global change, as it stores around 2,500 gigatons of carbon in its entirety, approximately two to three times more carbon than is contained in the atmosphere and plant mass (Stoorvogel et al., 2017). Therefore, analyzing the amount of carbon stored in Atlantic secondary forests soils, and improving the understanding of the factors related to its stock, is fundamental to emphasizing the relevance of conservation, recovery and management proposals for these forest areas (Guerrini et al., 2023; Mantovani et al., 2024). Climate, vegetation, land use history, organic matter input, temperature and soil moisture all are key drivers of soil organic carbon (SOC) stock (Doetterl et al., 2015; Fujisaki et al., 2018; Wallwork et al., 2022; Wiesmeier et al., 2019). In tropical forests, the amount of C stored in the soil can vary greatly depending on the type of forest, its edaphic and climatic characteristics (Gachhadar, Baniya, Mandal, 2022; Kouamé et al., 2023). Studies on naturally regenerated secondary forests that evaluate soil characteristics and focus on the relationship between soil carbon storage and the functional approach are still scarce (Ali & Yan, 2017).

The litter accumulated on the forest floor also performs important environmental functions, this dead matter is the major source of organic matter and nutrients for the soil microbiota (Keiser & Bradford, 2017; Wang et al., 2019). Litter also acts as a barrier against nutrient leaching by rain, maintains soil moisture and stores quantities of carbon, contributing to the regulation of the carbon cycle in forest ecosystems (Wang et al., 2019). In a subtropical forest it was found that litter stock is better explained by abiotic variables, such as slope elevation and soil moisture, than by biotic variables (vegetation) (Wang et al., 2019). However, there is a lack of studies that have investigated litter Carbon storage and its relationship with factors such as functional diversity and topographic variables, especially in tropical secondary forests (Fonsêca et al., 2024).

In this study we evaluated the multifunctionality of carbon storage of a secondary Atlantic tropical forest. We aimed to understand the relationship between C stock in three different forest compartments: aboveground-biomass, soil and litter with biotic and abiotic predictors. Some questions were raised: (i) how important is the soil contribution to carbon storage in the Atlantic Forest area studied? (ii) What are the main drivers (biotic and abiotic) of AGC, SOCS and LCS? Considering niche complementarity (Tilman et al., 2001; Loreau et al.,2001) and the mass ratio hypothesis (Grime, 1998) as one of the concepts that explains the ecosystem functioning, we have taken into account taxonomic richness, functional diversity, Community Weighted Mean (CWM) of functional traits (wood density, leaf phenology and maximum height), basal area, as well as abiotic variables such as topography, soil and litter nutrients. Other studies carried out in the same field have indicated that the mass ratio hypothesis seems to be dominant in explaining AGB (Rodrigues et al., 2023). Therefore, we hypothesize that carbon stocks in the different forest compartments - aboveground biomass (AGB), litter (LCS) and soil (SOCS), are mainly influenced by CWM of functional traits, stand structure characteristics, and also by soil characteristics like organic matter content.

2. MATERIALS AND METHODS

2.1 Study Area

The study area is located in the Zona da Mata region of Minas Gerais, Brazil. The region underwent major transformations, mainly due to the significant loss of Atlantic forest cover. The study area is among the regions in the state that have been most deforested for the implementation of coffee, sugar cane, and pasture crops (Meira-Neto, et al., 1997).

The studied vegetation, a 75-hectare of a Montane Seasonal Semideciduous Forest (Veloso; Rangel Filho; Lima, 1991) located in the municipality of Viçosa - MG (20°45'22.3"S 42°51'47.3"W) (Figure 04). The fragment belongs to the Federal University of Viçosa and has been undergoing natural regeneration since the abandonment of the coffee plantations in 1926, when the University was founded (Peloso, 2012), therefore, the fragment has almost 100 years. Despite this, the fragment has increased in forest cover over time, the most nuclear area N, has about 99 years of cover. Area S1 which in 1963 was still in a condition considered to be on the edge of the fragment, with around 62 years of vegetation cover, and finally area S2, which in 1963 almost half of the area had no tree cover yet, so it was still in the process of beginning to be covered with forest (Peloso, 2012). Each plot sampled is located in specific places within the fragment, which have their own local characteristics, for example, different patterns of topographical variation (Rodrigues et al., 2020, 2021). The climate is a humid mesothermal climate with rainy summers and dry winters, Cwa according to the Köppen classification (Alvares et al., 2013). The average annual rainfall is around 1,300 mm, with a relative humidity of around 80%, and an average annual temperature of 19 °C (Fialho & Santos, 2022). The elevation of the area is around 700m. The predominant soil types are Dystrophic Red-Yellow and Acrisols and Red-Yellow Cambisols (Ferreira-Júnior et al. 2007).

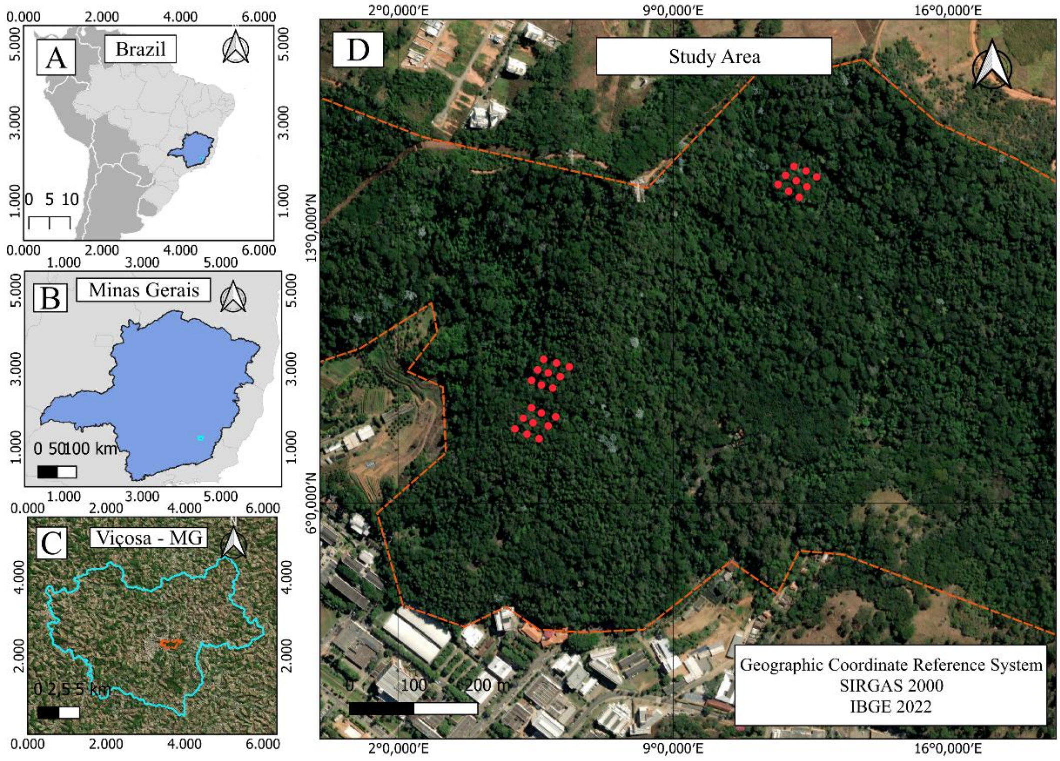


Figure 02. Location of the study area. A) Brazil. B) Minas Gerais state. C) Municipality of Viçosa. D) Location of the forest fragment studied.

2. 2 Data collection

2.2.1 Vegetation data

We sampled 27 permanent plots, each measuring 20 m x 20 m (400 m²), distributed over three different sites in the forest. Nine plots were established at each site: Southeast 1 (S1), Southeast 2 (S2) and Northeast (N). In each plot, all trees with a circumference at breast height (CBH) $\geq$ 10 cm were recorded and then converted to DBH, their height was measured, and all individuals were identified at species level.

For each plot, was calculated the basal area, above-ground biomass (AGB) and carbon stock in the above-ground biomass (AGC), following the general allometric model developed by Chave et al. (2014) for tropical forests. AGB is estimated in terms of DBH (in cm), wood density (WD, in g/cm3), and a measure of environmental stress (E):

$AGBest=\exp(-1.803-0.976E+0.976\ln(\rho)+2.673\ln(D)-0.0299[\ln(D)]2)$

For AGC we followed the formula:

Aboveground Carbon stock (AGC) = AGB * 0·47 (IPCC, 2006).

2.2.2 Taxonomic and Functional Diversity

We calculated the Shannon-Wiener and Simpson's diversity indices for each plot, and the species richness, which is the number of species found in each area in the year of sampling (Kent, 2011).

For each species we collected functional traits: Wood Density (WD; mg/m^3) and leaf phenology (evergreen, semi-deciduous and deciduous). Wood Density was obtained from the Global Wood Density Database (Zanne et al. 2009; Chave et al. 2014). We accessed leaf phenology by searching articles, books and plant databases.

For each plot, the Community-Weighted Mean (CWM) for the functional traits was calculated (Garnier et al. 2004; Lavorel et al. 2007). For this, we utilized the "functcomp" function from the "FD" package (Laliberté & Legendre 2010; Laliberté & Legendre 2014). Functional richness (FRic), a metric that represents the amount of functional space occupied by a set of species, functional divergence (FDiv), which defines how much species abundance diverges from the center of the functional space, functional uniformity (FEve), which represents the uniformity of the distribution of species abundance in the functional space (Mouchet et al. 2010), and functional dispersion (FDis), which defines the weighted average distance of individual species from the center of the functional space for all species, while the weights correspond to the relative abundances of the species (Laliberté & Legendre 2010), the package "fundiversity" was used for this (Gruson & Grenié, 2023).

2.2.3 Elevation data

Topographic variables (elevation, slope and convexity) were measured for each plot using a total station with the help of a surveyor. Elevation was calculated using the average elevation value of each of the four corners of the plots (see Rodrigues et al., 2020). The slope (°) was obtained by calculating 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 center of the plot from the average elevation of the eight surrounding plots (Wang et al., 2017).

2.2.3 Litter data

Litter contributes to the carbon stock in the soil and nutrient cycling, and the C content in the dry mass of the litter is significant for C analysis studies in tropical forests (Domke et al., 2016). For the litter carbon stock, to obtain the average for each plot, three litter samples were collected from each 20m x20m plot using a 25 cm x 25 cm (0,0625 m²) wooden box. All the accumulated matter inside the box up to ground level or up to the layer of intertwined fine roots was collected and dried in an oven at 60 ºC for 72 hours. The dry mass was recorded using a precision balance (0.001 g). Each litter sample was separated into "leaves", "branches and bark" and "miscellany" and had their weights recorded separately. The analyses for the estimation of carbon content and other nutrients were carried out by the Soil Departament Laboratory of the Federal University of Viçosa. The carbon stocks of the litter were calculated using the dry mass multiplied by carbon concentration, according to the formula presented in Lee et al. (2020).

Litter C storage (LCS) (Mg/ha) = dry mass (g m^{-2}) x C conc. (%) ÷ 100.

2.2.3 Soil assessment

We collected soil samples from each plot of 20mx20m at a depth of 0–10 cm, in three distinct points in each 10m x 10m subplots for a composite sample. The chemical and physical analysis was carried out by the Soil Departament Laboratory of the Federal University of Viçosa. Where soil pH, phosphorus (P), potassium (K), calcium ($Ca^{2+),}$ magnesium (Mg^{2+}), aluminum (Al^{3+}), exchangeable aluminum, Al^{3+} potential, sum of bases (SB), cation exchange capacity (T), effective cation exchange capacity (t), base saturation (V), aluminum saturation (m), organic matter (MO), organic carbon (C.org), remaining phosphorus (P-Rem), total sand, coarse sand, fine sand, silt and clay were determined. We calculated the average soil density for each plot by taking three samples at different points, where the soil was collected with a circular object of known volume.

To calculate the soil organic carbon stock (SOCS) we will use the formula presented in Fernandes et al (2020) based on the work of Veldkamp. (1994):

Est C = (CO x Ds x e)/10

Where:

Est C = stock of organic C at a given depth ($Mg.ha^{-1}$)

CO = total organic C content at the depth sampled ($g.kg^{-1}$)

Ds = soil density at depth ($kg.dm^{-3}$)

e = thickness of the layer considered (cm)

2.3 Data analysis

To analyze the normality of the data, Shapiro-Wilk test was applied. To compare the difference in the carbon stock between areas, Analysis of variance (ANOVA) was used for parametric data and the Kruskal-Wallis test for non-parametric data. To analyze the difference between the areas in terms of soil and litter properties, richness and functional diversity, we carried out a principal component analysis (PCA), where permutational multivariate analysis of variance (PERMANOVA) was performed to test the difference between the groups, the “FactoMineR” package was used (Husson et al. 2017).

To select predictor variables, to assess the correlation between the variables and to avoid multicollinearity problems, Pearson's correlation analysis was carried out. We used the function “ggcorr” from “GGally” package (Schloerke et al. 2024), and multicollonearity (VIF < 5) using the “car” package (Fox & Weisberg 2019). The effect of the main predictor variables selected from the correlations on AGC, LCS and SOCS was analyzed using multiple regression (LM) models. The LMs were performed using the “lme4” package (Bates et al. 2015). From global models with all selected variables, the best models were chosen using the function “*dredge*” from “MuMIn” package (Bartoń, 2024), and the Akaike's Information Criterion (AIC), where the best performing model had the lowest AIC value. To validate the models’ assumptions, “q-qplot” from “car” package was used (Fox & Weisberg 2019). The graphics were performed using the “GGplot2” and “sjPlot” package (Wickham 2016; Lüdecke 2024).

All analyses were carried out on the R studio platform v 4. 4.1 (RStudio Team, 2023)

3. RESULTS

3.2 Carbon stored in biomass, soil and litter

The amount of AGC differed between areas N, S1 and S2 and between the three different forest compartments (Table 01). Area S1 presented the highest amount of AGC, while area N showed a higher amount of LCS and S2 higher SOCS. Species richness, diversity indices and functional richness were relatively higher in the area with older vegetation cover N (Table 01).

Table 01. Average values per plot for each area: Species richness (Rich), diversity indices (Shannon and Simpson) and functional richness (Fric). Total values per site of carbon stored in above-ground biomass (AGC), litter (LCS), in the soil (SOC), standard deviation (SD) and total carbon stored in the three compartments of each area.

Area	**Rich**	**Shannon**	**Simp**	**Fric**	**AGC**	**SD**	**LCS**	**SD**	**SOCS**	**SD**	**TotalC**
N	25.89	2.80	0.89	0.61	110.26	±11.67	9.91	±0.51	24.66	±0.27	144.83
S1	22.89	2.11	0.74	0.53	126.92	±6.56	7.28	±0.24	26.91	±0.25	161.12
S2	23.22	2.57	0.84	0.57	47.16	±1.586	5.81	±0.09	29.13	±0.39	82.11

On average, area S1 has more AGC per plot than areas N and S2. (Kruskal-wallis, p= 0.004098) (Figure 02).

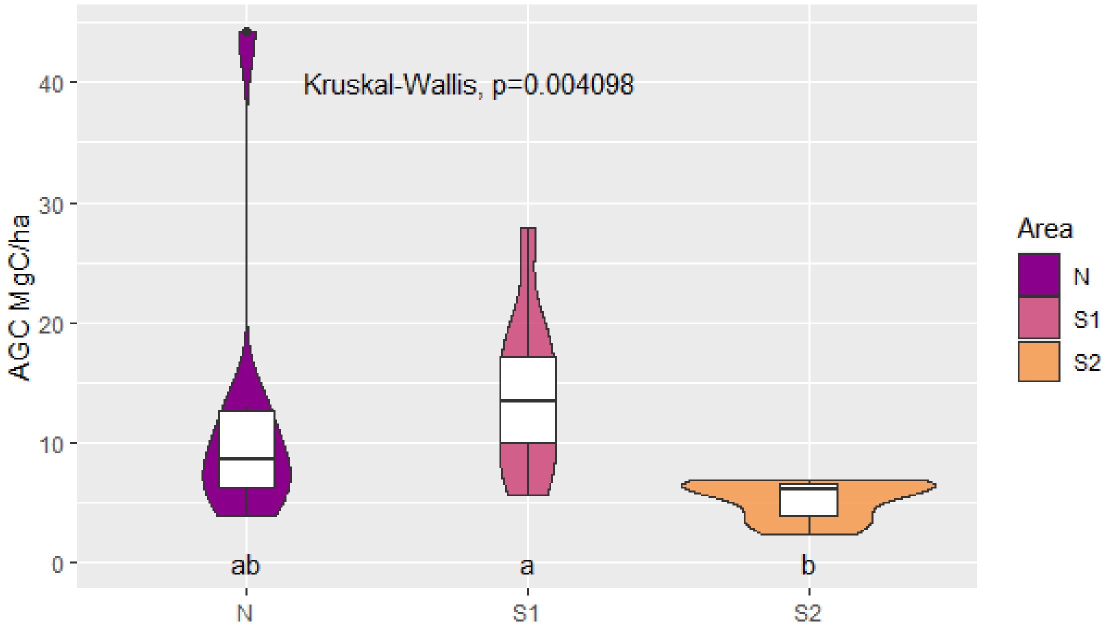


Figure 02. Average per plot of aboveground carbon stock (AGC) in the three different forest areas, Northeast (N), Southeast 1 (S1) and Southeast 2 (S2).

Among the three areas, on average per plot, S2 has the highest amount of C stored in the soil (Anova, p= 0.0157), while N has the lowest SOC (Figure 03). LCS was highest in area N, and the lowest value for area S2, while S1 was intermediate (Kruskal-wallis, p=0.04001) (Figure 04).

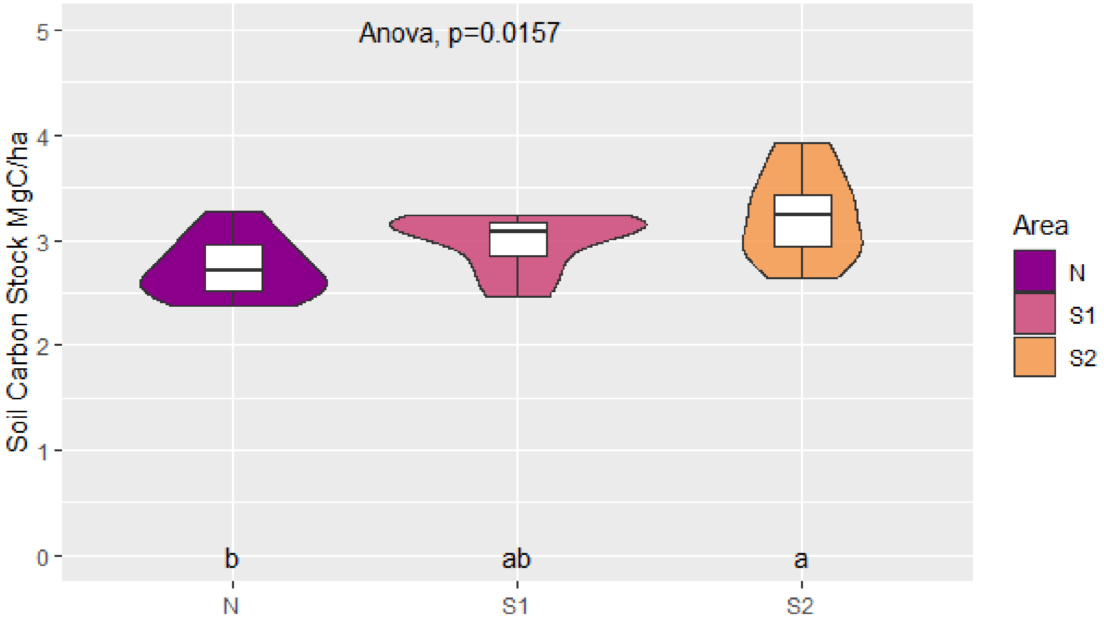


Figure 03. Average per plot of soil carbon stock in the three different forest areas, Northeast (N), Southeast 1 (S1) and Southeast 2 (S2).

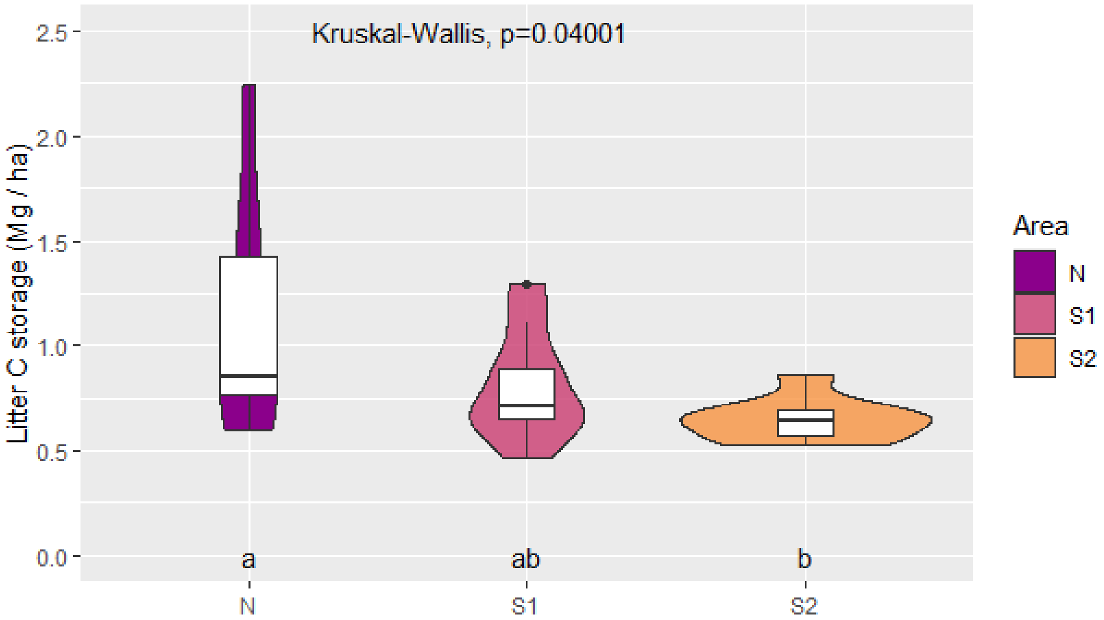


Figure 04. Average per plot of litter carbon (C) storage in the three different forest areas, Northeast (N), Southeast 1 (S1) and Southeast 2 (S2).

The total amount of carbon stored in the three areas was 388.07 Mg, where 73% was stored in the AGC, 21% in the soil and only 6% in litter (Figure 05).

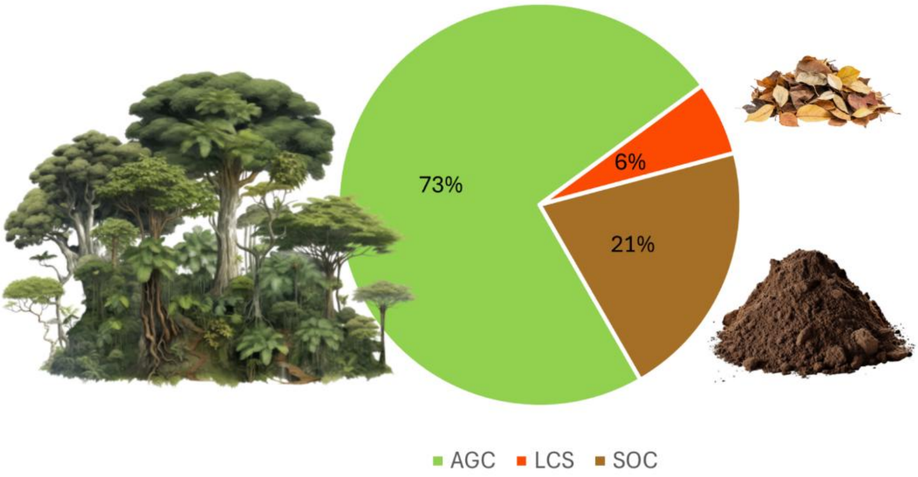


Figure 05. Percentage of C stored in each forest compartment, Mata da Biologia – Federal University of Viçosa – Minas Gerais, Brazil.

3.3 Differences between areas in terms of diversity, soil properties and litter characteristics

In terms of diversity metrics and CWM of functional traits, no significant differences were found between the areas (Permanova, p=0.957) (Figure 06).

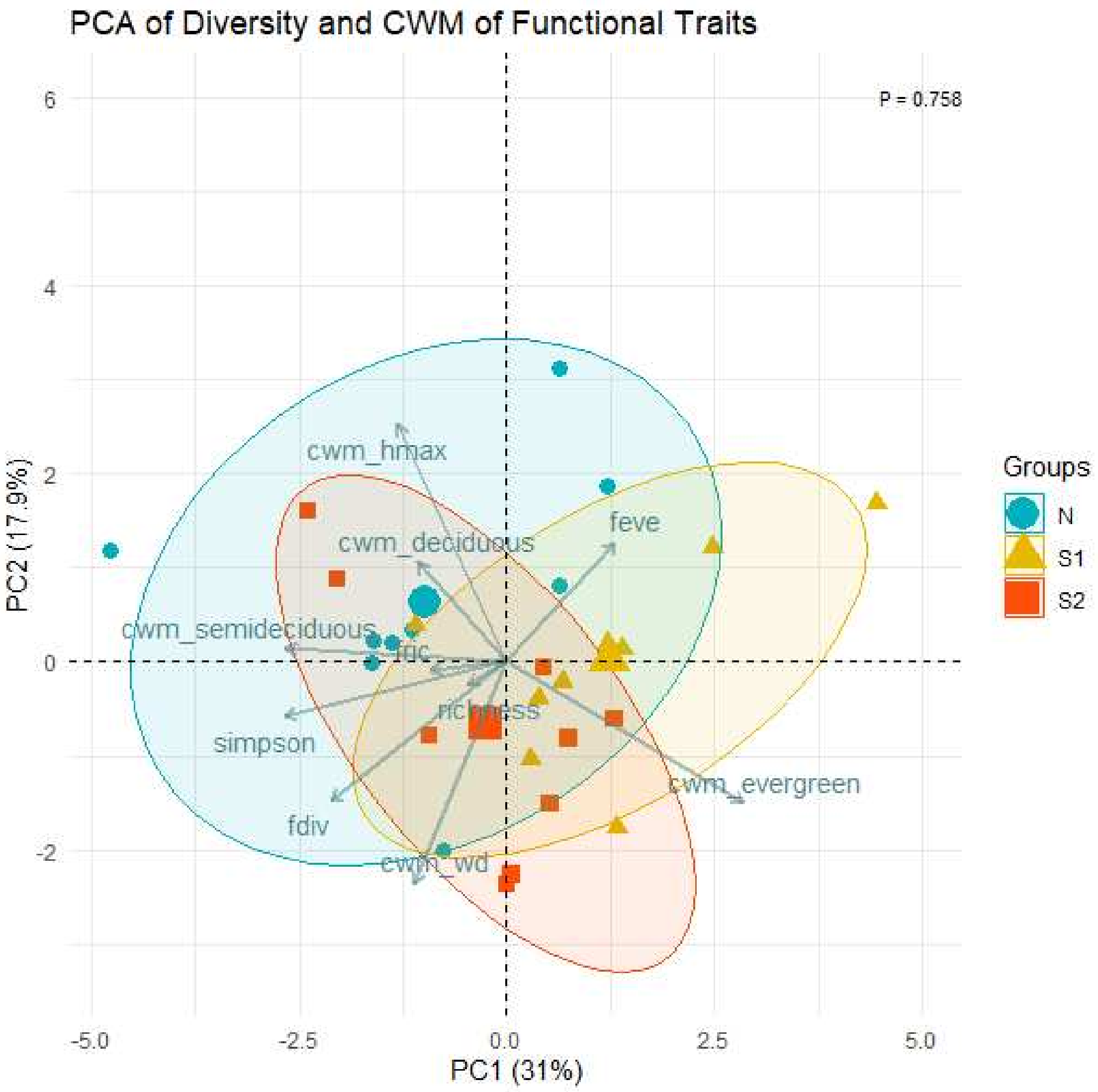


Figure 06. Principal component analysis of variables of diversity and CWM of functional traits in the three areas of the forest fragment.

Considering the characteristics of litter, a clear separation was found between areas N and S2, while area S1 was in an intermediate position (Permanova, p=0.001). Area N has more nutrient-rich litter, with higher amounts of N, Mg, Ca, K and C stock in the litter than the other areas (Figure 07).

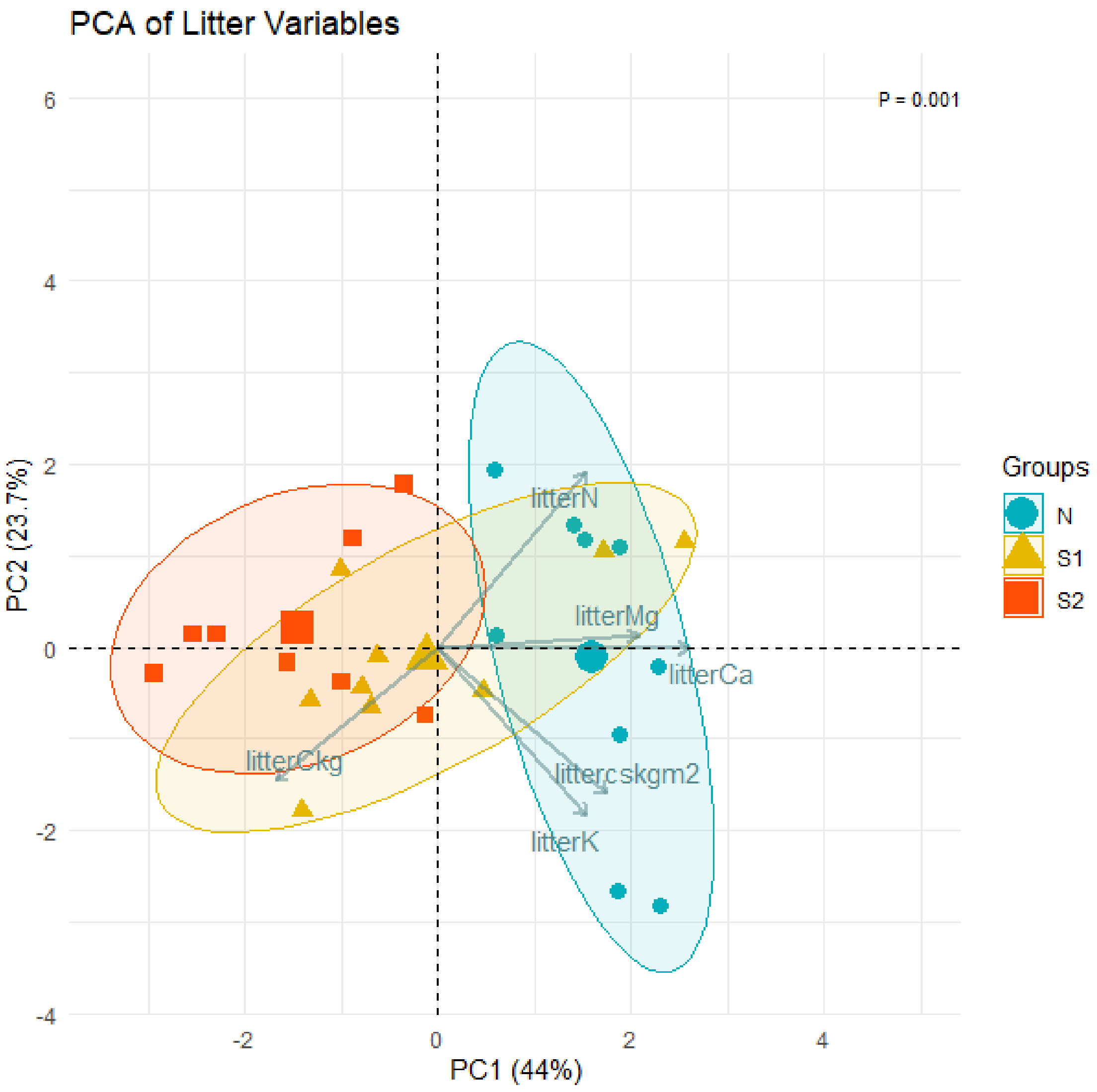


Figure 07. Principal component analysis of litter characteristics.

The areas also differed in terms of soil variables, in the same way as for litter, area N separated from area S2, and S1 was in an intermediate position (Permanova, p=0.001). Area S2 is more closely related to P, cation exchange capacity (ctc), soil moisture and soil carbon stock. Area N has a higher sand content and soil density (Figure 08).

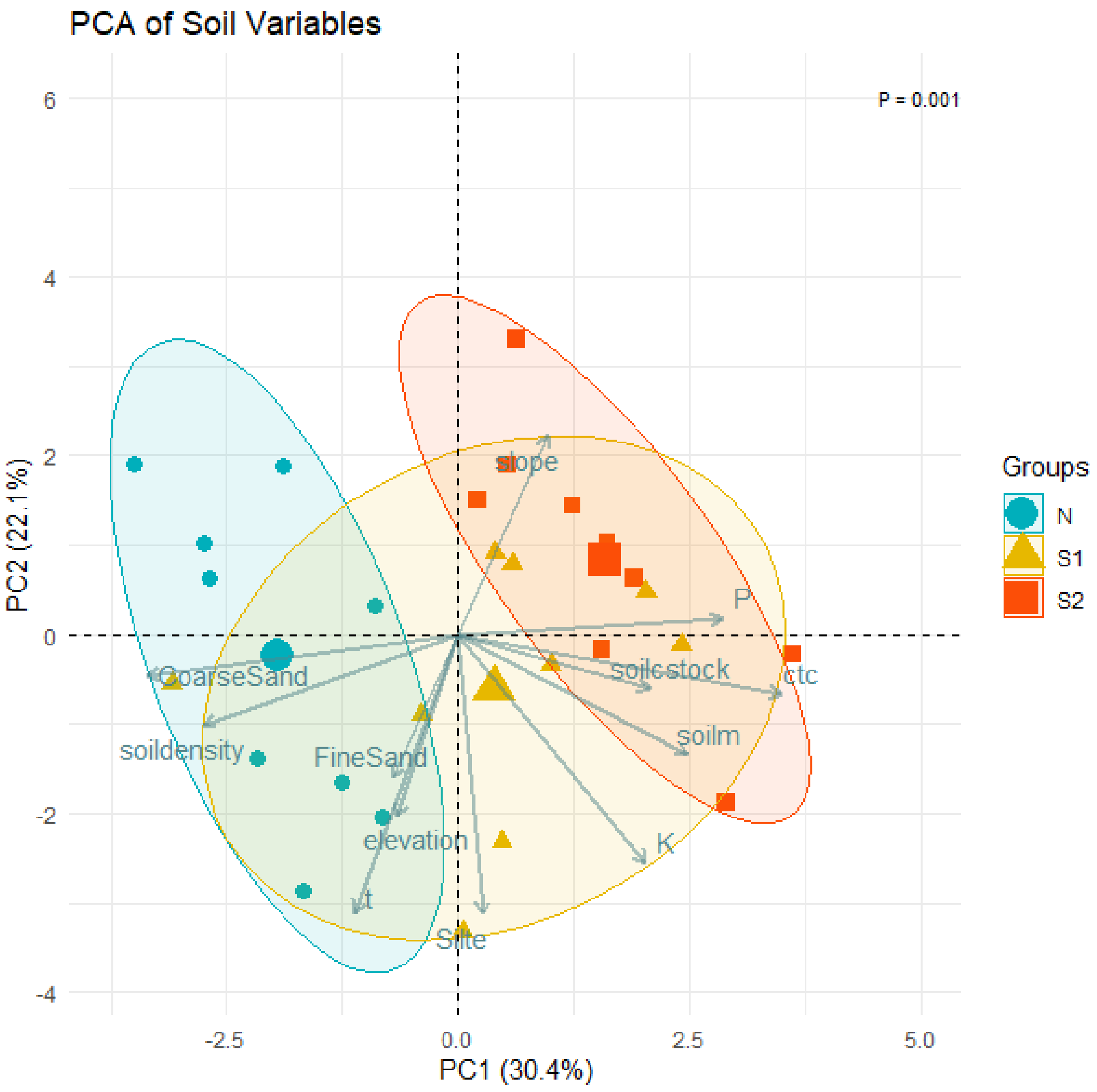


Figure 08. Principal component analysis of soil properties.

3.4 Influence of biotic and abiotic variables on carbon storage

The carbon stock in aboveground biomass was mainly positively influenced by basal area (p=6.64 e^{-16}), while clay content (p=0.0179), soil density (p=0.0119) and soil moisture (p=0.0389) had a negative effect on AGC (Figure 09).

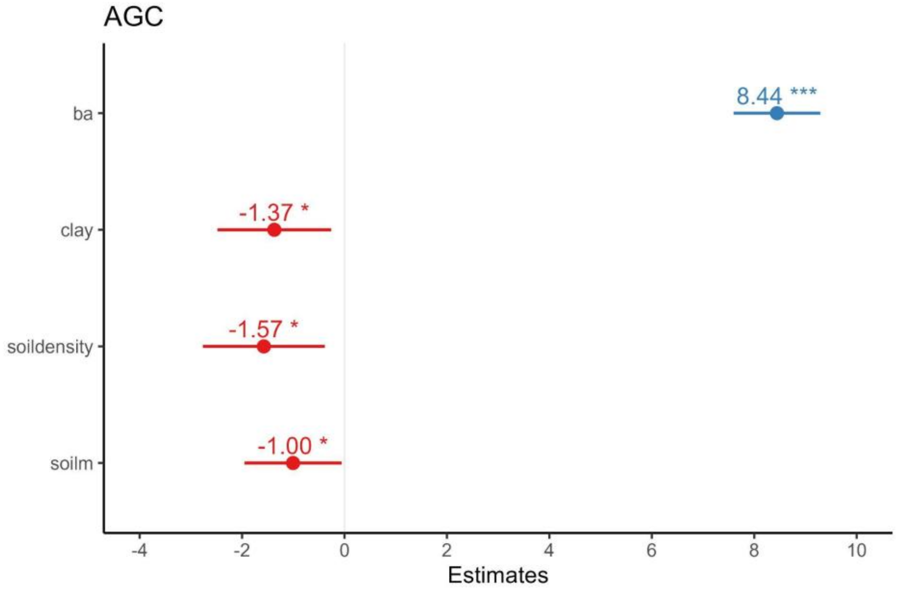


Figure 09. Effects of predictor variables (basal area, clay content, soil density and soil moisture) on AGC stock. The positive or negative position of the bars represents an effect of the predictor variable on AGC stock. * Represents significant effects ($p < 0.05$). The bars represent the adjusted standard errors. Adjusted R-squared: 0.9459. F-statistic: 114.6, p-value: 2.134e-14.

The carbon stock in the litter was mainly influenced by the CWM of wood density (p= 0.03) and the Ca content (p=4.1e^{-05}) of litter. The N content (p=0.06) and the Simpson index (p=0.14), despite showing a negative value, had no significant effect on LCS (Figure 10).

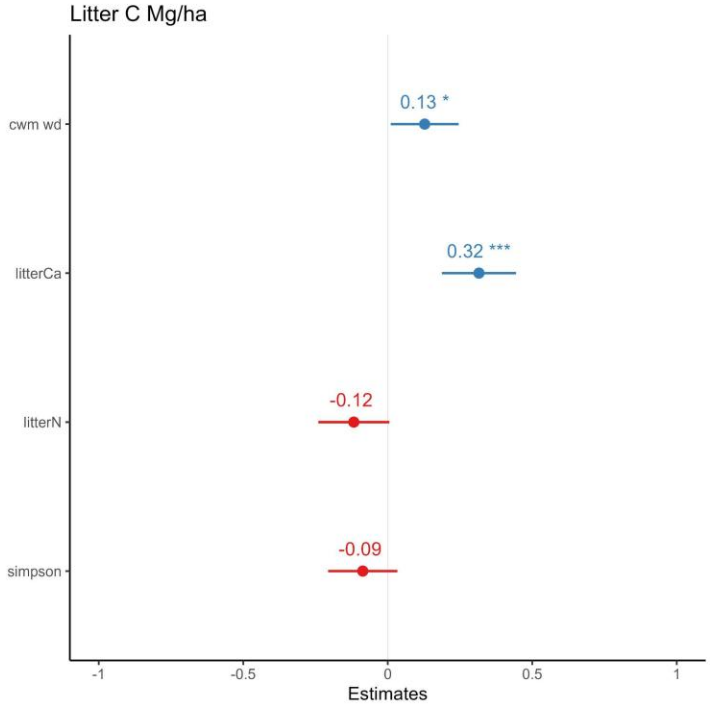


Figure 10. Effects of predictor variables (CWM of wood density, litter Ca, litterN and simpson) on Litter C stock. The positive or negative position of the bars represents an effect of the

predictor variable on Litter C stock. * Represents significant effects ($p < 0.05$). The bars represent the adjusted standard errors. Adjusted R-squared: 0.4916 F-statistic: 7.285 p-value: 0.0006787.

With regard to soil carbon stock, we found a high correlation only with organic matter content ($| r | \geq 0.7$), and a tendency towards a negative relationship with species richness and litter Ca content (Figure 11).

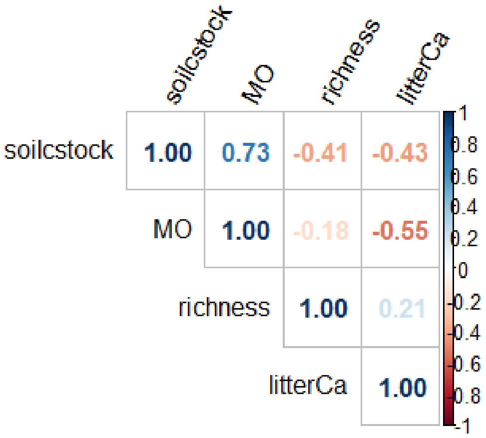


Figure 11. Correlation between predictor variables (organic matter, species richness, and litter Ca content) and soil carbon stock.

4.DISCUSSION

This study analyzed the multifunctionality of carbon storage in a tropical seasonal semideciduous forest and which factors drives C storage in aboveground biomass, soil and litter. We found the largest amount of C stored in the tree biomass compartment (73%), followed by soil (21%) and litter (6%). Each area of the fragment studied had different years of vegetation cover, thus, they differed in terms of soil and litter properties, but not in terms of diversity indices. AGC was positively affected by basal area and negatively by clay content, soil density and soil moisture. The C stored in litter, on the other hand, had a positive effect of CWM of wood density and Ca content of litter. Regarding SOCS, only a correlation with organic matter content was found. We found no relationship with species richness, functional diversity and CWM of the traits considered, besides wood density. It was clear that throughout succession in the natural regeneration process, older areas of cover are associated with more biomass and accumulation of litter, but this is not true for the C stored in the soil, which seems to depend more on factors relating to the structure of the soil itself (Jackson et al., 2017).

Studies indicate a great potential for carbon sequestration in secondary forests, with large amounts of C stored in the biomass at around 80 years of succession (Marín-Spiotta, Silver, Ostertag, 2007; Martin, Newton, Bullock, 2013). The average amount of AGC, when considering all three areas together, is similar to the values found in mature forests (Fonsêca et al., 2024). But when we analyze the areas separately, we can see the difference mainly between area S2, the last to be covered by forest vegetation, and the oldest areas. This difference is probably related to the age of the cover and the edge effect that the area S2 has suffered due to its position in relation to the other areas (Tian et al., 2023; Peloso, 2012). A study using imaging sensors to map AGB in fragmented Atlantic forests found that AGB at the edges is significantly lower than in the cores (Leite et al., 2023). In addition, area S1 has more basal area than the others, and higher percentages of individuals of *Sorocea bonplandii* (Baill.) W.C.Burger et al., *Myrciaria glomerata* O.Berg and a considerable amount of *Anadenanthera peregrina* (L.) Speg. *S. bonplandii* and *M. glomerata* are secondary, evergreen species with high wood density (Zanne et al. 2009; Chave et al. 2014) and together account for more than 50% of the individuals in area S1 (Figure S 02). *A. peregrina*, a deciduous species, carbon dominant, also with high wood density, has few, but individuals with DBH > 50 cm, some with DHB > 100 cm, thus contributing to a greater amount of C stored in its biomass (Rodrigues et al., 2023). Area S2 has fewer large individuals, and the largest tree in the area has a DBH of 64.6 cm.

The relationship between various factors that determine C storage in biomass can be complex, with some studies indicating a positive relationship between AGC and biodiversity (Van der Sande et al., 2017). On the other hand, other studies have reported a greater effect of variables related to forest stand structure, such as DBH and large trees (Wang et al., 2023). They also argue that large-diameter trees and dominant species, together with the stand structural complexity, would help to improve productivity (Wang et al., 2023). Our results are in line with the hypothesis that the structure of the stand and the presence of larger trees are fundamental for high levels of AGC.

The negative effect of clay, soil density and soil moisture on AGC, is in line with the results found in chapter one and with other studies that have found a negative effect of excess moisture, especially in the soil, on photosynthesis rate, affecting productivity as well (Chen; Liu; Liu, 2022; Schuur, 2003). This indicates that excessive humidity can also be a limiting factor (Fujita; Noguchi; Tange, 2021). Excess water can reduce plant growth, mainly due to the impact on oxygen in the soil, reducing gas exchange capacity, nutrient absorption and even producing toxic effects for plants (Chen; Liu; Liu, 2022). This may be true especially when we consider tropical forests located on really poor soils, which absorb nutrients mainly through fine, not suberized roots, often found tangled close to the soil surface, just below the litter layer (Fujita; Noguchi; Tange, 2021; Maycock; Congdon, 2000).

In relation to LCS, the effect of wood density on the carbon stock in the litter can be explained by the greater amount of biomass per unit volume of these trees, i.e. more C stored in the plant tissues (Nam; Anten; Van Kuijk, 2018). This contributes to a slower decomposition of the leaves, twigs and branches of the litter, thus allowing this C to be stored for longer before being decomposed (Nam; Anten; Van Kuijk, 2018). The positive effect of the calcium content in litter C stock provides interesting questions, since some studies report that higher Ca content is positively related to a faster rate of litter decomposition, while higher lignin is negatively related to litter decomposition (Hobbie et al., 2006; Zhou et al., 2021). In contrast, Gill & Lavender (1983) found that calcium nitrate slowed down the decomposition of litter during the first six months of the experiment. Calcium is an important constituent of plant structures, especially the cell wall and mitochondria, as well as accumulating in the vacuole and being used to form defense compounds against herbivory, such as calcium oxalate and calcium carbonates, being part of compounds responsible for the formation of recalcitrant carbon (González-Melo et al., 2025; Sá et al., 2024). Therefore, we believe that the interaction between Ca and C during litter decomposition or even in the structure of plant tissues promotes the production of carbonate compounds. In addition, studies have shown that wood density is positively related to higher levels of Ca, and this element accumulates mainly in the bark of the trees, which may also contribute to the slower decomposition and therefore longer time of C in litter tissues (Inagawa et al., 2023).

Of the total carbon stored in the Atlantic semideciduous forest studied, 21% were stored in the soil. We argue that the soils of semideciduous forests have great potential for storing C, since we found 21% of soil C stored considering only the first 10 centimeters of depth, i.e. if we had analyzed C storage at greater depths, 20 cm or even more, this potential would probably have doubled. This result is in line with the work carried out by Mantovani et al., (2024), who showed that 50% of the soil carbon stored in the Atlantic forest domain is found in the 0–30 cm layer.

The positive relationship between carbon stock and organic matter content evidence the potential benefit of introducing organic matter into the soil, promoting greater cation exchange capacity, more nutrients such as P and greater water retention (Gurmu, 2019). The lower sand content in area S2, higher soil humidity, P, and greater amount of clay promotes the accumulation of organic matter and storage of C (Sausen et al., 2014; Telles et al., 2003) in this area compared to the others.

Unlike Capellesso, Bayer & Sausen (2024), we found no relationship between SOCS and species richness or functional richness; probably because they compare naturally regenerating forests (which are richer in terms of the number of species) with monocultures. Other studies also found no relationship between richness and stock of organic matter in the soil (van der Sande et al., 2018). In our study, richness appears to have a slight negative correlation with SOCS, indicating that possibly less diverse areas and species characteristics may be more influential for the contribution of organic matter to the soil. Wallwork et al. (2022) found that SOCS is more associated with the presence of light-demanding species (or pioneers), which have higher SLA and leaf N, are more competitive and grow quickly. Area S2, which had more carbon stored in the soil due to being the most recent area in terms of vegetation cover, also has more light entering the forest and a higher proportion of early secondary and pioneer species (Figure S3).

In this view, we emphasize that natural regeneration, especially in a domain as fragmented and depleted as the Atlantic Forest, contributes to mitigating the effects of climate change, especially in a country where the main source of greenhouse gas emissions is land use changes, through the suppression of forests, farming and emissions from degraded pastures (SEEG, 2023). Furthermore, it is important that restoration and conservation projects that propose management practices pay attention to the role of soil carbon in natural climate solutions (Bossio et al., 2020). In addition, studies that seek to understand the multifunctionality of forests, are of utmost importance, especially in the most threatened Phyto physiognomies such as Atlantic semideciduous forests (Bergamin et al., 2017). In particular, there is a need to explore different variables, in a functional and group approach. Considering hard functional traits such as leaf traits, fruit and seed traits, wood properties, among others., as well as a species-level view, integrating multidisciplinary in the understanding of tropical ecosystems.

5.CONCLUSION

Our study has shown that naturally regenerated semideciduous Atlantic forests have great potential for multifunctionality in carbon storage, in biomass, soil and litter. Therefore, the forest fragment is of great importance for mitigating the effects of climate change, especially at a local scale. Stand age and structure were the main factors driving AGC, while soil moisture, density and clay had a negative effect. CWM of wood density and Ca content of litter positively affected LCS, while we only found a relationship between SOCS and organic matter content. We show that over the course of succession, the amount of carbon in the biomass and litter increases, but not necessarily the soil carbon stock. Our results provide important insights into the factors that drive forest multifunctionality. Providing contributions to the enrichment of practices and policies for the restoration and recovery of degraded areas based on natural regeneration, considering species characteristics, and soil properties. It is essential that the government invest more in public policies that support the conservation and the creation of new protection areas of Atlantic semideciduous seasonal forests.

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Supplementary Material

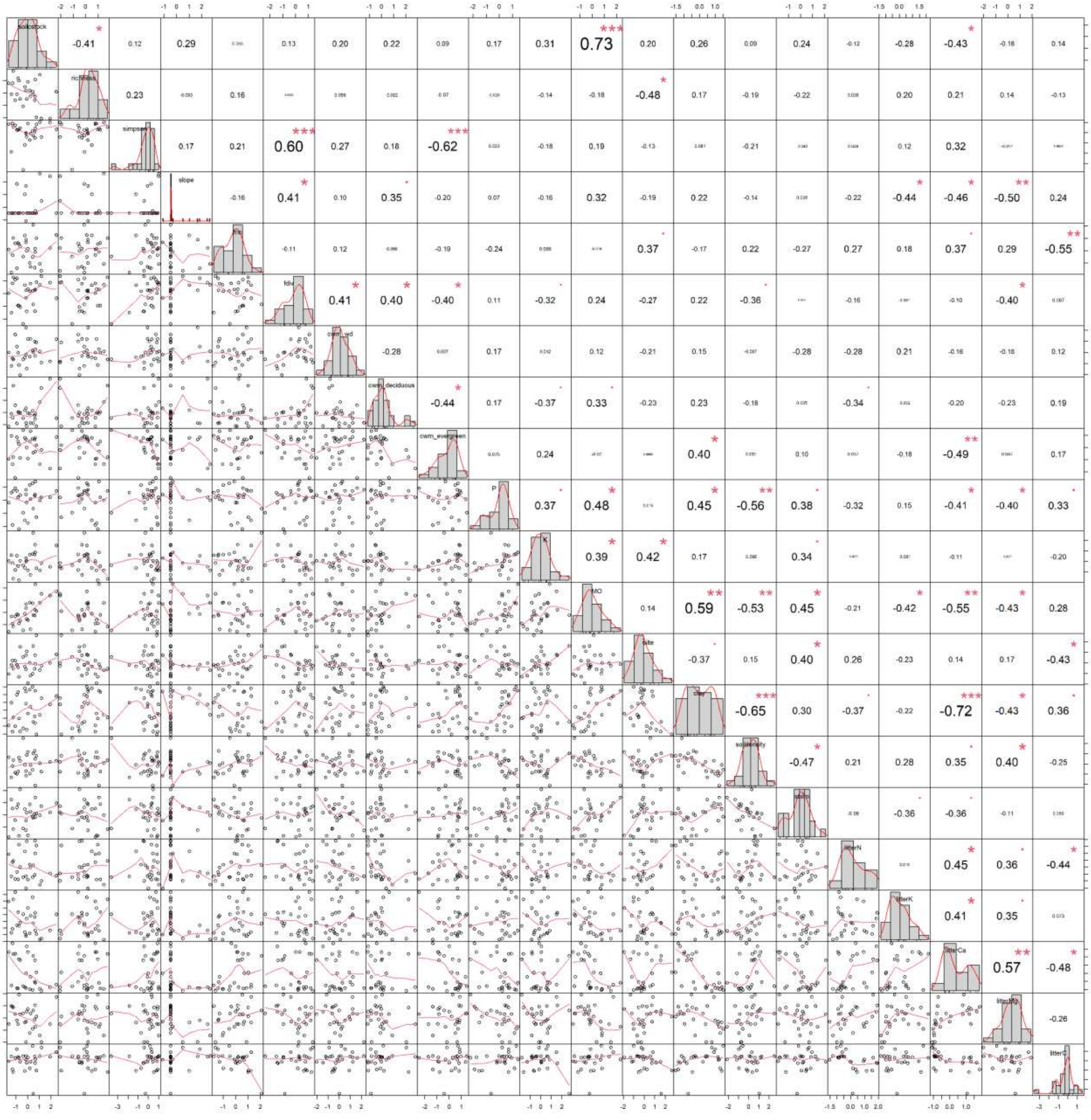
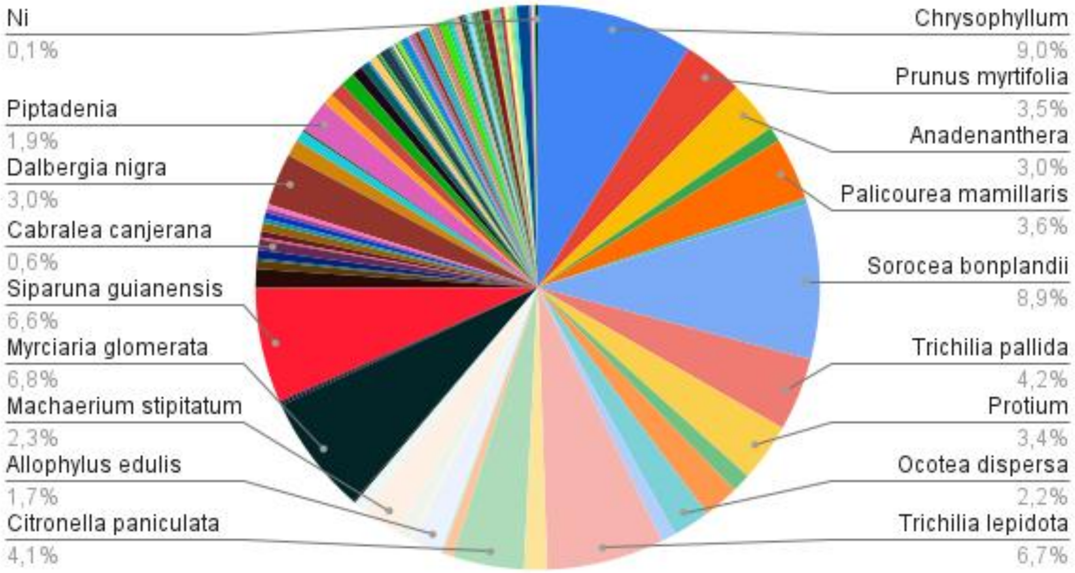
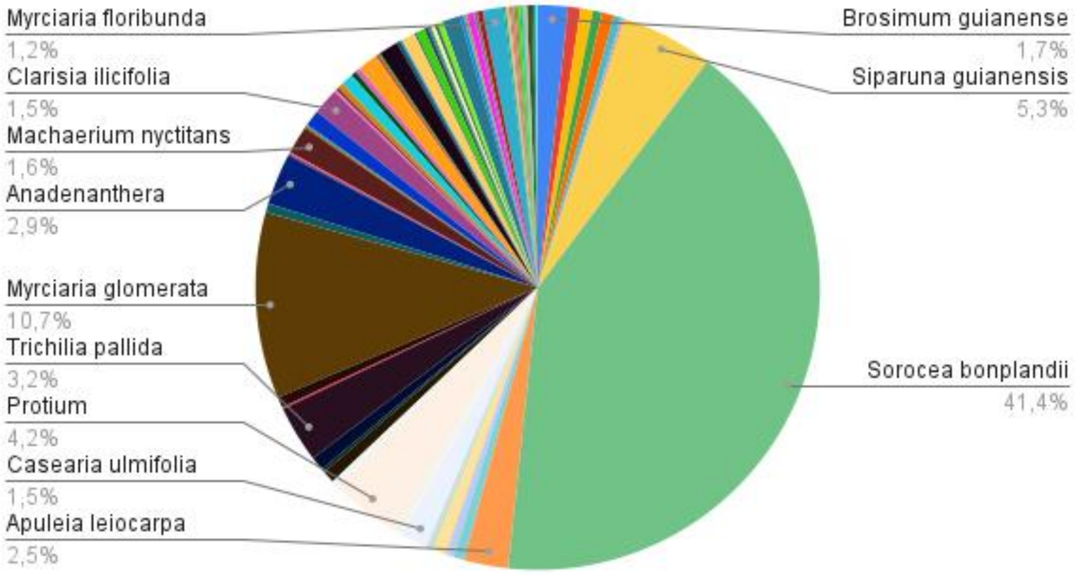


Figure S 01. Pearson's correlation for soil carbon stock.

Percentage of species - Area N



Percentage of species - Area S1



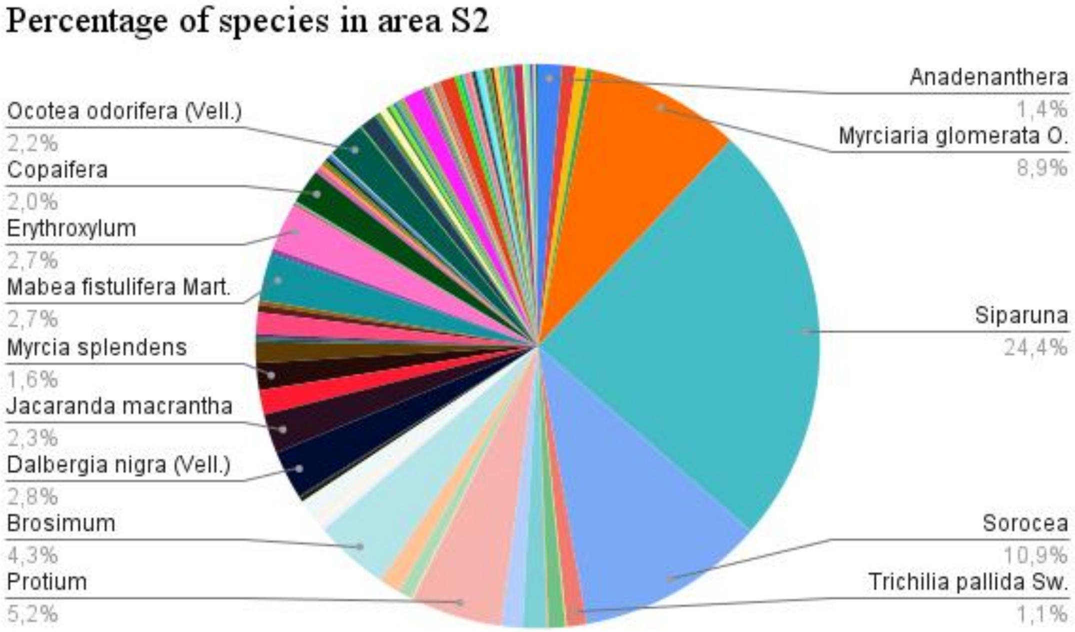


Figure S2. Percentage of species with the highest number of individuals in each area.

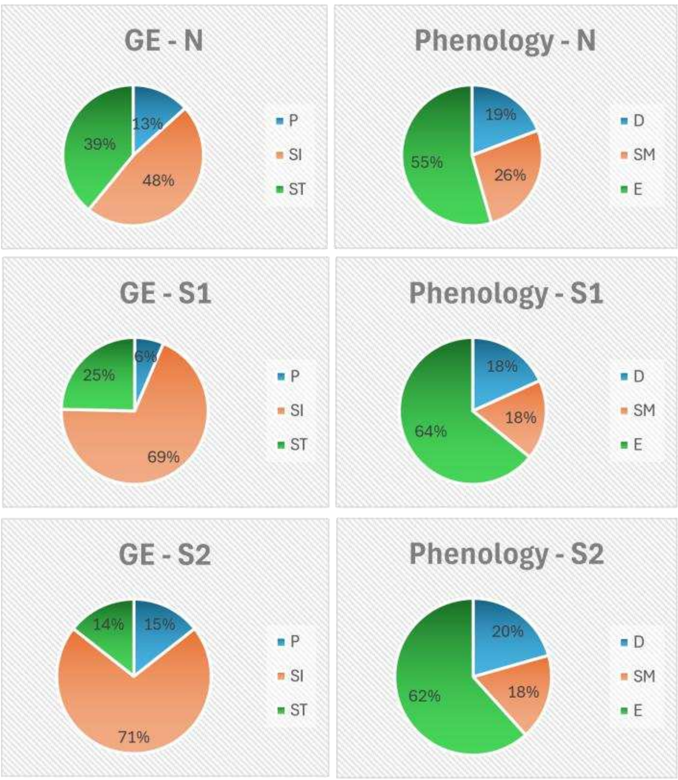


Figure S3. Percentage of species in relation to the ecological group of succession and leaf phenology. P= pioneer, SI= early secondary, ST= late secondary, D= deciduous, SM= semi-deciduous, E=evergreen.

GENERAL CONCLUSION

The aim of this study was to analyze the dynamics of demographic processes and the multifunctionality of carbon storage in an Atlantic semideciduous forest. Different climatic variables, a functional trait approach, species richness, as well as topographic, soil and litter characteristics were considered. We used permanent plots that were sampled over several periods, analyzing the mortality rates of growth, recruitment and survival of individuals in the community. We found that drought contributes to the increased mortality of the community's trees, while excess precipitation due to heavy rains also has a negative effect on the growth rate, recruitment and above-ground biomass stock in the forest. We can therefore conclude that climatic extremes can push semideciduous forests to their limits, which can drastically affect the carbon storage of this ecosystem in the future.

Despite this, the forest studied is still extremely important for absorbing and storing carbon dioxide, contributing to around 380 Megagrams of stored carbon, considering AGB, litter and soil carbon stock. We emphasize the potential of the soils of semideciduous seasonal forests to store carbon, since at a depth of just 10 cm we have seen that it has contributed to 21% of the forest's total carbon stock. Our work demonstrates that the conservation of remnant semideciduous seasonal forests as well as the creation of new protection areas is fundamental to mitigating the local effects of climate change. It is therefore a strategy based on natural solutions that cities should implement. There is knowledge gaps related to the dynamics of semideciduous forests in relation to climate change and the functional approach. Thus, it is essential that future studies consider the relationship between mortality rates, growth and recruitment with environmental variables, functional traits, especially traits that are more difficult to collect such as specific leaf area, traits related to wood hydraulics and below-ground root biomass, to also understand how climate changes impact forests at the species level.

Our study was important because its results show that when proposing reforestation and management techniques aimed at adapting to global change, it is important to focus on species that are well adapted to drought but also to excess rainfall. In addition to considering the relationship between the structure of the stand, functional traits such as wood density and organic matter, in order to optimize carbon storage. We also emphasize that these regeneration and management plans and public policies for conservation and adaptation must focus on considering the multiple facets of global change.