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Biodiversity and ecosystem functioning across Brazilian vegetation: from savannas to forests

Arthur da Cruz Silva
Doctor Scientiae

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

Adviser: Joao A. Alves Meira Neto

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À todas e todos que passaram pelo meu caminho,
Dedico.

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O trajeto da minha vida acadêmica, profissional e pessoal, é constituido de um grande quebra cabeça nada linear. São muitas experimentações em áreas diferentes, muita disposição em fechar ciclos e iniciar outros, muita abertura para experimentar o novo, muita vivência fora dos padrões estabelecidos como normais. Mas sem dúvida nenhuma, todas as relações vividas, construções durante o caminhar, me tornaram mais forte, e neste sentido há uma dificuldade muito grande em citar nomes especificos, pois são tantas pessoas em contextos tão diferentes na minha trajetória, que torna-se bem difícil fazer caber em poucos parágrafos todos/as que fizeram e fazem parte dessa trajetória.

Porém, é de suma importância citar minha família, em primeiro lugar minhas avós, pois sem dúvida nenhuma, minha família é matriarcal, não no sentido de ter superado o patriarcado estabelecido na sociedade, mas no sentido de que foram elas que sustentaram com muito custo a existência de tudo e todos/as que somos. Grandes exemplos de superação, força, resistência, grandes mulheres! Obrigado, Maria, Osmar e Vinícius primeiramente, e todos/as tios/as, primos/as – irmãos/ãs. E mais contemporâneo, a Beatriz, Isabela e Bruna, uma linda extensão da minha família nuclear. Minha família foi/é fundamental em me incentivar estudar/trabalhar e me proporcionar, a qualquer custo, o ambiente para que eu pudesse me dedicar à vida acadêmica – “Onde você que estar daqui cinco anos?”. Sou filho de uma família interracial e ambas partes tiveram um papel fundamental nessa trajetória. Obrigado aqueles/as que ajudaram com condições materiais minha família nuclear (consequentemente meus estudos), em momentos de instabilidade, muito obrigado à todos/as que disponibilizaram tempo de suas vidas para estar comigo me ensinando em diversos âmbitos da vida.

Nascer e ser criado em Orlândia, uma cidade pequena, teve muitas vantagens, e uma delas, sem dúvida, é poder ter me criado na “rua”. A maior parte da minha infância/adolescência, foi vivênciando a rua, com muitas amizades, recebendo muitas informações, vivendo muitas experiências, entre boas e ruins, mas que sem dúvida alguma, me formou e me transformou. Essa experiência fez com que pudesse enxergar de perto, caminhos que gostaria ou não de seguir, em ensinou empiricamente sobre como funciona algumas regras e leis da sociedade. Agradeço à todos/as que fizeram parte desse trajetória, são muitas pessoas, muitos

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ABSTRACT

SILVA, Arthur da Cruz, D.Sc., Universidade Federal de Viçosa, February, 2025. **Biodiversity and ecosystem functioning across Brazilian vegetation: from savannas to forests**. Adviser: Joao Augusto Alves Meira Neto.

Biodiversity, encompassing all life forms, is a critical driver of ecosystem processes, functioning, and services. Ecosystem functioning, shaped by biodiversity, has been studied through two paradigms: early studies focused on isolated biodiversity effects under controlled conditions, while current approaches emphasize nature-based, context-dependent studies. Key theories explaining biodiversity-ecosystem functioning relationships include niche complementarity, where species specialize in different niches, and the mass-ratio hypothesis, highlighting the role of dominant species' traits. These relationships vary across ecosystems, influenced by biotic and abiotic factors, such as diversity, species richness, competition, facilitation, soil fertility, water availability, fire regimes, and others, which shape vegetation structure and diversity. In tropical ecosystems, contrasting resource limitations (e.g., water in dry vegetation and light in wet vegetation) drive functional trait variation, from conservative strategies in dry forests to acquisitive strategies in wet forests, impacting biodiversity-ecosystem functioning dynamics. Functional and phylogenetic diversity have proven to be superior metrics over species richness in explaining biodiversity-ecosystem functioning relationships, while abiotic factors and topography also influence ecosystem processes. Understanding these patterns is vital to mitigate biodiversity loss and its effects on ecosystem services, particularly under global change scenarios, where biodiversity-ecosystem functioning research can guide restoration and conservation by prioritizing diversity and adaptive strategies. Thus, the thesis is divided in the following chapters: Chapter 1, titled: "Vegetation transition in the Central Brazilian Cerrado is better explained by structure than tree composition differences", and we propose two fundamental questions to be investigated in the Cerrado area of central Brazil: i) How variable is the vegetation structure and species between different Cerrado vegetation types? Second, ii) how strongly are vegetation structure and species composition linked? We hypothesize that vegetation types differ in both their structure and species composition, and that vegetation structure is tightly coupled to species composition, because of differences among species in how they deal with different types and degrees of different environments. Chapter 2, titled: " Taxonomic diversity, phylogenetic diversity and functional dominance drive aboveground carbon stock in the Brazilian Cerrado", and we aim to address three fundamental questions: 1) What is the difference in taxonomic diversity and carbon storage among the different vegetation types in the Cerrado? 2) Is taxonomic, functional, phylogenetic diversity or the community weighted mean of functional traits more important in driving AGC among the different vegetation types in the Cerrado? 3) Do relationships between diversity, functional traits and AGC differ among the different vegetation types in the Cerrado? We hypothesize that: i) taxonomic diversity and AGC follow the same pattern as the vegetation structure in the Cerrado, with higher levels in the taller vegetation types; and ii) the relationship between AGC and its drivers varies across vegetation types, primarily influenced by vegetation structure. Taller and denser vegetation exhibits a distinct pattern compared to other types. Finally, Chapter 3, titled: "Abiotic attributes outperform biodiversity in driving carbon storage across an environmental gradient in Brazilian tropical forests". For this chapter we aimed to answer two questions: 1) What is the pattern of resource use strategies in Tropical Forests along a climatic gradient? 2) How do abiotic and biotic attributes drive AGC in Tropical Forests along a climatic gradient? Based on the continuum between acquisition (fast return and low energy cost) and resource conservation (slow return and high energy cost), we expect that wet forests present a community of plant species with acquisitive traits compared to dry forests, which are composed of more conservative ones. The mass ratio hypothesis (based on functional composition) and structural diversity could play a more significant role in dry forests, as functional trait composition (e.g., drought resistance traits) might be more critical in determining aboveground biomass stock than resource availability. Thus, we expect that across forests, the abiotic attributes (e.g., soil fertility, climate, and water availability) have a positive and direct effect on biotic (species richness and stem structural diversity) and an indirect and positive effect on AGC.

Keywords: biodiversity ; functional traits; resource allocation

RESUMO

SILVA, Arthur da Cruz, D.Sc., Universidade Federal de Viçosa, fevereiro de 2025. **Biodiversidade e funcionamento ecossistêmico nas vegetações brasileiras: das savanas às florestas**. Orientador: Joao Augusto Alves Meira Neto.

A biodiversidade, que abrange todas as formas de vida, é um fator crítico na condução dos processos, funcionamento e serviços ecossistêmicos. O funcionamento dos ecossistemas, moldado pela biodiversidade, tem sido estudado por dois paradigmas: estudos iniciais focaram nos efeitos isolados da biodiversidade em condições controladas, enquanto abordagens atuais enfatizam estudos em contextos naturais e dependentes do ambiente. As principais teorias que explicam as relações entre biodiversidade e funcionamento do ecossistema incluem a complementaridade de nicho, onde as espécies se especializam em diferentes nichos, e a hipótese da razão de massa, que destaca o papel dos traços das espécies dominantes. Essas relações variam entre os ecossistemas, sendo influenciadas por fatores bióticos e abióticos, como diversidade, riqueza de espécies, competição, facilitação, como fertilidade do solo, disponibilidade de água, regimes de fogo, entre outros, que moldam a estrutura e a diversidade da vegetação. Nos ecossistemas tropicais, limitações contrastantes de recursos (por exemplo, água em vegetações secas e luz em vegetações úmidas) conduzem a variações nos traços funcionais, desde estratégias conservativas em florestas secas até estratégias aquisitivas em florestas úmidas, impactando as dinâmicas da relação entre biodiversidade e funcionamento ecossistêmico. A diversidade funcional e filogenética têm se mostrado métricas superiores à riqueza de espécies para explicar as relações entre biodiversidade e funcionamento ecossistêmico, enquanto fatores abióticos e topografia também influenciam os processos ecossistêmicos. Compreender esses padrões é fundamental para mitigar a perda de biodiversidade e seus efeitos sobre os serviços ecossistêmicos, especialmente em cenários de mudanças globais, a qual pesquisas sobre biodiversidade e funcionamento ecossistêmico BEF podem orientar esforços de restauração e conservação priorizando a diversidade e estratégias adaptativas. Assim, a tese está dividida nos seguintes capítulos: Capítulo 1, intitulado: “A transição da vegetação no Cerrado Brasileiro Central é melhor explicada pela estrutura do que pelas diferenças na composição das árvores”, propõe duas questões fundamentais a serem investigadas na área do Cerrado: i) Qual é a variabilidade na estrutura da vegetação e nas espécies entre os diferentes tipos de vegetação do Cerrado? ii) Quão fortemente estão

relacionadas a estrutura da vegetação e a composição de espécies? Nossa hipótese é que os tipos de vegetação diferem tanto em sua estrutura quanto em sua composição de espécies e que a estrutura da vegetação está fortemente acoplada à composição de espécies, devido às diferenças entre as espécies em como elas lidam com diferentes tipos e graus de ambientes distintos.. Capítulo 2, intitulado: “Diversidade taxonômica, diversidade filogenética e dominância funcional conduzem o estoque de carbono acima do solo no Cerrado brasileiro”, tem como objetivo abordar três questões fundamentais: 1) Qual é a diferença na diversidade taxonômica e no estoque de carbono entre os diferentes tipos de vegetação no Cerrado? 2) A diversidade taxonômica, funcional, filogenética ou a média ponderada da comunidade (CWM) de traços funcionais é mais importante para conduzir o carbono acima do solo (AGC) nos diferentes tipos de vegetação no Cerrado? 3) As relações entre diversidade, traços funcionais e AGC diferem entre os tipos de vegetação no Cerrado? Hipotetizamos que: i) A diversidade taxonômica e o AGC seguem o mesmo padrão da estrutura da vegetação no Cerrado, com níveis mais altos nos tipos de vegetação mais altos; e ii) a relação entre o AGC e seus fatores determinantes varia entre os tipos de vegetação, sendo influenciada principalmente pela estrutura da vegetação. Vegetações mais altas e densas exibem um padrão distinto em comparação com outros tipos. Por fim, o Capítulo 3, intitulado: “Atributos abióticos superam a biodiversidade na influência sobre o armazenamento de carbono ao longo de um gradiente ambiental em Florestas Tropicais Brasileiras”, propõe responder a duas questões: 1) Qual é o padrão de estratégias de uso de recursos em florestas tropicais ao longo de um gradiente climático? 2) Como os atributos abióticos e bióticos influenciam o AGC em florestas tropicais ao longo de um gradiente climático? Com base no contínuo entre aquisição (retorno rápido e baixo custo energético) e conservação de recursos (retorno lento e alto custo energético), esperamos que florestas úmidas apresentem comunidades de plantas com traços aquisitivos em comparação com florestas secas, compostas por espécies com traços mais conservativos. A hipótese da razão de massa (baseada na composição funcional) e a diversidade estrutural podem desempenhar um papel mais significativo em florestas secas, já que traços funcionais relacionados à resistência à seca podem ser mais críticos para determinar o estoque de biomassa acima do solo do que a disponibilidade de recursos. Assim, esperamos que, entre as florestas, os atributos abióticos (por exemplo, fertilidade do solo, clima e disponibilidade de água) tenham um efeito direto positivo nos fatores bióticos (riqueza de espécies e diversidade estrutural do caule) e um efeito indireto e positivo no AGC.

Palavras-chave: biodiversidade; atributos funcioanais; alocação de recurso

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1. General Introduction

Biodiversity can be defined as biological diversity, that includes all life forms, and it is considered one of the most important factor shaping the ecosystem processes, functioning, and services (IPBES 2019). Ecosystem processes can include (a)biotic components and their interactions, ecosystem functioning is a set of diverse ecological processes and interactions occurring within the ecosystems, and ecosystem services are the benefits that humans derive directly or indirectly from ecosystem functions and processes. Focusing on the ecosystem functioning, there are two paradigms trying to disentangle it relationship with biodiversity. In the past (old paradigm) studies including biodiversity and ecosystem functioning (BEF) were based on the role of climate and ecosystem functioning (biomass production, decomposition rates, herbivory, pollination) influencing biodiversity, also focusing on the isolated effects of biodiversity on ecosystem functioning (Naeem et al. 1994; Tilman et al. 1996). However, nowadays, we face a new paradigm, which researches and theories migrated from theoretical and experimental to nature based researches (Naeem 2002; Tilman et al. 2014; Van Der Plas 2019). Thus, started a discussion to interpret the results, arising different theories to explain the influence of biodiversity and abiotic attributes on the ecosystem functioning. On one hand, the niche complementarity theory postulates that species can be specialized to occupy different niches (niche differentiation), coexisting and influencing the ecosystem functioning (Tilman et al. 2014), on the other hand, the mass-ratio theory postulates that the traits of the dominant species coordinate the functioning of the ecosystem (Grime 1998). Those theories are widely used to understand the BEF relationship in different ecosystems worldwide, and there are different and sometimes controversial results found, because it is dependent on the continent, biome, vegetation type, vegetation structure (Van Der Plas 2019). For instance, in the tropical vegetation of Brazil, some researchers found positive relationships of BEF in tropical forest (dry and wet), while others found negative relationships of BEF in Cerrado (Brazilian savanna) (Pellegrini et al. 2016; Morandi et al. 2020; Righi et al. 2023). Better understand these patterns is fundamental, nowadays, because the humans are impacting negatively, local and global, on the ecosystems, causing biodiversity loss, and a replacement of species and it functional traits, also increasing the CO2 level in the atmosphere. Hence, understand this shift is fundamental to promote actions to store carbon on the vegetation and mitigate all other effects of global changes.

Human-driven invasions and extinctions have altered ecosystem goods and services, often with irreversible consequences. The effects of species loss vary across ecosystems, depending on functional redundancy, the specific contributions of species to the specific ecosystem, and abiotic controls. Moreover, biodiversity is essential to ensure the stability of ecosystem services in the face of spatial and temporal variability. Biodiversity loss is a problem of the Century, and researches focusing on it, have been using species richness as a proxy of biodiversity (Hooper et al. 2005), however, it’s known that other diversity metrics, can better explain the BEF relationships, such as functional and phylogenetic diversity. Species show functional traits that significantly influence ecosystem properties in various ways, and the functional diversity quantifies the variation in those morphophysiological characteristics among co-occurring species (Magnago et al., 2014; Villéger et al., 2008), while, the phylogenetic diversity quantifies to which extent co-occurring species on average have a recent (low phylogenetic diversity) or distant (high phylogenetic diversity) common ancestor (Cadotte et al. 2010). Besides, there are more diversity metrics, such as stem structural diversity that can be also used to understand the BEF relationships (Zhai et al. 2024).

In addition, abiotic factors are also fundamental in BEF studies, because it can drive both, diversity and ecosystem functioning, through limiting the resource availability, shaping the diversity of the plant community, its structure, hence, the ecosystem functioning (Van Der Sande et al. 2017; Galván-Cisneros et al. 2023; Villa et al. 2023). For example, within *Cerrado*, the tree species composition is expected to change along gradients of soil, water availability and the presence of fire (Hoffmann et al. 2003; Dantas et al. 2013; Lehmann et al. 2014). While high soil fertility is the main predictor shaping dry forest vegetation, high water availability drives evergreen and semi deciduous forests (Bueno et al. 2018). Comparing dry versus wet forest, it is possible to see a tendency that soil fertility explain a large variance in the former than in the latter (Peña-Claros et al. 2012), thus, when analyzing the effects of abiotic factors, herein, soil conditions, it shows different effects on the vegetation in a climatic gradient. Moreover, in tropical forests, soil and climatic conditions are important drivers of the forest dynamic (Quesada et al. 2012). Furthermore, topography also play a role in the vegetation dynamics, for instance, in the Tropical Atlantic Forest, elevation and convexity affect the soil fertility (Rodrigues et al. 2021), shaping the plant communities.

A large number of researches of BEF relationships, specially, on biomass productivity were made in the tropical wet forests, that can differ from dry forests and savannas (Van Der Plas 2019). The functioning of these vegetations are different because the resources limitation differ. For instance, in terms of water and light dynamics, dry vegetation types (such as dry forests and Cerrado savanna-like vegetation) experience water limitations and high light availability, whereas the opposite is true for wet tropical forests (Lohbeck et al. 2013; Prado-Junior et al. 2016). Therefore, the functional traits also change, which in the more harsh environments (dry vegetation) the species shows higher wood density, low specific leaf area, and others, that are considered a conservative strategy. The wet forests, shows higher specific leaf area, low wood density to deal with the specific environment, that is considered acquisitive strategy. Hence, these different resource use strategies directly impact on BEF relationships. Thus, the BEF approach can provide valuable insights for restoration, emphasizing functional, and species resource strategies, over taxonomic diversity, to bring back health ecosystems. Thus, incorporating functional diversity into restoration efforts is critical, especially under climate change scenarios that predict extreme events, additionally, phylogenetic diversity also play significant roles in ecosystem functioning.

Thus, based on the challenges to deal with the climate change, biodiversity loss, and the CO2 increment in the atmosphere, this thesis was structured to disentangle some gaps in plant ecology in the Brazilian vegetation. The first two chapters are focused on *Cerrado*, the most diverse savanna worldwide (Simon et al. 2009), that we tried to understand the difference between *Cerrado*'s vegetation types and it relationship with the functioning of the ecosystem using only biotic (diversity) attributes. In the third chapter we expanded along a climatic gradient in the Brazilian tropical forest (dry and cloud forest), using both, biotic (diversity) and abiotic (climate and soil) attributes to deeper understand it effects on the functioning of the ecosystem, focused on the tree aboveground storage. Thus, we, specifically, divided the thesis in the following chapters: Chapter 1, titled: “Vegetation transition in the Central Brazilian Cerrado is better explained by structure than tree composition differences”, and we propose two fundamental questions to be investigated in the Cerrado area of central Brazil: i) How variable is the vegetation structure and species between different Cerrado vegetation types? Second, ii) how strongly are vegetation structure and species composition linked? We hypothesize that vegetation types differ in both their structure and species composition, and that vegetation structure is tightly coupled to species composition, because of differences among species in how they deal with different types and degrees of different environments. Chapter 2, titled: “ Taxonomic diversity, phylogenetic diversity and functional dominance drive aboveground carbon stock in the Brazilian Cerrado”, and we aim to address three fundamental questions: 1) What is the difference in taxonomic diversity and carbon storage among the different vegetation types in the Cerrado? 2) Is taxonomic, functional diversity, phylogenetic diversity or the community weighted mean of functional traits more important in driving AGC among the different vegetation types in the Cerrado? 3) Do relationships between diversity, functional traits and AGC differ among the different vegetation types in the Cerrado? We hypothesize that: i) the taxonomic diversity and AGC follow the same pattern of the Cerrado vegetation structure, which high levels are found in the highest vegetation types; additionally, ii) the drivers of AGC differ among vegetation types, due to and following the pattern of AGC, finally iii) there are different process of community assembly that structures the vegetation depending on the vegetation type considered. Finally, Chapter 3, titled: "Abiotic attributes outperform biodiversity in driving carbon storage across an environmental gradient in Brazilian tropical forests". For this chapter we aimed to answer two questions: 1) What is the pattern of resource use strategies in tropical forests along a climatic gradient? 2) How do abiotic and biotic attributes drive AGC in tropical forests along a climatic gradient? Based on the continuum between acquisition (fast return and low energy cost) and resource conservation (slow return and high energy cost), we expect that wet forests present a community of plant species with acquisitive traits compared to dry forests, which are composed of more conservative ones. The mass ratio hypothesis (based on functional composition) and structural diversity could play a more significant role in dry forests, as functional trait composition (e.g., drought resistance traits) might be more critical in determining aboveground biomass stock than resource availability. Thus, we expect that across forests, the abiotic attributes (e.g., soil fertility, climate, and water availability) have a positive and direct effect on biotic (species richness and stem structural diversity) and an indirect and positive effect on AGC.

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2. Chapter 1 - Vegetation Transition in the Central Brazilian Cerrado is Better Explained by Structure than Tree Composition Differences

2.1. Abstract

The *Cerrado* biome encompasses different vegetation types, ranging from savanna-like vegetation to forest-like vegetation, represented by a vegetational continuum from *Cerrado Típico*, *Cerrado Denso* and *Cerradão,* respectively. Nevertheless, there are still uncertainties on whether these different vegetation types do not only differ in their vegetation structure, but also in their species compositions. Based on vegetation surveys from 167 plots in the central Brazilian *Cerrado*, we addressed two questions: i) How variable is the vegetation structure and species between different *Cerrado* vegetation types? Second, ii) how strongly are vegetation structure and species composition linked? To answer these questions, we performed hierarchical clustering for species composition and vegetation structure. Our results showed that for species composition only 18% of the variance was explained by hierarchical clustering, while for vegetation structure 82% of variance was explained. Additionally, there was a significant difference in the structure metrics between clusters, showing that it is possible to clearly identify different *Cerrado* vegetation types based on vegetation structures, but not by species composition. Finally, we suggest that trait plasticity in *Cerrado* trees should drive structural differences among vegetation types, which could be the focus of future studies.

Key-words: Cerrado vegetation types, Brazilian savanna**,** species overlapping, tree species composition.

2.2. Introduction

The *Cerrado* is considered a conservation priority due to the high plant diversity and the high degree of endemism (Cardoso Da Silva and Bates 2002; Abreu et al. 2017; de Castilho Silva et al. 2024). It encompasses different vegetation types, ranging from treeless environments up to forested areas (Ribeiro and Walter 1998). Within the spectrum of *Cerrado's* vegetation types, *Cerrado lato sensu* (savanna formation) can be divided into five vegetation types (Ribeiro and Walter 1998). Of these, *Cerrado Típico (stricto sensu)* stands out as a savanna formation characterized by sparse, small and tortuous trees, with thick barks adapted to fire, accompanied by a continuous herbaceous and grass layer (Miranda et al. 2009). Moreover, the tree height ranges from around 3 to 6 meters, and around 20 % of canopy cover (Ribeiro and Walter 1998; Torello-Raventos et al. 2013). In contrast, *Cerradão* (forest formation) is considered the transition between savanna and forest formation. This vegetation type consists of a blend of *Cerrado Típico*, gallery and dry forest tree species (Oliveira-Filho and Ratter 1995; Marimon Junior and Haridasan 2005; Ribeiro and Walter 2008; Solórzano et al. 2012), featuring taller trees ranging from 8 to 20 meters, higher tree density, and a sparser herbaceous and grass layer (Moreira 2000). Additionally, *Cerradão* exhibits greater tree diversity (Toppa 2004), and a canopy cover ranging from 50 to 90% of the areas (Ribeiro and Walter 1998). Finally, a transitional savanna-like vegetation between *Cerrado Típico* and *Cerradão*, is the *Cerrado Denso* (*stricto sensu*), that is characterized predominantly by trees with a height ranging from around 5 to 8 meters, and covering around 50 % of the canopy (Ribeiro and Walter 1998). Consequently, there is a coexistence of a large number of tree species, and some of these species can be considered key for different vegetation types (Ribeiro and Walter, 1998) which could be associated to the conservation value of the species they hold. However, we are still unsure about the extent to which composition and vegetation structure can explain the transitional vegetation of the *Cerrado-Típico-Cerradão* system. Therefore, the extent to which we can rely on vegetation variation to formulate and plan conservation actions for the Cerrado remains unclear.

Different *Cerrado* vegetation types may represent specific ecological dynamics and species pools (Ribeiro and Walter 1998), depending on the biogeographic region (Françoso et al. 2020). Felfili et al. (2004) reported that throughout the Cerrado there is a large overlap in woody species occurrence but with high variation in their abundances associated with soil variation. Ongoing discussions persist regarding which factors are driving variation in vegetation structure and species composition among vegetation types (Marimon Junior and Haridasan 2005; Pinheiro and Durigan 2012). Within *Cerrado*, the tree species composition is expected to vary along abiotic gradients (Hoffmann et al. 2003; Dantas et al. 2013; Lehmann et al. 2014). While high soil fertility is the main predictor shaping dry forest vegetation, high water availability drives evergreen and semi deciduous forests (Bueno et al. 2018). Finally, the fire frequency and intensity changes vegetation structure, density of tree individuals and canopy cover among vegetation types (Júnior et al. 2014; Bueno et al. 2018). Favorable edaphic and abiotic drivers also play an important role in driving vegetation structure (Torello-Raventos et al. 2013; Veenendaal et al. 2015; Gonçalves et al. 2021). However, none of these studies clarify whether the structural changes resulting from the gradients correspond to compositional changes.

The floristic composition of the Brazilian *Cerrado* varies and can be divided into geographic areas, with each region presenting a characteristic floristic composition (Ratter et al. 2003; Françoso et al. 2020). In central Brazil, encompassing Goiás and Minas Gerais States, there are two phytogeographic core regions (Amaral et al. 2017). However, different vegetation structural types, such as *Cerrado stricto sensu* (Cerrado Típico and Cerrado Denso) may have a different species composition and species richness compared to taller vegetation, such as *Cerradão* (Ferreira Ribeiro and Tabarelli 2002). Various abiotic factors have been shown to explain the differences in species composition between the vegetation types (Ratter et al. 2003; Durigan and Ratter 2016). However, it remains unclear whether structural differences in vegetation are consistently linked to differences in species composition. This uncertainty underscores the need for further studies to better understand the relationship between vegetation structure and species composition in the *Cerrado* biome.

The *Cerrado* is threatened by land-use change (logging, deforestation for agriculture, changed fire regimes) as well as by climate change (Velazco et al. 2019). At a fine and regional scale, it is possible to reduce the impacts of such disturbances by applying restoration and conservation strategies and policies. For instance, preserving original and critical areas could preserve more than 500 threatened animal and plant species (Strassburg et al. 2017). For such policies to be effective, it is necessary to improve the knowledge about the relationship between plant species composition and vegetation structure in the *Cerrado* vegetation mosaic, thus we could know which species grow where, and which locations should be prioritized for conservation. Therefore, we propose two fundamental questions to be investigated in the *Cerrado* area of central Brazil: i) How variable are vegetation structure and species composition between different vegetation types within the *Cerrado*? ii) How strongly are vegetation structure and species composition related? We hypothesize that vegetation types differ in both their structure and species composition, and that vegetation structure is tightly coupled to species composition, because of differences among species in how they deal with different types and degrees of different environments.

2.3. Material and Methods

Study area

Data were used from a survey of 19 tree communities in the *Cerrado* biome, 12 in Minas Gerais (MG), and 7 in Goiás (GO) States, Brazil (Fig. 1. For details see Júnior et al. (2021). The areas were chosen based on different tree structures, varying from smaller to taller trees inside the areas, representing open to closed Cerrado vegetation on flat terrains with deep soils. For the analysis we made use of an existing data set of previously sampled plots, ranging from 100 m^2 to 500 m^2, totaling 167 plots (Table S1), for details see Júnior et al. (2021). The study encompassed all living tree species with a diameter at breast height (DBH) equal to or exceeding 5 cm. Such a method may create a skew towards species that do not have a trunk. Each tree was identified down to the species level. The diameter at breast height (DBH) was measured using a metric tape, and the heights of the trees were compared using the tallest ones as a reference, employing a 5.5-meter tree pole pruner.

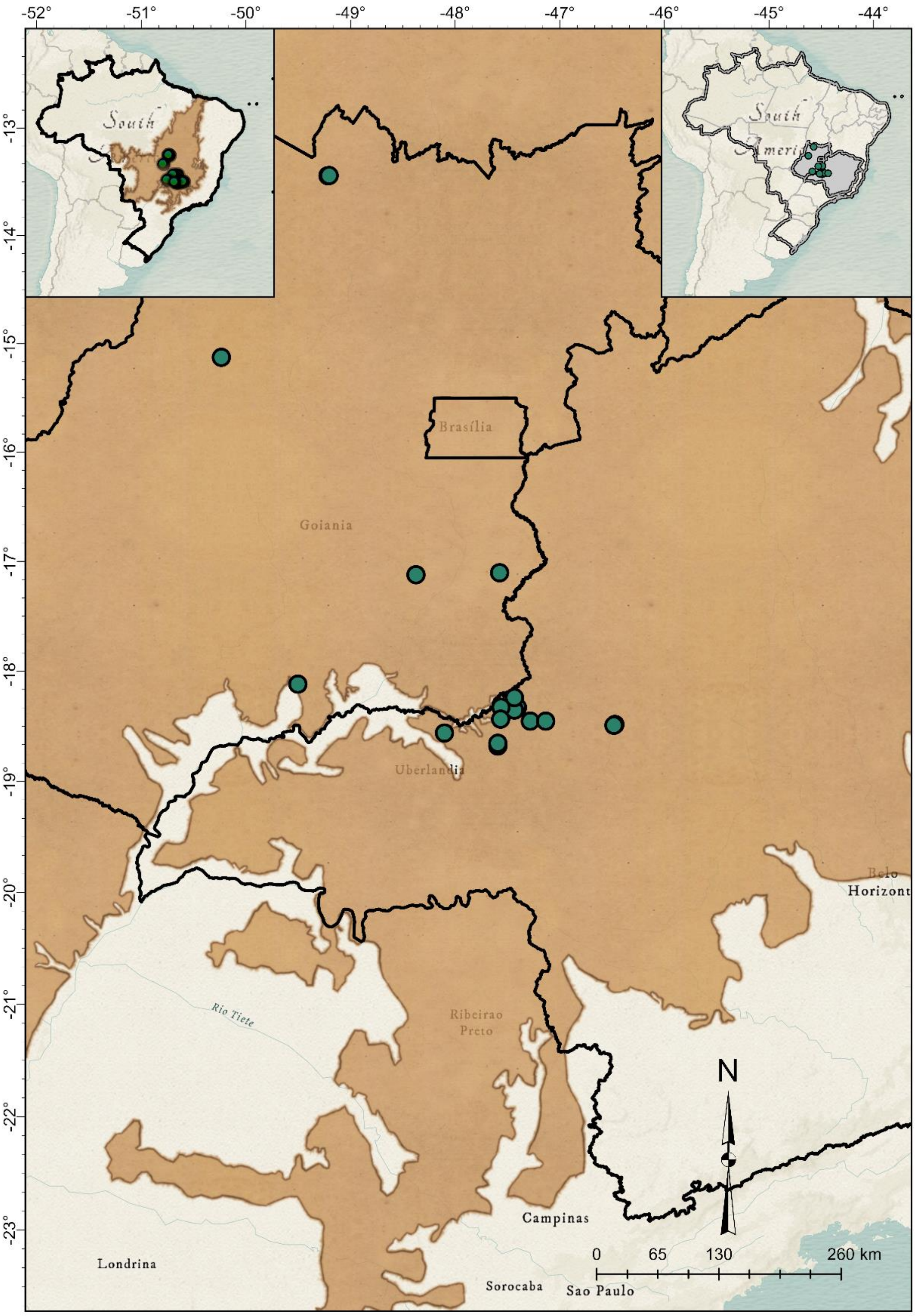


Figure 1. Map of the studied areas in the *Cerrado*. The green points indicate the study locations. The *Cerrado* biome domain is highlighted in light brown. The two areas outlined in black the Brazilian states of Goiás, in the top left, and Minas Gerais, in the bottom right.

The study area (Fig. 1, S2, and S3) is characterized by the typical seasonality of Brazilian savanna with an extended dry season, annual precipitation below 1400 mm, and rainfall concentrated during summers, classified as type Aw in the Koppen system (Köppen, 1936).

However, according to Françoso et al. (2020), the study areas encompass two different biogeographic districts, whereas the areas located in the north part of GO state, are in the Central-west (CW) district characterized by high temperatures with low seasonal variation, and with high radiation during the dry season. The areas in the Southeast (SE) district have an intermediate mean annual temperature and radiation, and a high seasonality compared to the other districts (Françoso et al. 2020). Additionally, the soils in the study areas are Yellowish Red to Yellow Latosols.

Tree species composition and vegetation structure

We utilized the hierarchical clustering method with the Jaccard similarity index (Real and Vargas 1996), also accounting for the abundance, and Ward's minimum variance method "ward.D2" to group the plots and assess the similarity in tree species composition among them. The R package "stats" and its "hclust" function were used in the analysis. We used the Jaccard distance, since it is most suitable for handling the many zeros in the abundance matrix. To define the number of clusters, the elbow method analysis (Fig. S1) was conducted, using the "K-means" function of the "stats" R package. To test the difference between clusters, a Permutational analysis of variance (PERMANOVA), with 1000 permutations, was conducted using the "adonis2" function from the R package "vegan".

Furthermore, to examine the similarity in vegetation structure among plots, we performed hierarchical clustering using Euclidean distance and Ward's minimum variance method "ward.D2" to group the plots. The R package "stats" and its "hclust" function were used in the analysis. For vegetation structure, the variables maximum and mean height (m), stand basal area (m^2/ha), and stand basal area for DBH less than, bigger or equal to 10 cm (to account for variability in tree size) were used as input variables for the hierarchical clustering procedure. Again, to define the number of clusters, the elbow method analysis (Fig. S1) was conducted, using the "K-means" function of the "stats" R package. To test the difference between clusters, a PERMANOVA, with 1000 permutations, was conducted using the "adonis2" function from the R package "vegan". Additionally, to analyze differences in vegetation structural parameters, and tree density between clusters, Kruskal-Wallis tests were performed using the "Kruskal.test" package, followed by "dunn.test" using the "stats" and "dunn.test" packages, respectively.

Finally, we tested the of species composition between each structural cluster, to analyze if the different structures contain different tree species compositions. Thus, we performed an Analysis of similarities (ANOSIM), using the " anosim" function of the "vegan" R package.

Spatial correlation

A Mantel test was performed to assess the correlation between spatial distances and two sets of ecological data: (i) species composition and (ii) vegetation structure. Spatial distances between plots were calculated using Euclidean distance based on geographic coordinates. Species composition dissimilarity was calculated using the Jaccard index, while vegetation structure dissimilarity was derived using Euclidean distances from plot-level metrics (maximum height, mean height, stand basal area, basal area for stems < 10 cm, and basal area for stems ≥ 10 cm). Distance matrices were compared using the mantel function from the "vegan" package in R (R Core Team, 2024), with 999 permutations to test the significance of the Mantel statistic (r).

2.4. Results

Species composition

In total there were 204 tree species, and 7,455 tree individuals belonging to 54 families (Table S2). Only 13 species represented 50% of all individuals: *Tachigali subvelutina, Astronium urundeuva, Tapirira guianensis, Xylopia aromatica, Qualea grandiflora, Myrcia splendens, Emmotum nitens, Siparuna guianensis, Xylopia sericea, Curatella americana, Matayba guianensis, Astronium fraxinifolium* and *Qualea parviflora*, respectively. Additionally, four families represented 52% of all species: Fabaceae, Anacardiaceae, Vochysiaceae and Annonaceae.

Hierarchical clustering

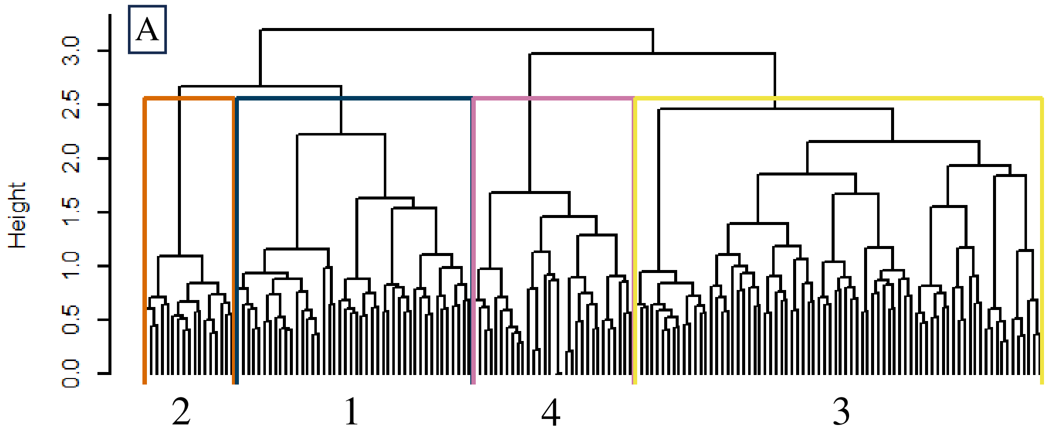
For species composition, based on the elbow method (Fig. S1) we identified four vegetation clusters (Fig. 2 A). In contrast, for vegetation structure we found three clusters (Fig. 2 B). The PERMANOVA analysis showed a significant difference between clusters in species composition and vegetation structure, both p-values were 0,000999. There were strong differences in explained variation (R^2): while for the species composition, 18% of variation was explained by the clusters, for vegetation structure 82% (Table 1) of variance was explained by the clusters.

Table 1 Result of a PERMANOVA by species composition and vegetation structure

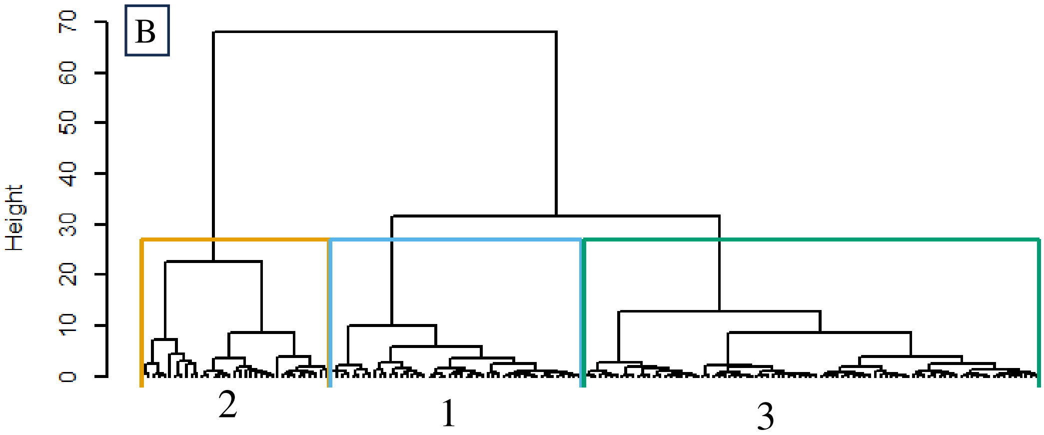
Term	Df	Sum of Squares	R2	F	Pr(>F)
		Species composition			
Clusters	3	13,085	0,1787	11,819	0,000999 ***
Residual	163	60,152	0,8213		
Total	166	73,237	1,0000		

Vegetation structure					
Clusters	2	2819,0	0,8242	384,43	0,000999 ***
Residual	164	601,3	0,1758		
Total	166	3420,4	1,0000		

Based on hierarchical clustering of species composition, 3% of all species are shared by all clusters, while 13% belongs only to cluster 1, 8% only to cluster 2, 20% only to cluster 3, and 7% only to cluster 4, and 48% shared between at least two clusters (Table S5). When only focusing on 70% of most abundant species of each cluster, in the cluster 1 there were 13 species (of which 4 were exclusive to cluster 1), in cluster 2 there were 9 species (of which 4 were exclusive to cluster 2), in cluster 3 there were 34 species (of which 24 were exclusive to cluster 3), and in cluster 4 there were 10 species (of which 5 were exclusive to cluster 4) (Table S4, S5).



Species Composition



Vegetation Structure

Fig. 2 Hierarchical clustering for species composition (A) and vegetation structure (B). The numbers on the X-axis represent the clusters.

According to ANOSIM results, significant differences in species composition were observed between clusters (p-value = 0.001) with 13% of the variance explained by the clusters. Thus, considering 70% of most abundant species of each cluster, in the Cluster 1 there were 23 species (7 exclusive), in Cluster 2 there were 14 species (7 exclusive), in Cluster 3 there were 27 species (13 exclusive), showing that the Cluster 1 showed less dominance, followed by Cluster 3, and Cluster 2, respectively (Table S3). Based on hierarchical clustering of vegetation structure, 35% of all species are shared by all clusters, while 9% belongs only to cluster 1, 13% only to cluster 2, 14% only to Cluster 3. Furthermore, 10% of species were shared between clusters 1 and 2, 17% shared between clusters 1 and 3, and 2% shared between cluster 2 and 3 (Table S2). Additionally, the 13 species most abundant in the surveyed areas belong to all three clusters.

The tree density of the structural clusters was 996 n/ha for the Cluster 1, 1530 n/ha for the Cluster 2 and 665 n/ha for the Cluster 3.

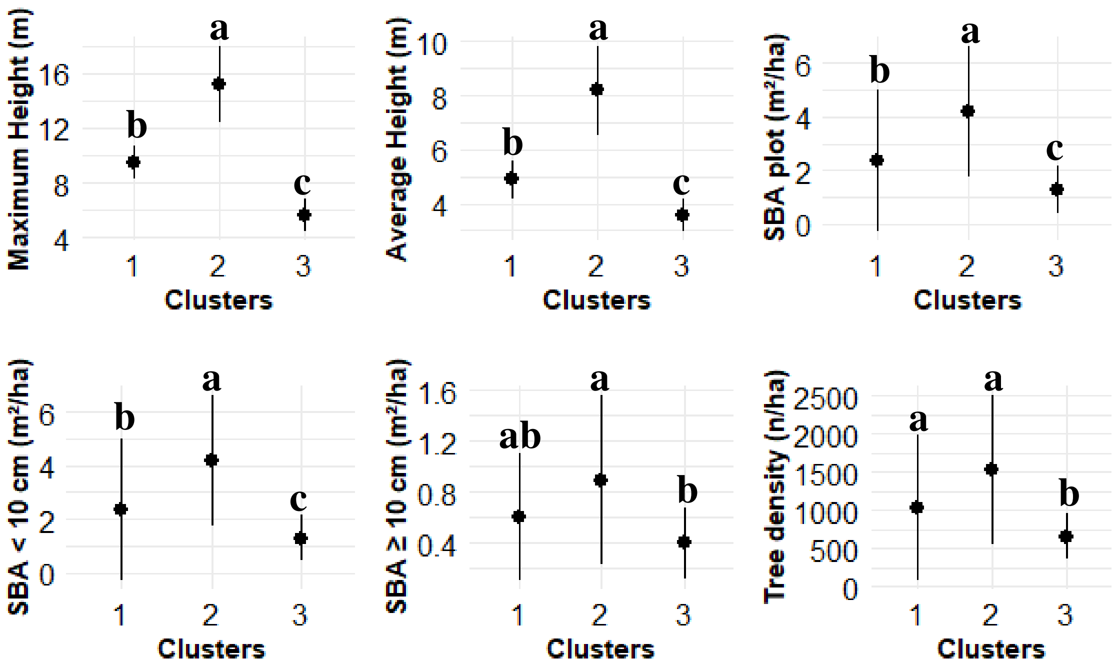


Fig. 3 Graphs representing the difference between vegetation structure variables and tree density by clusters. The dots represent the mean and the lines the standard error. SBA plot = stand basal area per plot; SBA < 10 cm = total stand basal area for all trees lower than 10 cm of DBH per plot; SBA ≥ 10 cm = stand basal area for all trees higher or equal than 10 cm of DBH per plot. Different letters mean that the values are statistically different (p-value < 0,05), based on Kruskal-Wallis, and Dunn test.

Based on the Kruskal-Wallis' test for vegetation structure, and tree density there was a significant difference ($p < 0.05$) between clusters for all metrics used (Fig. 3; Table S6). For maximum/ mean height, stand basal area, and stand basal area smaller than 10 cm, the Cluster 2 showed the highest values followed by Cluster 1 and Cluster 3. However, for stand basal area for trees equal or bigger than 10 cm, there was only difference between clusters two and three (Fig. 3; Table S6). Thus, the Cluster 2 showed the highest values of vegetation structure, followed by the Cluster 1 and Cluster 3, respectively (Fig. 3; Table S6). Additionally, for tree density Cluster 1 and Cluster 2 did not show statistical differences, but both were higher than Cluster 3 (Fig. 3; Table S6).

Therefore, we classify the clusters based on Ribeiro and Walter (1998). Cluster 3 of the vegetation structure-based clustering approach we classified as *Cerrado Típico*, since the average height was around 4. Cluster 1 showed intermediate values of the structural metrics, such as five meters of average height, thus we classified it as *Cerrado Denso*. Finally, Cluster 2, had the highest values of structural metrics, such as maximum tree height around 15 meters. Therefore, we classified it as *Cerradão*. The tree density was the same between Cluster 2 and Cluster 1, higher than Cluster 3.

Spatial correlation

We performed a Mantel test to evaluate the correlation between species composition (community dissimilarity – Jaccard index) and geographic distance (Haversine method). Additionally, we also performed a Mantel test to evaluate the correlation between vegetation structure (Euclidean distance) and geographic distance. The analysis for species composition (Mantel statistic r = 0.1532, p- value = 1e-04, based on 9999 permutations), and vegetation structure (Mantel statistic r = 0.1158, p-value = 0.0072, based on 9999 permutations) revealed a statistically significant positive correlation, indicating that community dissimilarity increases with geographic distance. To represent graphically the spatial correlation result, we plotted the representation of clusters of species composition and vegetation structure in the map of the studied areas (Fig. S2 and S3). The positive relations of geographic distances with both, vegetation structure and species composition, do not challenge the overall results found.

2.5. Discussion

In this study we used tree surveys from 167 *Cerrado* plots in 19 sites to investigate whether i) their tree communities can be categorized based on species composition and/or structural differences, and ii) whether variation in tree species composition among plots correlates with variation in vegetation structure. Our results confirmed our hypothesis that *Cerrado* plots can be clustered based on differences in vegetation structure, with three distinct clusters representing *Cerrado Típico, Cerrado Denso* and *Cerradão*. We found a positive relationship between geographic distances among sites and both vegetation structures and species composition, which does not challenge the overall results. While we could also identify plot clusters based on species compositional differences, these explained little (13%) of variation among communities, which is very little compared to the >80% of variation among plots that could be explained based on differences in vegetation structure. As a result, clusters based on vegetation structure varied little in their species composition.

We identified 204 tree species, which represents approximately 25% of the species classified by Françoso et al. (2020) for the entire *Cerrado* biome. Despite the classification by Françoso et al. (2020) referring only to savannic *Cerrado* compositions, the little variation explained by species composition in the *Cerrado strictu sensu* - *Cerradão* transition in our results supports the inclusion of *Cerradão* in the same comparison. Therefore, only 142 of these 204 species match the 814 species identified in their survey, representing just 17% of the woody species. In our study the families with highest tree abundances were Fabaceae, Anacardiaceae, Vochysiaceae and Annonaceae, congruently with results of other studies (Almeida et al. 2014). The Fabaceae and Vochysiaceae families were expected, because the former is frequently found in studies of the Brazilian Cerrado, and the latter present many species able to accumulate aluminum (Nogueira et al. 2019), a mineral very present in soils of the biome (Oliveira et al. 2020).

We found that only 13% of the variance was explained with species composition hierarchical clustering, indicating a significant overlap of species between clusters. Specifically, 52% of all species were present in at least two clusters, encompassing 89% of all tree individuals. Specific *Cerrado* tree species might be linked to climate and soil characteristics (Ribeiro and Walter 1998; Ratter et al. 2003; Pinheiro and Durigan 2012; Neri et al. 2012; Françoso et al. 2020), but the species clusters showed a great overlap, suggesting this might not be the case in our study area in central Brazil. However, the complex relationship between woody species and the soils of *Cerrado* is far from being completely understood. Contrasting with the clustering based on species composition, the clustering based on vegetation structure showed great difference between clusters, with the model explaining 82% of the variance. This indicates a clear differentiation between the three clusters in terms of vegetation structure, and based on the structural characteristics of our clusters, they mostly coincide with the following vegetation types: *Cerrado Típico* (cluster 3), *Cerrado Denso* (cluster 1) and *Cerradão* (cluster 2). The vegetation was taller, and the tree density was higher in our clusters representing *Cerradão* and *Cerrado Denso* than in the cluster representing *Cerrado Típico*, congruently with studies showing that the canopy cover increases in a gradient from *Cerrado sensu stricto* to *Cerradão* (Torello-Raventos et al. 2013). Moreover, our results are congruent with findings of Pinheiro and Durigan (2012), which concluded that SBA per plot is among the most reliable predictors for distinguishing between Cerrado vegetation types.

We found that vegetation clusters categorized based on vegetation structure hardly varied from each other in their species composition. Hence, vegetation structure and species composition seem to be largely decoupled in the *Cerrado*. This is in line with our findings that vegetation plots can be categorized based on differences in vegetation structure, but hardly based on differences in species composition. Indeed, 64% of the species in our study, representing 94% of all tree individuals, are shared by at least two clusters. Pinheiro and Durigan (2012) also found no differentiation in species composition between types of savanna vegetation (*Cerrado Típico* and *Cerrado Denso*) but in contrast to our study, they reported different species for *Cerradão*. Our study is congruent with studies that report many *Cerrado* species with great ecological amplitude regarding to a variation in response to water availability, soil and climate conditions, shade and fire (Neri et al. 2012; Dantas et al. 2013; Cianciaruso et al. 2013; Maracahipes et al. 2018). Our results which are obtained in *Cerrados* on flat terrains with deep soils in central Brazil differ from reports of studies focused on contrasting substrates as deep soils typically found in the *Cerrado* compared to alluvial soils (Carrijo et al. 2021) or deep soils typically found in the Cerrado compared to rocky substrates (Abadia et al. 2018). However, in our study, we did not measure soil-related properties, so that still some uncertainties remain how the different vegetation clusters vary regarding soil type.

Some species show distributions associated to specific *Cerrado* biogeographic districts due to climate differences between regions (Françoso et al. 2020). Again, despite the classification by Françoso et al. (2020) referring only to savannic *Cerrado* compositions, the little variation explained by species composition in the *Cerrado strictu sensu* - *Cerradão* transition in our results supports the inclusion of *Cerradão* in the same comparison. In our study we couldn't find the same pattern, since more than 50% of these species are found in the three hierarchical vegetation structure clustering, belonging to two different biogeographic region according Françoso et al. (2020). Moreover, according Bueno et al. (2018) there are key indicator species of *Cerrado Típico*, and we found some of them (*Byrsonima coccolobifolia, Dalbergia miscolobium, and Palicourea rigida*) shared by the three clusters, meanwhile others were shared by two clusters (*Davilla elliptica* and *Kielmeyera coriacea*). Finally, only one *Cerrado Típico* specialist species (*Zeyheria montana*) was found in our *Cerrado Típico* vegetation (Table S3), reinforcing that in our study the classification based on specific species distributions would not be effective. Nevertheless, patterns in species composition should receive further attention in the *Cerrado* to understand how classifications based on species composition might aid in conservation practices and policies. There are some tree species that have been reported to have particularly high abundance in unburned areas, such as *Blepharocalyx salicifolius* (Machida et al. 2021), and *Miconia cuspidata* (fire-sensitive). Our study is congruent with these earlier findings, since both species were found only in our *Cerradão* areas. Nevertheless, another species known as fire-sensitive, *Copaifera langsdorffii,* was found both in *Cerradão* and *Cerrado Denso* areas, suggesting that our *Cerrado Denso* areas could be less affected by fire, or alternatively, that within our region this species is more tolerant to fires (Dantas et al. 2013; Cianciaruso et al. 2013). Finally, our *Cerrado Típico* areas showed lower values of height and SBA, indicating that these plots might have experienced a high fire frequency that reduces the community stand basal area (Machida et al., 2021) or these plots present low soil fertility that only support this kind of vegetation structure, with scattered and small trees (Veenendaal et al. 2015). Independently whether there are gradients of fire frequency, soil, or climatic conditions in between *Cerrado Típico*, *Cerrado Denso* and *Cerradão* and despite various studies have shown that across different environmental conditions (e.g. gradients in natural fire, drought, or shade), different species are found, with different traits enabling these species to cope with their local environment (Cornelissen et al. 2003; Hoffmann et al. 2012), in our study area the species seem to have intraspecific variability or plasticity that makes it possible for many species to occur in varying environments (Dantas et al. 2013; Cianciaruso et al. 2013; Souza et al. 2018). However, investigating how environmental gradients were responsible for our observed findings would have required various additional measurements that were outside the scope of the current study, although we recommend that future studies dive deeper into this.

2.6. Conclusion

Our findings, which are confined to the tree species of the *Cerrado,* suggest that the *Cerrado* presents a mosaic of different vegetation types that can be categorized based on vegetation structure rather than species composition. The presence of the same species in different vegetation types suggests a high phenotypic variability or plasticity of these species that deserve further studies to be elucidated.

We encourage studies exploring intra- and inter-specific variation in functional traits of species occurring from savanna-like environments to forested areas. Such studies would help in understanding the relationship between disturbance, traits, and diversity in transitional vegetation types.

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2.8. Supplementary Information

Table S1. Characteristics of the *Cerrado's* biome areas.

Cerrado's areas	Plots (n)	Plot size (m^2)	Area size (m^2)	Species Richness
Area 1	3	500	1500	28
Area 2	9	500	4500	53
Area 3	24	500	12000	60
Area 4	10	500	5000	47
Area 5	19	400	7600	36
Area 6	16	500	8000	56
Area 7	11	400	4400	26
Area 8	13	400	5200	29
Area 9	11	500	5500	51
Area 10	6	500	3000	41
Area 11	6	400	2400	15
Area 12	4	500	2000	45
Area 13	9	500	4500	54
Area 14	13	500	6500	54
Area 15	5	500	2500	43
Area 16	1	400	400	10
Area 17	2	500	1000	29
Area 18	5	400	2000	23
Area 19	1	100	100	22

Table S2. Species by hierarchical clustering of the species composition and vegetation structure and the total abundance of the tree individuals.

Families and Species	**Clusters Sp. composition**	**Clusters Veg. structure**	**Total abundance**
Anacardiaceae			
Astronium fraxinifolium Schott	1, 2, 3, 4	1, 2, 3	129
Astronium graveolens Jacq.	3, 4	1, 2	2
Astronium urundeuva (Allemão) Engl.	1, 2, 3	1, 2, 3	408
Lithraea molleoides (Vell.) Engl.	1, 3	1, 3	29
Schinus terebinthifolia Raddi	4	3	1
Tapirira guianensis Aubl.	1, 2, 3	1, 2, 3	398
Tapirira obtusa (Rich.) C.DC.	1	2	4
Annonaceae			
Annona bahiensis R.E. Fr.	1	2	2
Annona coriacea Mart.	1, 2, 3	1, 2, 3	14
Annona crassiflora Mart.	2, 3, 4	2, 3	13
Guatteria sellowiana A.DC.	1	3	1
Xylopia aromatica (Lam.) Mart.	1, 2, 3	1, 2, 3	368
Xylopia emarginata Mart.	2	1, 2	66
Xylopia sericea A.St.-Hil.	1, 4	1, 2, 3	215
Apocynaceae			
Aspidosperma macrocarpon Muell. Arg.	1, 3	1, 3	29
Aspidosperma parvifolium A.DC.	1, 3	1, 3	17
Aspidosperma subincanum Mart.	2	2	5
Aspidosperma tomentosum Mart.	1, 2, 3	1, 2, 3	23
Hancornia speciosa Gomes	1, 2, 3, 4	1, 2, 3	15
Aquifoliaceae			
Ilex conocarpa R. Br.	3	3	6
Araliaceae			
Dendropanax cuneatus (Benth.) Frodin	1	2	2
Didymopanax macrocarpus Rizzini	1, 3	1, 2, 3	46
Arecaceae			
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	3	1, 2, 3	17
Asteraceae			
Eremanthus glomerulatus Less.	3, 4	3	10
Piptocarpha macropoda (Less.) Baker	1	1	1
Piptocarpha rotundifolia (DC.) Baker	1, 2, 3	1, 2, 3	105
Bignoniaceae			

Handroanthus albus (Cham.) Mattos	3	1	5
Handroanthus impetiginosus (Mart. ex DC.) Mattos	3	1	1
Handroanthus ochraceus (Cham.) Mattos	1	2	1
Handroanthus serratifolius (Vahl) S.O.Grose	1, 3	1, 3	11
Jacaranda caroba (Vell.) DC.	2	2	1
Tabebuia aurea (Silva Manso) Benth. ***& Hook.f. ex S. Moore***	2	1, 2	5
Tabebuia roseoalba (Ridl.) Sandwith	3	3	1
Zeyheria montana Mart.	3	3	2
Boraginaceae			
Cordia sellowiana Cham.	1	1	6
Cordiera macrophylla Mart.	1	1	1
Cordiera sessilis (Vell.) Kuntze	2, 3	1, 2	54
Burseraceae			
Protium altissimum (Aubl.) Marchand	1, 2	1, 2	97
Protium heptaphyllum (Aubl.) Marchand	1	1	2
Calophyllaceae			
Calophyllum brasiliense Cambess.	1	2	1
Cannabaceae			
Trema micrantha (L.) Blume	2	2	1
Caryocaraceae			
Caryocar brasiliense Cambess.	1, 2, 3, 4	1, 2, 3	78
Celastraceae			
Cardiopetalum calophyllum R.S. Cowan	1, 2	1, 2	2
Salacia crassifolia (Mart. ex Schult.) ***G.Don***	3	3	5
Chrysobalanaceae			
Hirtella glandulosa Spreng.	1	1, 2	2
Hirtella martiana Hook.f.	1	2	2
Clusiaceae			
Kielmeyera coriacea Mart.	3	3	15
Kielmeyera speciosa Mart.	3, 4	1, 3	28
Platonia insignis Mart.	3	1, 2	4
Combretaceae			
Terminalia argentea Mart. & Zucc.	1, 2, 3	1, 2, 3	68
Terminalia glabrescens Mart.	1, 3	1, 3	8
Connaraceae			

Connarus suberosus Planch.	1, 2, 3	1, 2, 3	21
Dilleniaceae			
Curatella americana L.	1, 3, 4	1, 2, 3	186
Davilla elliptica A.St.-Hil.	1, 3	1, 3	7
Ebenaceae			
Diospyros hispida A.DC.	3	1	1
Diospyros lasiocalyx Mart. ex Miq.	1, 3	1, 3	75
Erythroxylaceae			
Erythroxylum campestre A.St.-Hil.	3	3	7
Erythroxylum daphnites Mart.	3	1, 3	4
Erythroxylum deciduum A.St.-Hil.	1, 2, 3	1, 2, 3	29
Erythroxylum suberosum A.St.-Hil.	1, 2, 3	1, 2, 3	29
Euphorbiaceae			
Croton urucurana Baill.	4	1	1
Pera glabrata (Schott) Poepp. ex Baill.	1	2	6
Sapium glandulosum (L.) Morong	3	1, 3	4
Fabaceae			
Adenanthera pavonina L.	3	1, 2, 3	3
Anadenanthera colubrina (Vell.) Brenan	1, 3, 4	1, 2, 3	36
Anadenanthera peregrina (L.) Speg.	1, 3, 4	1, 3	47
Andira vermifuga (Mart.) Benth.	3	1, 3	2
Apuleia leiocarpa (Vogel) J.F. Macbr.	3	1, 2	5
Bauhinia curvula Benth.	3	1, 2	15
Bauhinia forficata Link	1, 3	1, 3	9
Bauhinia rufa (Bong.) Steud.	4	3	1
Bauhinia variegata L.	2	2	3
Bowdichia virgilioides Kunth	1, 2, 3	1, 2, 3	85
Chamaecrista orbiculata (Benth.) H.S.Irwin & Barneby	4	3	1
Copaifera langsdorffii Desf.	1, 2	1, 2	31
Dalbergia miscolobium Benth.	1, 2, 3	1, 2, 3	14
Dimorphandra mollis Benth.	1, 2, 3, 4	1, 2, 3	98
Dipteryx alata Vogel	1, 3	2	2
Enterolobium contortisiliquum (Vell.) Morong	1	3	2
Enterolobium gummiferum (Mart.) J.F. Macbr.	1, 2, 3	1, 2, 3	24
Hymenaea courbaril L.	3, 4	1, 2, 3	14
Hymenaea stigonocarpa Mart. ex Hayne	1, 3, 4	1, 2, 3	20

***Hymenolobium heringerianum* Ducke**	1	1	12
***Inga cylindrica* (Vell.) Mart.**	2	2	1
***Inga edulis* Mart.**	3	1, 3	6
***Inga nobilis* (Vell.) Mart. ex Benth.**	1	1, 2, 3	7
***Leptolobium dasycarpum* (Vogel) Ducasse**	1, 2, 3	1, 2, 3	29
***Machaerium acutifolium* Vogel**	1, 2, 3	1, 2, 3	13
***Machaerium hirtum* (Vell.) Stellfeld**	1	1, 2, 3	3
***Machaerium opacum* Vogel**	1, 2, 3	1, 2, 3	20
***Mimosa claussenii* Benth.**	4	3	4
***Mimosa hebecarpa* Benth.**	3, 4	1, 2, 3	28
***Ormosia arborea* (Vell.) Harms**	2	2	5
***Parkia platycephala* Benth.**	3, 4	1, 2, 3	19
***Peltophorum dubium* (Spreng.) Taub.**	4	1	1
***Piptadenia gonoacantha* (Mart.) J.F.Macbr.**	3 , 4	1, 2, 3	25
***Plathymenia reticulata* Benth.**	1, 2, 3	1, 2, 3	107
***Platycyamus regnellii* Benth.**	2	2	12
***Platymiscium floribundum* Vogel**	3	3	1
***Platypodium elegans* Vogel**	1, 3	1, 2, 3	60
***Pterodon emarginatus* Vogel**	1, 3, 4	1, 2, 3	8
***Pterodon pubescens* Benth.**	2	2	1
***Salvertia convallariodora* (Vell.) Sleumer**	3, 4	1, 2, 3	47
***Senegalia polyphylla* (DC.) Britton & Rose**	1, 3	1	6
***Stryphnodendron adstringens* (Mart.) Coville**	1, 2, 3	1, 2, 3	52
***Stryphnodendron pulcherrimum* (Willd.) Hochr.**	4	3	15
***Tachigali aurea* (Spire) Hutch.**	1, 3, 4	1, 2, 3	42
***Tachigali subvelutina* (Mart.) G.P.Lewis & G.S.Bunting**	1, 2, 3	1, 2, 3	505
***Tachigali vulgaris* (Benth.) Hutch.**	3	1, 3	25
***Vatairea macrocarpa* (Benth.) Ducke**	1, 3	1, 3	102
Icacinaceae			
***Emmotum nitens* Mart. ex Berg**	1, 2, 3	1, 2, 3	293
Lamiaceae			
***Aegiphila integrifolia* Jacq.**	2	2	1
***Aegiphila verticillata* Vell.**	3	1, 3	12
***Vitex megapotamica* (Spreng.) Moldenke**	3	1, 2	10

Lauraceae			
Endlicheria paniculata (Spreng.) J.F. Macbr.	2	2	7
Nectandra cissiflora Nees	3	3	5
Ocotea corymbosa Mez	3	1	1
Ocotea spixiana (Nees & Mart.) Mez	3	1	1
Loganiaceae			
Strychnos pseudoquina A.St.-Hil.	2, 3, 4	1, 2, 3	29
Lythraceae			
Lafoensia pacari A. St.-Hil.	1, 3	1, 2, 3	9
Malpighiaceae			
Byrsonima coccolobifolia Kunth	1, 2, 3	1, 2, 3	14
Byrsonima crassifolia (L.) Kunth	3	1, 3	36
Byrsonima laxiflora Griseb.	1,3	1, 2, 3	13
Byrsonima pachyphylla A.Juss.	1, 2, 3, 4	1, 2, 3	39
Byrsonima verbascifolia (L.) DC.	1, 3, 4	1, 2, 3	37
Heteropterys byrsonimifolia A.Juss.	1, 3	1, 3	15
Malvaceae			
Apeiba tibourbou Aubl.	3	1, 3	19
Eriotheca gracilipes (K. Schum.) A. Robyns	3	1	5
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	1, 2, 3	1, 2, 3	26
Guazuma ulmifolia Lam.	1, 3	1, 2, 3	24
Luehea divaricata Mart.	4	1	1
Pseudobombax longiflorum (Mart. & Zucc.) A. Robyns	1, 3	1, 3	9
Pseudobombax tomentosum (Mart. & Zucc.) A. Robyns	2	2	2
Sterculia striata A.St.-Hil.	3	1, 2, 3	10
Melastomataceae			
Miconia albicans (Sw.) Triana	2, 3	1, 2	9
Miconia burchellii (Naudin ex Cogn.) Naudin	1, 4	1, 3	16
Miconia cuspidata (Ruiz & Pav.) D. Don	1	2	17
Miconia ferruginata DC.	3	3	45
Miconia leucocarpa (Sw.) DC.	4	3	7
Miconia rubiginosa Naudin	4	3	1
Monteverdia floribunda (A.St.Hil.) J.F.Macbr.	1	2	1
Meliaceae			
Guarea guidonia (L.) Sleumer	1, 4	2, 3	8
Guarea kunthiana A.Juss.	3	1, 3	6

Moraceae			
Brosimum gaudichaudii Trecul	3	3	1
Ficus goiana Miq.	2	2	87
Myristicaceae			
Virola sebifera Aubl.	1	1, 2	7
Myrtaceae			
Blepharocalyx salicifolius (Kunth) O.Berg	1, 2, 3	2	10
Campomanesia lineatifolia R. Br.	3	1, 2	4
Campomanesia velutina (A.St.-Hil.) O.Berg	1	1, 3	82
Eugenia dysenterica DC.	1, 2, 3	1, 2, 3	25
Eugenia florida DC.	1	2, 3	14
Myrcia splendens (Sw.) DC.	1, 3	1, 2, 3	329
Myrcia tomentosa (Aubl.) DC.	3	1	1
Psidium laruotteanum Cambess.	1, 3, 4	1, 3	41
Psidium myrsinites Mart. ex DC.	1, 2, 3	1, 2, 3	51
Psidium rufum Mart. ex O.Berg	1	1	3
Siphoneugena densiflora (O.Berg) Kausel	4	3	9
Nyctaginaceae			
Guapira graciliflora (Spreng.) Little	3, 4	3	10
Guapira noxia (Vell.) Lundell	1, 2, 4	1, 2, 3	106
Neea theifera (Planch. & Triana) Baill.	3	3	13
Ochnaceae			
Ouratea castaneifolia (Mart. ex DC.) Engl.	2	2	59
Ouratea hexasperma (A.St.Hil.) Baill.	1, 3	1, 3	19
Opiliaceae			
Agonandra brasiliensis Miers	1, 3	1, 3	5
Primulaceae			
Myrsine coriacea (Sw.) R.Br.	1, 2	1, 2	36
Myrsine gardneriana A.DC.	3	1, 2, 3	9
Myrsine guianensis (Aubl.) Kuntze	1, 3	1, 2, 3	72
Myrsine parvifolia Benth.	1	1, 2, 3	5
Myrsine umbellata Mart.	1, 3	2, 3	22
Proteaceae			
Roupala montana Aubl.	1, 2, 3, 4	1, 2, 3	61
Rhamnaceae			
Rhamnidium elaeocarpum (Rich.) DC.	1, 3	1, 2, 3	6
Rubiaceae			

Alibertia edulis (Rich.) A. Rich.	1, 3, 4	1, 2, 3	115
Coussarea hydrangeaefolia Mart.	1, 2	2, 3	3
Faramea hyacinthina DC.	4	3	1
Ferdinandusa elliptica (Poir.) Standl.	3	3	1
Guettarda viburnoides A.St.-Hil.	3, 4	1, 2	12
Palicourea rigida Kunth	1, 2, 3	1, 2, 3	7
Palicourea tetraphylla Cham.	2	2	2
Rudgea viburnoides Cham.	1, 2, 3	1, 2, 3	22
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	3	1, 3	2
Rutaceae			
Zanthoxylum rhoifolium Lam.	1, 3, 4	1, 2, 3	32
Salicaceae			
Casearia sylvestris Sw.	3	1	1
Sapindaceae			
Cupania vernalis Cambess.	1	3	3
Diatenopteryx sorbifolia Radlk.	3	1, 3	5
Dilodendron bipinnatum Radlk.	1, 3	1, 2, 3	10
Magonia pubescens A.St.-Hil.	1, 3, 4	1, 2, 3	35
Matayba guianensis Aubl.	1, 2, 3	1, 2, 3	156
Sapotaceae			
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	1	1, 3	14
Pouteria ramiflora (Mart.) Radlk.	1, 3	1, 3	17
Pouteria torta (Mart.) Radlk.	1, 3	1, 3	2
Simaroubaceae			
Simarouba amara Aubl.	4	2	1
Siparunaceae			
Siparuna guianensis Aubl.	1, 2	1, 2, 3	238
Solanaceae			
Solanum lycocarpum A.St.-Hil.	4	3	7
Styracaceae			
Styrax ferrugineus Nees & Mart.	1	1	12
Ulmaceae			
Plenckia populnea (Jacq.) Radlk.	1, 3	1, 2	2
Urticaceae			
Cecropia pachystachya Trécul	1, 3, 4	1, 3	15
Verbenaceae			
Physocalymma scaberrimum (DC.) Kuhlm.	3, 4	1, 2, 3	18
Vochysiaceae			
Callisthene major (Mart. ex DC.) Baill.	1, 2, 3	1, 2, 3	69
Qualea dichotoma Mart.	2, 3	1, 2	16

***Qualea grandiflora* Mart.**	1, 2, 3, 4	1, 2, 3	359
***Qualea multiflora* Mart.**	1, 3	1, 2, 3	9
***Qualea parviflora* Mart.**	1, 2, 3	1, 2, 3	116
***Vochysia elliptica* Mart.**	1, 3, 4	3	8
***Vochysia rufa* Mart.**	1, 3	1, 3	52
***Vochysia tucanorum* Mart.**	2	1, 2	13

Table S3. Species specific for each vegetation structural clustering, based on the 70% most abundant species.

Species		
Cluster 1	**Cluster 2**	**Cluster 3**
Anadenanthera colubrina	*Callisthene major*	*Aspidosperma macrocarpon*
Anadenanthera peregrina	*Ficus goiana*	*Byrsonima crassifolia*
Campomanesia velutina	*Guapira noxia*	*Byrsonima verbascifolia*
Diospyros lasiocalyx	*Ouratea castaneifolia*	*Caryocar brasiliense*
Guazuma ulmifolia	*Protium altissimum*	*Miconia ferruginata*
Magonia pubescens	*Siparuna guianensis*	*Psidium laruotteanum*
Myrsine guianensis	*Xylopia emarginata*	*Psidium myrsinites*
Physocalymma scaberrimum		*Qualea parviflora*
Piptadenia gonoacantha		*Stryphnodendron adstringens*
Platypodium elegans		*Vochysia rufa*
Tachigali aurea		
Terminalia argentea		
Zanthoxylum rhoifolium		

Table S4. Species specific for each species composition clustering, based on the 70% most abundant species.

Species			
Cluster 1	**Cluster 2**	**Cluster 3**	**Cluster 4**
Campomanesia velutina	*Ficus goiana*	*Acrocomia aculeata*	*Byrsonima pachyphylla*
Matayba guianensis	*Guapira noxia*	*Anadenanthera colubrina*	*Byrsonima verbascifolia*
Myrcia splendens	*Protium altissimum*	*Anadenanthera peregrina*	*Psidium laruotteanum*
Myrsine guianensis	*Siparuna guianensis*	*Apeiba tibourbou*	*Salvertia convallariodora*
		Aspidosperma macrocarpon	*Stryphnodendron pulcherrimum*
		Astronium fraxinifolium	
		Bowdichia virgilioides	
		Byrsonima crassifolia	
		Caryocar brasiliense	
		Connarus suberosus	
		Didymopanax macrocarpus	
		Dimorphandra mollis	
		Diospyros lasiocalyx	
		Enterolobium gummiferum	
		Erythroxylum deciduum	
		Guazuma ulmifolia	
		Leptolobium dasycarpum	
		Miconia ferruginata	
		Piptocarpha rotundifolia	
		Plathymenia reticulata	
		Platypodium elegans	
		Psidium myrsinites	
		Qualea parviflora	
		Stryphnodendron adstringens	
		Tachigali vulgaris	
		Terminalia argentea	
		Vochysia rufa	

Table S5. Percentage of species shared by each species composition clustering.

Clusters	**% of species shared**
1	13,24
2	8,33
3	20,10
4	7,35
1, 2	2,94
1, 2, 3	14,22
1, 2, 3, 4	3,43
1, 2, 4	0,49
1, 3	14,22
1, 3, 4	6,37
1, 4	1,47
2, 3	1,96
2, 3, 4	0,98
3, 4	4,90

Table S6. Dunn test for structural vegetation and tree individual density measurements by vegetation structural clusters.

Structural measurements	Clusters	z-test Statistic	p-value	Kruskal-Wallis chi-squared	Kruskal-Wallis p-value
Maximum height (m)	1 vs 2	-3.699781	0.0006 *	137.5876	2.2E-16
	1 vs 3	7.539013	0.0000 *		
	2 vs 3	10.936260	0.0000 *		
Mean Height (m)	1 vs 2	-4.177723	0.0001 *	124.3038	2.20E-16
	1 vs 3	6.612179	0.0000 *		
	2 vs 3	10.628730	0.0000 *		
Stand basal area (m^2/ha)	1 vs 2	-3.948305	0.0002 *	53.1348	2.90E-12
	1 vs 3	3.147914	0.0049 *		
	2 vs 3	7.238300	0.0000 *		
Stand basal area < 10 cm (m^2/ha)	1 vs 2	-3.994989	0.0002 *	52.7639	3.49E-12
	1 vs 3	3.071642	0.0064 *		
	2 vs 3	7.221166	0.0000 *		
Stand basal area ≥ 10 cm (m^2/ha)	1 vs 2	-1.590390	0.3352	15.9942	0.0003364
	1 vs 3	2.290963	0.0659		
	2 vs 3	3.841472	0.0004 *		
Tree Individual Density (n/ha)	1 vs 2	-2.329223	0.0595	23.9438	0.0000
	1 vs 3	2.443391	0.0436 *		
	2 vs 3	4.800770	0.0000 *		

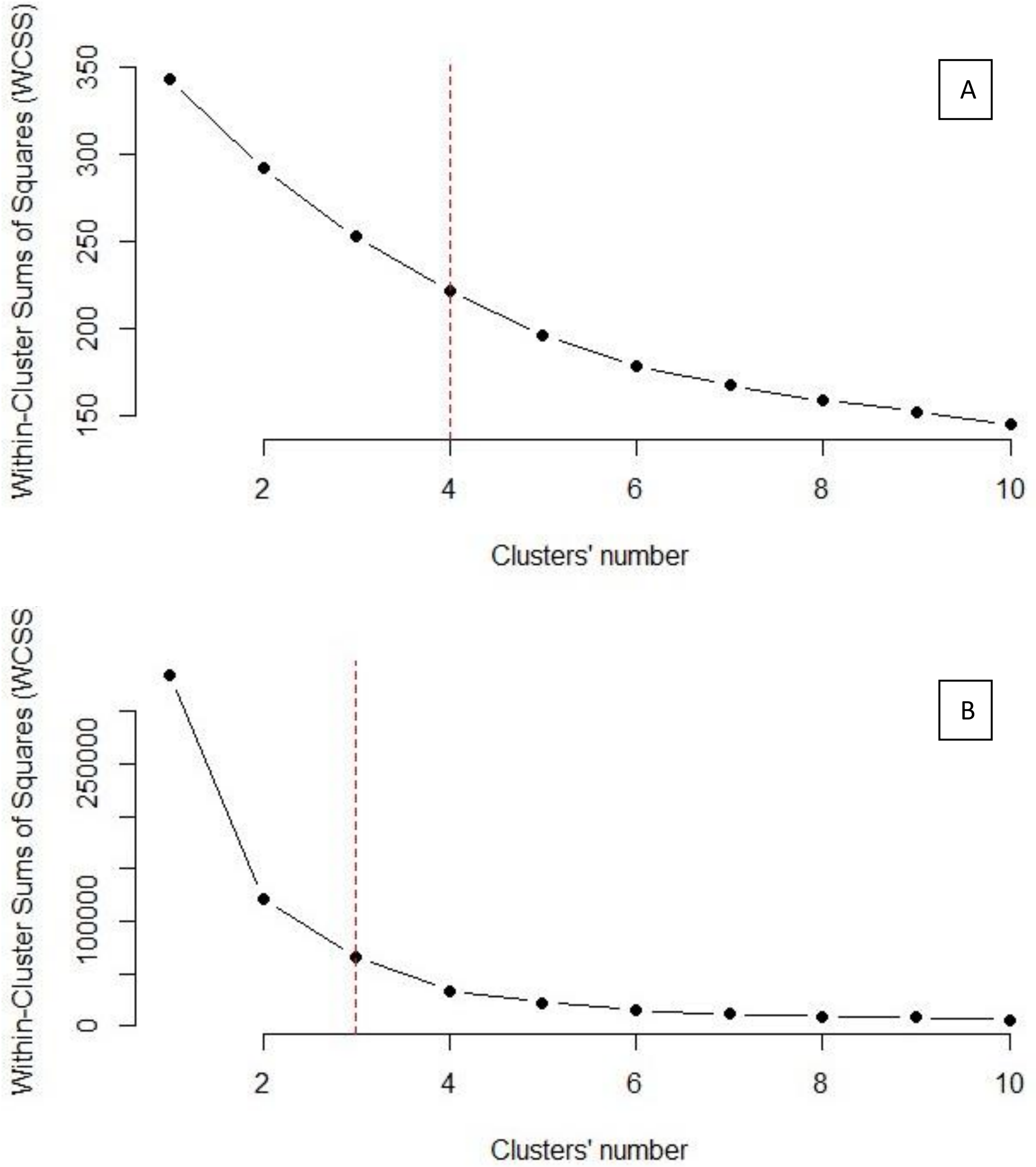

Figure S1. Elbow method analysis to choose the cluster’s number. The chart A represents the species composition, while B represents vegetation structure.

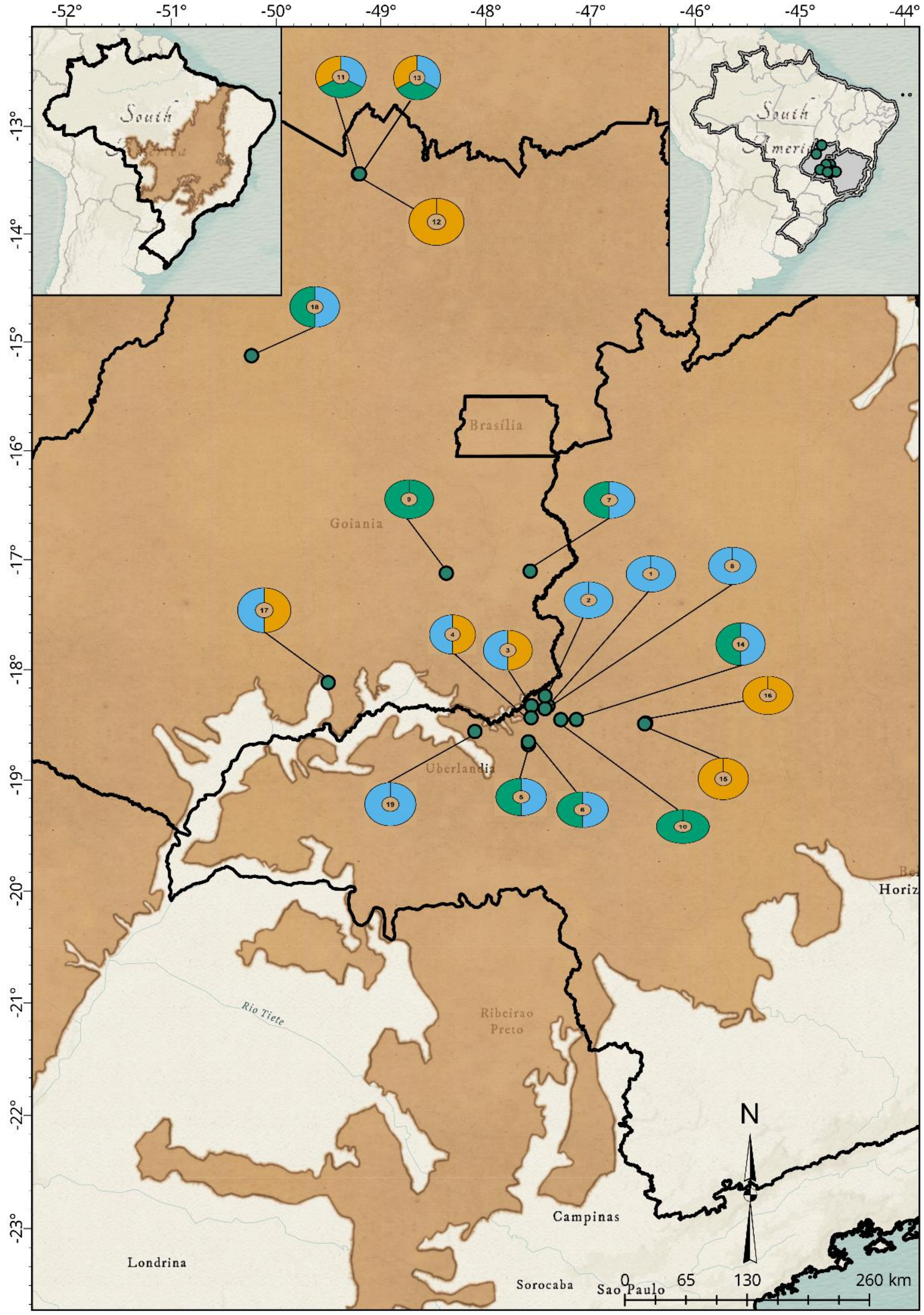

Figure S2. Map of the studied areas in the *Cerrado*. The green points indicate the study locations. The *Cerrado* biome domain is highlighted in light brown. The two areas outlined in black the Brazilian states of Goiás, in the top left, and Minas Gerais, in the bottom right. The circles in the map represents the vegetation structure clusters, whereas Blue: Cluster 1, Orange: Cluster 2, Green: Cluster 3.

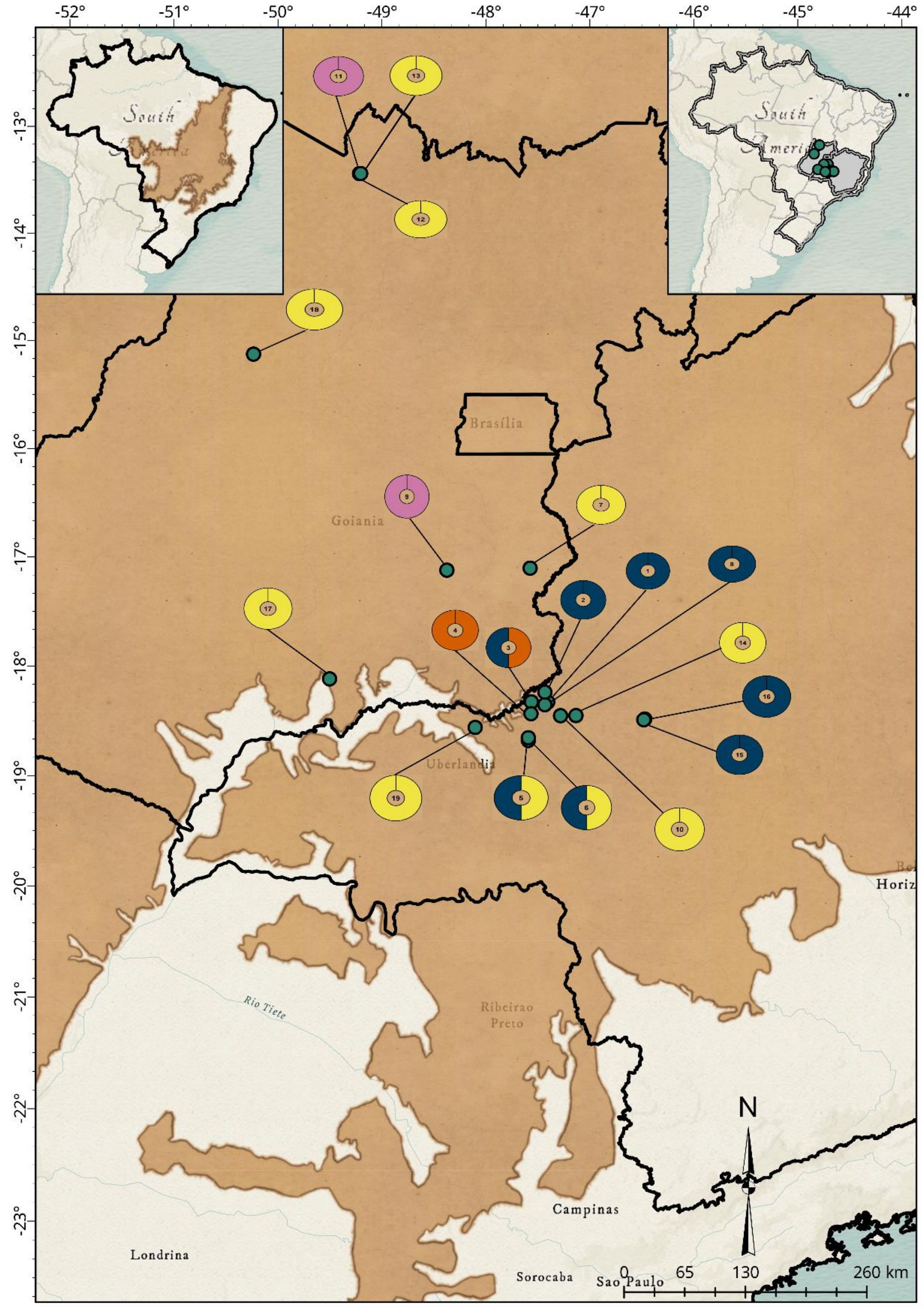

Figure S3. Map of the studied areas in the *Cerrado*. The green points indicate the study locations. The *Cerrado* biome domain is highlighted in light brown. The two areas outlined in black the Brazilian states of Goiás, in the top left, and Minas Gerais, in the bottom right. The circles in the map represents the species composition cluster, whereas, Blue: Cluster 1, Orange: Cluster 2, Yellow: Cluster 3, Pink: Cluster 4.

3. Chapter 2 - Taxonomic and phylogenetic diversity, along with functional dominance drive aboveground carbon stock in the Brazilian Cerrado

3.1. Abstract

Carbon storage is a crucial ecosystem function supporting climate change mitigation, which varies across ecosystems and vegetation types. Despite recent studies showing that biodiversity can drive tree aboveground carbon stocks, we still have limited knowledge on the importance of different components of biodiversity (e.g. species richness, phylogenetic diversity or the traits of dominant species) for carbon storage in different vegetation types within the Brazilian savanna (Cerrado). Using surveys on woody species from 167 plots in Brazilian Cerrado, this study addressed three questions: 1) What is the difference in taxonomic diversity and carbon storage among the different vegetation types in the *Cerrado*? 2 Which is the most influential factor in driving AGC across the different vegetation types in the Cerrado: taxonomic diversity, functional diversity, phylogenetic diversity, or the community-weighted mean of functional traits? 3) Do relationships between diversity, functional traits, and AGC differ among the different vegetation types in the *Cerrado*? Our results showed that vegetation with taller trees present the lowest species richness and highest tree dominance. Besides, there was a distinct biodiversity-AGC relationships among the different Cerrado vegetation types: in *Cerrado stricto sensu Típico* (the vegetation type with lowest density), species richness was one of the drivers of AGC, with a higher species richness associated to a high AGC, while, phylogenetic diversity was negatively related to AGC. In *Cerrado stricto sensu Denso* (the vegetation type with intermediate density), species richness was also positively related to AGC. In *Cerradão* (the most taller and dense vegetation type), communities dominated by tree species with a low wood density had highest AGC. These findings suggest that niche complementarity among species explains aboveground carbon stock-diversity relationships in lower-structure vegetation, while the dominance of species with particular traits is most important in driving AGC in taller vegetation.

Keywords: Biodiversity, ecosystem functioning, tree biomass, functional traits, savanna.

3.2. Introduction

Carbon storage is a crucial ecosystem function supporting climate change mitigation and biodiversity recovery, that can vary depending on the ecosystem and vegetation type (Bustamante et al. 2016; Salete Capellesso et al. 2021; Hilmi et al. 2021; Zhou et al. 2022). Tropical ecosystems are one of the biggest carbon reservoirs. These ecosystems sequester substantial amounts of carbon, primarily within the soil. Additionally, they store significant quantities of carbon in both the aboveground biomass (such as trunks, branches, and leaves) and the belowground biomass (Silveira et al. 2019; Zhou et al. 2022). However, their capacity to store carbon can be hampered by deforestation and degradation (Mitchard 2018). Conservation and restoration activities can help in maintaining or recovering the species richness (Rozendaal et al. 2019). However, there is an open debate if this also increases carbon sequestration. Various studies have investigated the role of biodiversity in driving aboveground carbon stocks (AGC) in recent years (van der Plas 2019), and some of these studies have demonstrated positive relationships, in some cases driven by resource partitioning (i.e. different coexisting species using different resources in the same environment) and niche complementarity, where species differences in resource use, phenology, or functional traits enhance overall ecosystem functioning. (Loreau and Hector 2001; Cardinale et al. 2007; van der Plas 2019). However, most of these studies have been carried out in tropical rainforests. In contrast, relationships between biodiversity and AGC are comparatively understudied in savannas (van der Plas 2019; but see Carvalho et al. 2014; Loiola et al. 2015; Pellegrini et al. 2016). In the few studies carried out so far in the vegetational mosaic of the Brazilian *Cerrado*, both positive and negative relationships have been observed between diversity and AGC (Pellegrini et al. 2016; Morandi et al. 2020; Righi et al. 2023). A potential explanation for these seemingly contrasting results, is that within the Brazilian *Cerrado*, which encompasses different vegetation types with different vegetation structures, different diversity components have different effects on AGC (Zhou et al. 2022; Zhai et al. 2024).

While most studies that investigate the role of biodiversity in driving AGC have focused on taxonomic measures of biodiversity (most often species richness), functional and phylogenetic diversity may be even more important in driving ecosystem functioning (Tilman et al. 1997; Cadotte et al. 2008; van der Plas 2019). Functional diversity indices quantify the variation in morphophysiological characteristics among co-occurring species (Magnago et al., 2014; Villéger et al., 2008), while phylogenetic diversity quantifies to which extent co-occurring species on average have a recent (low phylogenetic diversity) or distant (high phylogenetic diversity) common ancestor (Cadotte et al. 2010). The potential effects of biodiversity on ecosystem functioning could be explained by different theories. First, when different species specialize in different resources, higher species diversity can enhance biomass production through resource partitioning (Tilman 2001; Tilman et al. 2014), driven by the functional traits of species within the community (i.e., morphological, phenological, or physiological characteristics). The relationship between species and resource utilization can also be influenced by the evolutionary history of the species in the community, as closely related species are expected to use similar resources, while more distantly related species may facilitate better resource partitioning (Cadotte et al. 2009; Hao et al. 2018). In contrast to this phylogenetic perspective, the mass ratio theory posits that ecosystem functioning is primarily driven by the functional traits of the dominant species in the area (Grime 1998), meaning that a few species with a higher number of individuals or greater biomass per unit area exert the strongest influence.

The Brazilian *Cerrado* features a range of vegetation types, from treeless areas to forests, and the differences among them are attributed to species composition and vegetation structure (Ribeiro and Walter 2008, Da Cruz Silva et al. unpublished). The tree height and stand basal area, increase from savanna-like to forest-like vegetation: *Cerrado stricto sensu Típico, Cerrado stricto sensu Denso* and *Cerradão*, respectively. Thus, with this study, we aim to find out how different diversity indexes (taxonomic, functional, phylogenetic diversity indicators, and trait diversity) drive carbon storage within different Cerrado subtypes. Specifically, we aim to address three fundamental questions: 1) What is the difference in taxonomic diversity and carbon storage among the different vegetation types in the *Cerrado*? 2) Which is the most influential factor in driving AGC across the different vegetation types in the Cerrado: taxonomic diversity, functional diversity, phylogenetic diversity, or the community-weighted mean of functional traits? 3) Do relationships between diversity, functional traits, and AGC differ among the different vegetation types in the *Cerrado*? We hypothesize that: i) taxonomic diversity and AGC follow the same pattern as the vegetation structure in the Cerrado, with higher levels in the taller vegetation types; and ii) the relationship between AGC and its drivers varies across vegetation types, primarily influenced by vegetation structure, which taller and denser vegetation exhibits a distinct pattern compared to other types.

3.3. Material and Methods

Study area

The study area in the Cerrado exhibits the typical seasonality of the Brazilian savanna climate, classified as type AW in the Köppen climate system. Data were collected from a survey of 19 tree communities in the Cerrado biome, with 12 located in Minas Gerais (MG) and 7 in Goiás (GO), Brazil. (Fig. 1. For details see Júnior et al. (2021)). The areas were chosen based on different tree structures, varying from smaller to taller trees inside the areas, representing open to closed Cerrado vegetation. For the analysis we made use of three *Cerrado* different vegetation types: *Cerrado s.s. Típico*, *Cerrado s.s. Denso* and *Cerradão* (details on Da Cruz Silva et. al. 2024). The plots' area within the vegetation types ranged from 100 m^2 to 500 m^2, totalizing 167 plots. Tree height and tree diameter were measured of all living individuals with a diameter at breast height (DBH) $\geq$ 5 cm, and each tree was identified down to the species level. A metric tape was used to measure the DBH, and the heights of the trees were compared using the tallest ones as a reference, employing a 5.5-meter tree pole pruner.

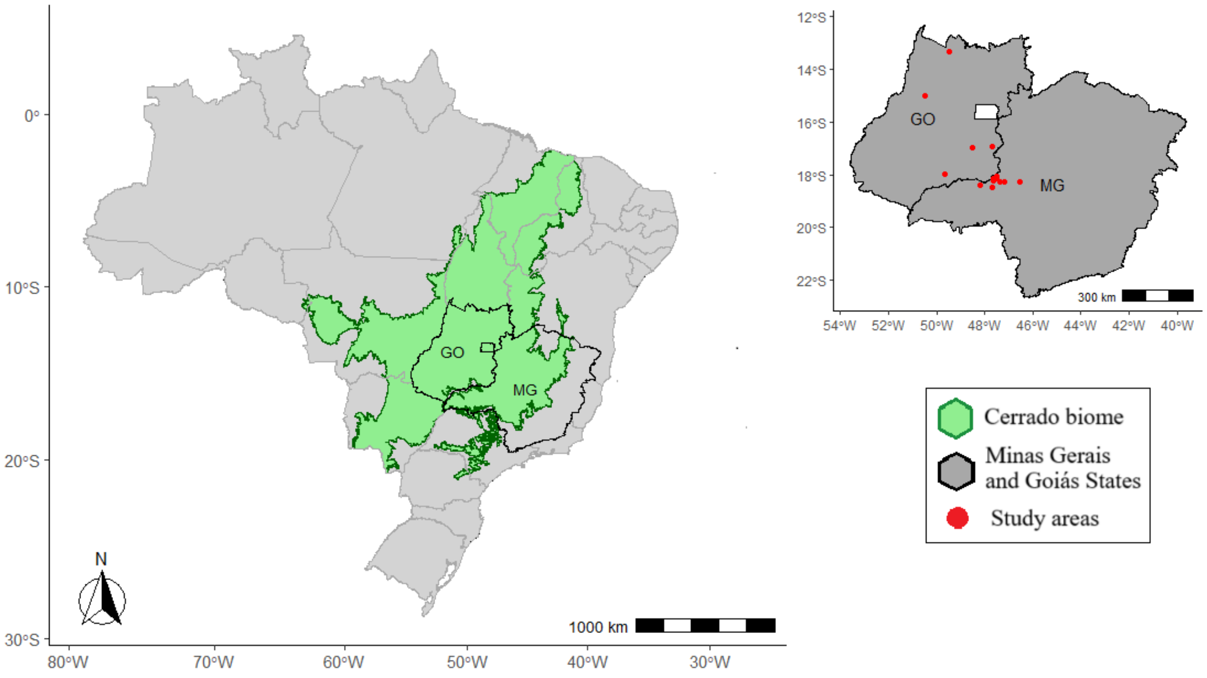

Figure 1. Brazil with Cerrado biome in green and the studied areas location represented by the red dots. GO = Goiás State, MG = Minas Gerais State, Brazil.

Taxonomic diversity

To analyze the tree diversity differences between *Cerrado s.s. Típico*, *Cerrado s.s. Denso* and *Cerradão*, we performed an individual-based rarefaction and extrapolation method. The method allows comparing diversity indices between communities when the sample size, sample efforts, or the number of individuals are not equal. We developed curves that represent the observed number of tree individuals with a confidence interval (0.95) based on 300 replicate bootstrapping runs. Extrapolations were made based on the double of tree individuals of each vegetation type, which in *Cerrado s.s. Típico* is 2,658, in *Cerrado s.s. Denso* it is 2,175 and in Cerradão it is 2,622 tree individuals. We used the first three Hill's numbers (Colwell et al. 2012; Chao et al. 2014): species richness (q = 0), the Shannon index (q = 1), and Simpson index (Order q = 2), and whenever the 95% confidence intervals did not overlap, diversity indexes did not differ significantly at $p < 0.05$ (Colwell et al. 2012). The Shannon index (q = 1) considers the species richness and abundance, showing higher values when the species are equally distributed in the community, and thus can be considered as the effective number of common species in the community (Hsieh et al. 2016). The Simpson index (Order q = 2) is more weighted by rare species, showing higher values in communities with lower dominance. The analysis was done using the 'iNEXT' package (Hsieh et al. 2016) in R software.

Tree aboveground carbon stock

We calculated the carbon (C) stock for each plot, summing up the values of each tree and quantifying based on the C stock per hectare. To estimate C stock of individual trees based on DBH and height measurements, we used allometric equations (Scolforo et al., 2008) for Cerrado vegetation types. For *Cerrado s.s. Típico and Cerrado s.s. Denso* we used Equation 1, and for Cerradão we used Equation 2:

1. Equation for *Cerrado s.s. Típico* and *Cerrado s.s. Denso*

$$Ln(C) = -11.13 + 2.38 * Ln(DBH) + 0.61 * Ln(H)$$

2. Equation for *Cerradão*

$$Ln(C) = -10.88 + 2.64 * Ln(DBH) + 0.09 * Ln(H)$$

Where C = aboveground carbon stock in Mg/ha; DBH = diameter at breast height in cm and H = height in meters.

To test the differences in tree aboveground carbon stock between the vegetation types, we performed a Kruskal Wallis and Dunn test in R.

Functional trait data

We used the following functional traits: wood density, length and width of the leaf, fruit, and seed of each tree species. We used these traits to cover different ecological aspects: dispersal and colonization potential through seed and fruit traits, stress tolerance through wood density, and resource acquisition through leaf traits. We accessed wood density through the Global Wood Density Database, virtual herbaria, and literature (Lorenzi 1992, 2000, 2009, Zanne et al. 2009). The other functional traits, i.e. length and width of the leaf, fruit, and seed were measured using plant images of *Reflora* virtual herbaria (Reflora, 2023), and the ImageJ software (Schneider et al. 2012). In each exsiccate image there was a scale, which was used to calibrate the ImageJ ruler, transforming the pixel values in centimeters. After the ruler calibration, we used it to measure the length and width of five leaves, fruits, and seeds of five repetitions per species, following standardized protocols proposed by Pérez-Harguindeguy et al. (2013).

Functional Diversity

Based on the functional traits described above, we calculated three indexes of functional diversity: functional richness (FRic); functional evenness (FEve); and functional dispersion (FDis), where FRic represents the amount of functional space filled by the community, while FEve quantifies the regularity by which the functional space is filled by species, weighting their abundances (Villéger et al. 2008). Low values of FRic and FEve can indicate the performance of environmental filters reducing the richness of features in the community and the abundance of these traits, respectively (Mouchet et al. 2010; Mason et al. 2013). FDis refers to the average distance of a species in the multidimensional functional space to the centroid of all species (Laliberte and Legendre 2010). FDis is recommended to assess patterns of divergence and convergence of traits, and low values also can indicate the presence of environmental filters (Ricotta and Moretti 2011; Ribeiro et al. 2019). All functional diversity indices were calculated using the “FD” package (Laliberte and Legendre 2010) from R software (R Core Team 2022).

Additionally, we calculated the community weighted mean (CWM) of the traits weighting by the species abundance in the community of each plot, using the packages “tidyr” and “dplyr” of R software.

Phylogenetic Diversity

For phylogenetic diversity we used six indices: phylogenetic diversity (PD), mean phylogenetic distance (MPD), mean nearest taxon distance (MNTD) based on abundance, and their standardized size effects, sesPD, sesMPD and sesMNTD, respectively. The PD is the sum of the branches connecting all species in the community, and it is the most used metric in phylogenetic studies (Faith 1992). The MPD quantifies the mean distance of the kinship between pairs of species, considering species of different families (Webb et al. 2002). MNTD quantifies the mean value of the distance to the rearrest neighbor, weighting the relationship at the end branches of the phylogeny (Webb et al. 2002). These measurements are complementary to each other, since they focus on different dimensions of the evolutionary history in the community. Additionally, in order to reduce the effect of species richness, the standardized effect size was calculated based on 999 null model randomizations of the community matrix by selecting species from a species pool occurring in the phylogeny with equal probability, using the algorithm "*phylogeny pool*". All woody individuals identified at the species, genus, or family level were considered for the construction of the phylogeny. The phylogenetic tree was built by cutting the megatree R20120829mod.new (Gastauer and Meira-Neto 2016) for all sampled woody species. These metrics were calculated using functions PD, MPD, MNTD, sesPD, sesMPD and sesMNTD from the "picante" package in R software version 3.2.1 (R Core Team, 2022).

Relationship between diversity and aboveground carbon stock

Initially, a Mantel statistic test was conducted to assess the need for a model using the areas as random effects using "mantel" function, "vegan" package (R Core Team 2019). Based on the Mantel test result, it was necessary to consider area as a random effect, thus we designed a Linear Mixed Model (LMM) to investigate the relationship between tree aboveground carbon stock, diversity components, and the community weighted mean of the functional traits for each vegetation type (Table 1). In this test, "lmer" function in the "lme4" package in R was used. Due to different units of measurements, we Z-scaled all the predictors to a mean equal to zero and a standard deviation of one. Besides, multicollinearity of the model was tested using the "vif" function in the "car" package in R, leading to the exclusion of variables exhibiting VIF values higher than five (James et al. 2022). After excluding the variables with multicollinearity, we used the "dredge" function in the "MuMIn" package of R, to perform model averaging the models (Grueber et al. 2011) (Table 1), and selecting the best model, based on AIC.

Table 1. Response variable, predictors, and random effect of the Linear Mixed Model of each Cerrado vegetation type. F. richness = Functional richness, F. Evenness = Functional Evenness, F. Divergence = Functional Divergence; ses = standardized effect size, PD = Phylogenetic Diversity, MPD = Mean pairwise distance, MNTD = Mean near taxon distance; CWM = community weighted mean, WD = wood density.

Variables	**Cerrado Vegetation Types**		
	Tipico	**Denso**	**Cerradão**
Response	Aboveground Carbon Stock	Aboveground Carbon Stock	Aboveground Carbon Stock

Predictors	**Taxonomic**	Species Richness	Species Richness	Simpson index
	Functional	FRic FEve FDiv	FRic FEve FDiv	FRic Feve FDiv
	Phylogenetic	MPD ses.PD ses.MPD	MPD ses.PD ses.MNTD	ses.PD ses.MPD ses.MNTD
	CWM Traits	CWM WD CWM fruit length CWM fruit width CWM seed length CWM leaf length	CWM WD CWM fruit length CWM fruit width CWM seed width CWM leaf length	CWM WD CWM fruit width CWM leaf length

3.4. Results

Taxonomic diversity

Based on the rarefaction analyses, the species richness across plots of *Cerrado s.s. Típico* was 140 (± 10.96), in *Cerrado s.s. Denso* it was 146 (± 14.25), and in *Cerradão* it was 124 (± 15.78) (Table 2), and according to the observed values (comparation between vegetation types standardized by the smallest number of individuals) of the rarefaction analysis (Fig. 2), there was non-significant difference between *Cerrado s.s. Típico* and *Cerrado s.s. Denso*, however, were significant higher than *Cerradão*. Nevertheless, when extrapolated to the double number of tree individuals of each vegetation type (*Cerrado s.s. Típico*: 2212 individuals, *Cerrado s.s. Denso*: 2621 individuals, *Cerradão*: 2622 individuals) there was no difference between the vegetation types (Fig. 2).

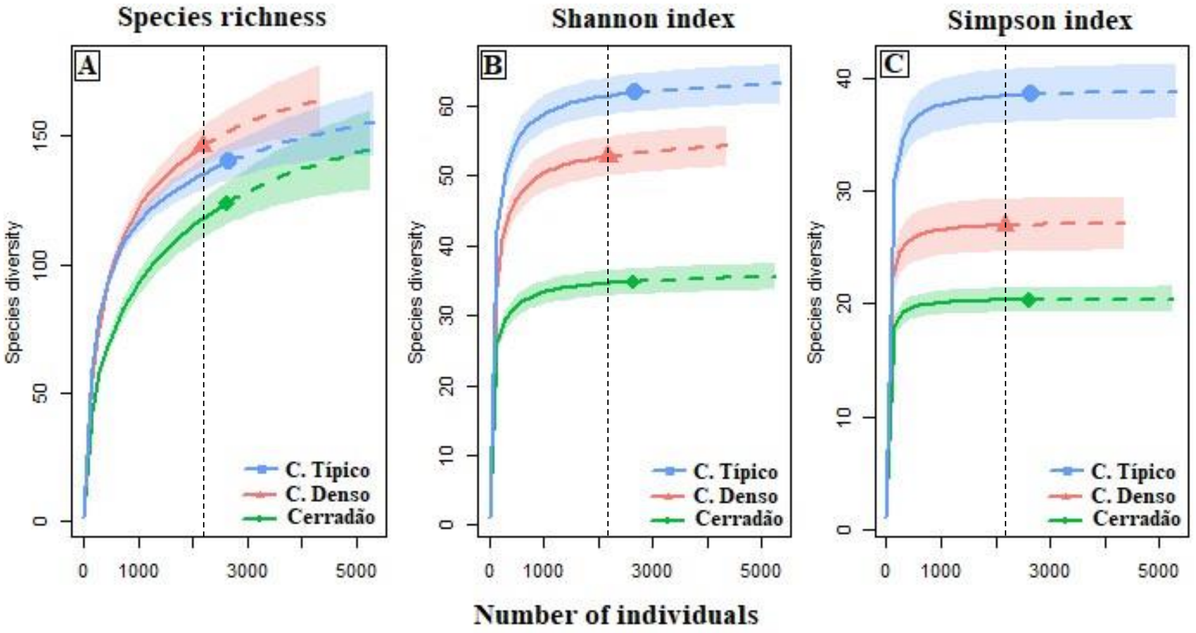

Figure 2. Rarefaction (solid line) and extrapolation (dashed line) curves based on the number of individuals for three Cerrado vegetation types. The shade in the curves represent the 95% of interval confidence, and where there is an overlap means that there are no statistical differences between the curves. C. Típico: *Cerrado s.s. Típico*, C. Denso: *Cerrado s.s. Denso*.

For the rarefied Shannon index (Hill's number q=1), considering the observed and extrapolated value, there was a difference between vegetation types across plots, with *Cerrado s.s. Típico* having a value of 61.37 (± 1.38), which was higher than in the *Cerrado s.s. Denso* 52.81 (± 1.51) and *Cerradão* 34.87 (± 1.04), respectively. Finally, the Simpson index (Hill's number q=2) showed the same pattern as Shannon, which in *Cerrado s.s. Típico* was 39.07 (± 1.28), and therefore higher than in *Cerrado s.s. Denso*, where it was 27.27 (± 1.23) and also higher than in *Cerradão*, where it was 20.35 (± 0.63).

Table 2. Result of rarefaction analyses, based on the three Cerrado's vegetation types and species richness, Shannon index, and Simpson index.

Vegetation Type	**Diversity indexes**	**Observed values**	**Estimator**	**Standard error**	**Lower Confidence Limit**	**Upper Confidence Limit**
Cerrado s.s. Típico	Species richness	140,00	163,99	10,96	142,51	185,47
Cerrado s.s. Denso	Species richness	146,00	174,11	14,25	146,18	202,04
Cerradão	Species richness	124,00	156,02	15,78	125,08	186,95
Cerrado s.s. Típico	Shannon	61,87	63,93	1,38	61,23	66,63
Cerrado s.s. Denso	Shannon	52,81	55,14	1,51	52,18	58,10

Cerradão	Shannon	34,87	36,01	1,04	33,98	38,05
Cerrado s.s. Típico	Simpson	38,52	39,07	1,28	36,57	41,58
Cerrado s.s. Denso	Simpson	26,95	27,27	1,23	24,87	29,68
Cerradão	Simpson	20,35	20,50	0,63	19,27	21,73

Tree aboveground carbon stock

The tree aboveground carbon stock varied between the vegetation types (Table 3, Fig. 3, p-value: 9,368E-16). It was highest in *Cerradão*, intermediate in *Cerrado s.s. Denso*, and lowest in *Cerrado s.s. Típico*. In the *Cerradão*, the tree aboveground carbon stock ranged from 9 Mg/ha to 74 Mg/ha (mean 33.3 ± 16.9), in the *Cerrado s.s. Denso* from 3 Mg/ha to 114 Mg/ha (mean 15.1 ± 19.0), and in *Cerrado s.s. Típico* from 1 Mg/ha to 23 Mg/ha (6.96 ± 5.28) (Fig.3).

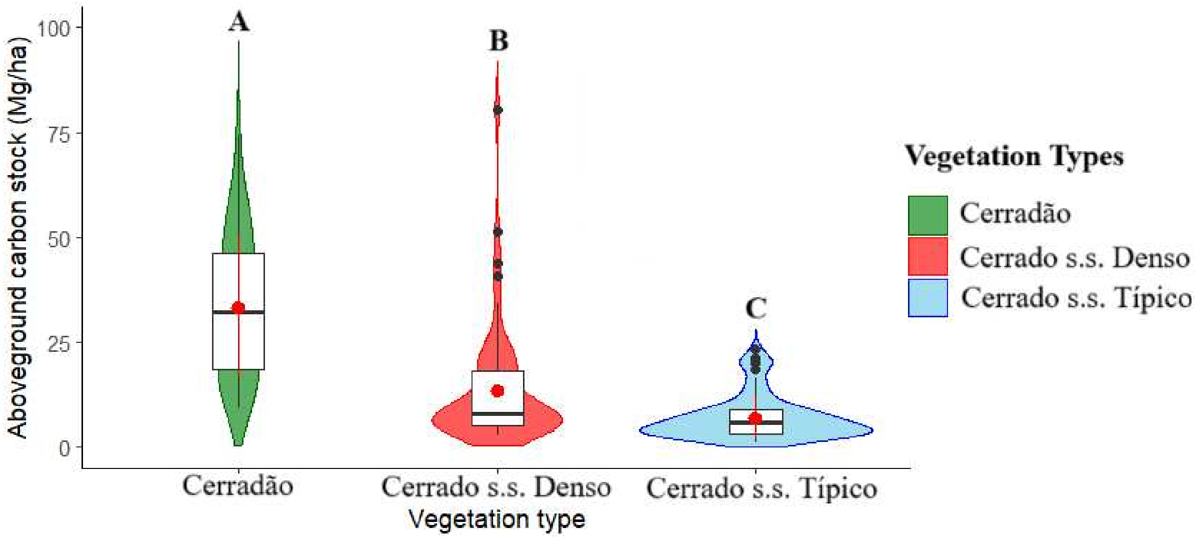

Figure 3. Boxplot analysis of Cerrado's tree aboveground carbon stock of three different vegetation types. Different letters represent statistically significant differences between groups. The red dot represents the means. The abbreviation "s.s." means stricto sensu.

Table 3. Results of Kruskal-Wallis and Dunn test of Cerrado's tree aboveground carbon stock by three different vegetation types.

Measurement	Vegetation type	z-test Statistic	p-value	Kruskal-Wallis chi-squared	Kruskal-Wallis p-value
Tree aboveground carbon stock	1 vs 2	5,086684	0.0000*	69,151	9,368E-16
	1 vs 3	3,553976	0.0002*		
	2 vs 3	8,304842	0.0000*		

Relationship between diversity and tree aboveground carbon stock

Relationships between tree diversity and tree aboveground carbon stocks varied among vegetation types. In *Cerrado s.s. Típico*, species richness (taxonomic diversity, p-value <2e-16) was significantly positively related to aboveground carbon stock, while MPD was significantly negatively related (phylogenetic diversity, p-value = 0.0142). In *Cerrado s.s. Denso*, only species richness was significantly and positively related to aboveground carbon stock (taxonomic diversity, p-value = 0.023). Last, in *Cerradão*, the CWM of wood density was significantly and negatively related to the aboveground carbon stock (functional trait, p-value = 5.7e-6) (Table 5, Fig. 4).

Table 5. Linear mixed models results by Cerrado vegetation types and the significant variables for each model. MPD = Mean Pairwise Distance, CWM WD = Community Weighted Mean of Wood Density

Variables	**Vegetation types**				
			Cerrado s.s. Típico		
	Estimate	**Std. Error**	**Adjusted SE**	**Z value**	**Pr(>|z|)**
Intercept	2.673.918	0.151547	0.153902	17.374	< 2E-16
Species richness	0.590674	0.096971	0.098278	6.010	< 2E-16
MPD	-0.206253	0.063772	0.064662	3.190	0.00142
			Cerrado s.s. Denso		
	Estimate	**Std. Error**	**Adjusted SE**	**Z value**	**Pr(>|z|)**
Intercept	2.995.987	0.261376	0.268907	11.141	<2e-16
Species richness	0.475481	0.205907	0.209129	2.274	0.023
			Cerradão		
	Estimate	**Std. Error**	**Adjusted SE**	**Z value**	**Pr(>|z|)**
Intercept	392.154	0.09749	0.10144	38.657	2,00E-16
CWM WD	-0.52594	0.11170	0.11593	4.537	5.7e-06

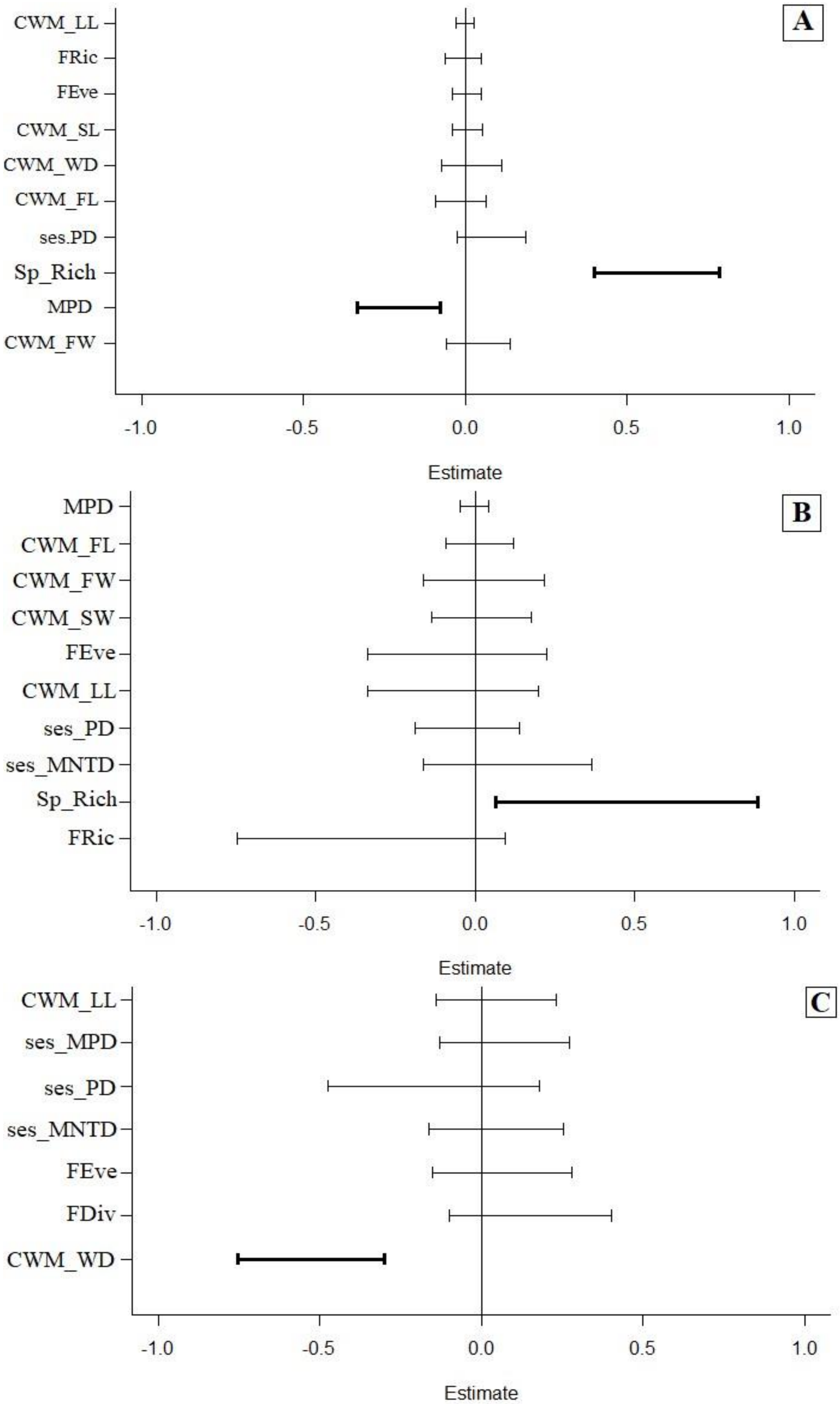

Figure 4. Result of the model averaging of the Linear Mixed Model between *Cerrado* tree aboveground carbon stock, diversity metrics and functional traits community weighted. CWM: community weighted mean, LL: Leaf Length, FRic: Functional Richness, FEve: Functional Evenness, SL: Seed Length, WD: Wood density, FL: fruit length, ses: standard effect size, PD: Phylogenetic Diversity, Sp_Rich: Species richness, MPD: Mean Pairwise Distance, FW: Fruit Width, SW: Seed Width, MNTD: Mean Near Taxon Distance, FDiv: Functional Divergence. A: Cerrado s.s. Típico, B: Cerrado s.s. Denso, C: Cerradão

3.5. Discussion

The different vegetation types of the Cerrado exhibit distinct patterns in diversity, tree species dominance, and aboveground carbon stock (AGC). *Cerradão* has the lowest tree species richness but the highest tree dominance and AGC values compared to *Cerrado s.s. Típico* and *Cerrado s.s. Denso*. Moreover, the relationship between functional dominance, diversity, and AGC varies across these vegetation types. In *Cerradão*, AGC is primarily influenced by the traits of dominant species, aligning with the mass ratio theory (Grime 1998). In contrast, in *Cerrado s.s. Típico* and *Cerrado s.s. Denso*, species richness is positively associated with AGC, supporting the niche complementarity theory (Tilman et al. 2014b).

Based on the observed values of species richness in the rarefaction curves, we found similarly to Batalha et al. (2001), that *Cerrado s.s. Típico* (but in our case, also *Cerrado s.s. Denso*) showed higher values of species richness than *Cerradão*. However, when the curves were extrapolated this difference between the vegetation types disappears, emphasizing the importance of scale in species richness studies in the Cerrado biome. Their study attributed the lack of difference between species richness to both the recruitment of new species and a reduction in mortality observed over a 5-year period among species within the *Cerrado s.s. Típico*. Da Cruz Silva et al. (unpublished) found a small difference in species composition between the three vegetation types, meaning that the strong overlap in species composition also reflected in similar values of species richness. Although there are specific species occurring in each vegetation type, the number of species is approximately the same. The other two parameters in the Hill's number (Shannon and Simpson) showed a higher tree dominance in the *Cerradão* (taller vegetation) compared to the others, similar to Abreu et al. (2017). Due to the change in the edaphic conditions from *Cerrado s.s. Típico* to *Cerradão* (i.e. higher soil fertility, higher soil water content, low aluminum content), in the *Cerradão* the trees can grow taller and faster (Ratter et al. 2003), presenting higher stand basal area (Da Cruz Silva et al., 2024). Hence, the condition created by these trees negatively influence the trees adapted to savanna environments. This pattern is also confirmed with the regression analysis, since the carbon stock was more influenced by the traits of the dominant species in the *Cerradão*.

Our finding that *Cerradão* had the highest carbon stock was expected, as previous studies have shown that in *Cerradão* trees are on average taller and have a higher total stand basal area compared to the other vegetation types (Da Cruz Silva et. al., unpublished), showing a close relationship between structure and tree aboveground biomass along this structural gradient (De

Castro and Kauffman 1998). Studies not distinguishing between different vegetation types report values around 20 Mg/ha of tree aboveground carbon stock in Cerrado (Grace et al. 2006; Bainard et al. 2011; Terra et al. 2023), similar to the range of values that we observed, which were 7, 15, and 33 Mg/ha for *Cerrado s.s. Típico, Cerrado s.s. Denso* and *Cerradão*, respectively. *Cerrado* stores high vales of carbon in the belowground part, so if we would have accounted for tree belowground carbon stock and the carbon of herbaceous-shrub vegetation, the results would likely have differed, if considered all the carbon content in the system (Zhou et al. 2022; de Oliveira et al. 2019; Terra et al. 2023). The belowground carbon stock correspond to a proportion of the total carbon stock, however, the root to shoot ratio is higher in shorter vegetation compared to taller vegetation structures (Zhou et al. 2022). Hence, in order to disentangle how biodiversity drives carbon storage accurately, it is important that future studies consider the whole carbon stocks in the system, from grasses, herbs, and trees.

Our result about the relationship between AGC, diversity and functional traits, contradicts Morandi et al. (2020), who found a negative relationship between species richness and AGC of woody plants in *Cerrado*. In their study they just considered *Cerrado stricto sensu*, while we split in different vegetation types, which could explain these differences in findings. *Cerrado s.s. Típico* also presented a negative relationship between tree AGC and MPD Our results showed that both environmental filtering and biotic interactions (e.g. competition, attack by specialist herbivores or pathogens) structure the plant community. Hence, the negative relationship between AGC and MPD found in the *Cerrado s.s. Típico*, means that the AGC is primarily driven by the presence of high species richness of related tree species. Despite the results found, there are abiotic factors that were not addressed to our study that can also influence the carbon storage in the natural systems, such as the soil fertility (Pastor et al. 1984; Coelho et al. 2024).

In the *Cerradão*, there was a different result from the other vegetation types, which the community weighted mean of wood density was negatively related to AGC, meaning that following from the lowest to highest vegetation structure, the niche complementary hypothesis is less important to the community assembly in the *Cerradão* ("forest-like" vegetation), and the traits of the dominant species are the main drivers of the ecosystem functioning (Grime 1998). Although the differences in species composition between vegetation types were low (Da Cruz Silva et al., 2024) the specific species for each vegetation type probably are influencing the ecosystem functioning in the areas. As showed by Maracahipes et al. (2018) the species present different strategies to deal with contrasting environments, thus, forest species have acquisitive traits, with higher competitive ability, fast resource acquisition to deal with light-limited environments, since soil nutrients and soil water availability are not limiting resources. Contrasting, savanna species present conservative strategies, to deal with disturbance effects, such as fire, drought and low soil fertility. The *Cerradão* vegetation tend to suffer less stress and disturbance compared to *Cerrado s.s. Denso* and *Cerrado s.s. TípicoCerrado s.s. Típico*, respectively (Ratter et al. 2003). Thus, it is supposed that the *Cerradão* characteristics are contributing to the establishment of trees with acquisitive characteristics, such as lower wood density.

3.6. Conclusion

Within *Cerrado* vegetation types there is a positive relationship between vegetation structure, tree species dominance and tree aboveground biomass, where taller vegetation types present a higher tree dominance (less evenness) and highest carbon stocks. Finally, we found that there is different effects on aboveground carbon storage in different vegetation types. The tallest vegetation, *Cerradão*, is mostly the dominant species that drive carbon storage, whereas in the medium and the smallest vegetation types, *Cerrado s.s. Denso* and *Cerrado s.s Típico*, especially tree species richness is positively associated with a high carbon storage.

3.7. References

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3.8. Supplementary Information

Table S1. Leaf, fruit and seed functional traits by specie.

Specie	Flower Lenght (cm)	Flower Width (cm)	Seed Length (cm)	Seed Width (cm)	Wood Density (cm3)	Leaf Length (cm)	Leaf Width (cm)
Acrocomia aculeata	3,87	3,80	1,35	1,11	0,46	280,00	93,00
Adenanthera pavonina	13,00	1,50	0,80	0,60	0,80	2,35	1,22
Aegiphila integrifolia	0,80	0,50	0,63	0,36	0,66	14,92	6,98
Aegiphila verticillata	1,00	0,90	0,70	0,40	0,65	8,64	4,77
Agonandra brasiliensis	3,00	1,70	1,50	1,50	0,90	4,64	2,62
Alibertia edulis	8,00	8,00	0,60	0,50	0,76	16,43	6,64
Anadenanthera colubrina	24,47	1,97	1,29	1,37	0,87	16,37	10,03
Anadenanthera peregrina	16,64	1,05	1,21	1,13	0,87	19,43	13,70
Andira vermifuga	5,00	3,20	2,20	1,00	0,71	7,22	4,16
Annona bahiensis	3,00	3,50	1,00	0,60	0,51	13,54	6,66
Annona coriacea	16,00	18,00	2,00	1,00	0,51	11,22	7,60
Annona crassiflora	20,00	15,00	1,50	1,00	0,56	12,41	8,15
Apeiba tibourbou	8,67	9,33	0,76	0,66	0,20	14,48	6,38
Apuleia leiocarpa	7,58	2,82	1,65	0,77	0,80	13,33	8,80
Aspidosperma macrocarpon	18,00	20,00	9,00	9,00	0,68	14,95	8,94
Aspidosperma parvifolium	4,00	5,00	3,00	2,00	0,74	11,73	5,36
Aspidosperma subincanum	5,03	2,77	2,25	1,75	0,82	11,58	5,98
Aspidosperma tomentosum	8,00	4,50	4,00	3,00	0,74	21,40	6,12
Astronium fraxinifolium	1,26	0,28	1,14	0,28	0,85	21,15	17,80
Astronium graveolens	2,00	2,00	0,90	0,40	0,82	8,70	3,43
Astronium urundeuva	0,33	0,35	0,39	0,38	1,10	19,53	12,83

Bauhinia curvula	10,20	1,10	0,70	0,40	0,82	4,53	5,27
Bauhinia forficata	25,50	2,61	0,79	0,47	0,66	9,75	7,11
Bauhinia rufa	12,00	2,00	1,20	1,00	0,66	11,72	11,63
Bauhinia variegata	20,00	2,50	1,50	1,50	0,70	10,18	10,37
Blepharocalyx salicifolius	1,00	0,60	0,50	0,40	0,60	5,25	2,21
Bowdichia virgilioides	7,00	1,50	0,50	0,40	0,79	5,24	1,84
Brosimum gaudichaudii	3,00	3,00	2,00	1,50	0,56	7,50	2,84
Byrsonima coccolobifolia	1,00	1,00	0,60	0,60	0,62	9,93	6,45
Byrsonima crassifolia	2,00	2,00	1,20	1,00	0,58	12,24	5,18
Byrsonima laxiflora	0,65	0,65	0,50	0,40	0,59	10,41	4,89
Byrsonima pachyphylla	1,50	1,50	0,50	0,50	0,56	13,99	7,75
Byrsonima verbascifolia	2,50	2,50	1,00	1,00	0,75	14,73	8,38
Callisthene major	2,10	1,40	1,20	0,70	0,75	3,61	1,56
Calophyllum brasiliense	3,00	3,00	2,20	2,20	0,62	10,75	5,05
Campomanesia lineatifolia	5,00	6,50	0,60	0,40	0,71	11,17	6,11
Campomanesia velutina	2,50	1,50	0,50	0,22	0,82	6,66	2,56
Cardiopetalum calophyllum	4,00	2,00	0,80	0,50	0,50	10,05	3,27
Caryocar brasiliense	10,00	6,00	4,00	3,00	0,65	13,90	18,43
Casearia sylvestris	0,50	0,50	0,20	0,15	0,68	29,30	13,57
Cecropia pachystachya	6,30	1,55	0,20	0,10	0,41	23,53	26,27
Chamaecrista orbiculata	5,00	1,10	0,55	0,35	0,90	4,90	4,32
Chrysophyllum marginatum	0,88	0,43	0,50	0,30	0,59	4,98	2,50
Connarus suberosus	2,00	1,80	1,50	0,60	0,45	6,96	4,43

Copaifera langsdorffii	1,73	1,80	1,32	0,85	0,65	12,23	8,75
Cordia sellowiana	3,00	2,00	1,20	1,00	0,41	17,32	7,31
Cordiera macrophylla	3,00	2,00	0,50	0,40	0,76	13,81	6,60
Cordiera sessilis	2,75	2,80	0,74	0,54	0,88	8,03	3,55
Coussarea hydrangeaefolia	1,08	0,76	0,92	0,55	0,65	13,00	8,48
Croton urucurana	0,60	0,60	0,40	0,30	0,41	12,62	10,43
Cupania vernalis	1,10	1,80	0,87	0,59	0,66	22,60	16,23
Curatella americana	1,50	1,50	0,40	0,30	0,65	13,93	8,43
Dalbergia miscolobium	5,40	1,48	1,25	0,60	0,79	6,57	2,70
Davilla elliptica	1,50	1,50	1,00	1,00	0,65	7,38	5,14
Dendropanax cuneatus	0,93	1,03	0,50	0,12	0,42	16,90	5,30
Diatenopteryx sorbifolia	3,50	1,00	2,50	0,66	0,80	5,48	1,73
Didymopanax macrocarpus	0,80	1,50	0,70	0,40	0,58	11,20	3,89
Dilodendron bipinnatum	0,73	0,48	1,24	0,77	0,52	10,53	7,03
Dimorphandra mollis	15,00	3,20	1,50	0,70	0,74	1,53	0,69
Diospyros hispida	6,00	6,00	2,00	1,00	0,57	13,52	7,00
Diospyros lasiocalyx	3,27	3,83	1,07	0,83	0,62	11,78	7,00
Dipteryx alata	5,06	3,86	2,34	1,03	0,98	20,60	15,13
Emmotum nitens	2,50	3,00	1,60	1,60	0,70	11,04	5,16
Endlicheria paniculata	1,90	1,23	2,23	1,23	0,63	11,00	3,73
Enterolobium contortisiliquum	6,00	5,00	1,53	1,00	0,40	8,88	3,80
Enterolobium gummiferum	10,00	7,00	1,50	1,00	0,54	2,60	1,13
Eremanthus glomerulatus	1,00	0,10	0,20	0,10	0,57	9,55	3,84

Eriotheca gracilipes	5,95	5,22	0,82	0,65	0,43	11,23	4,86
Eriotheca pubescens	7,00	5,50	1,10	0,90	0,46	13,36	5,52
Erythroxylum campestre	1,00	1,00	0,90	0,60	0,71	9,54	4,67
Erythroxylum daphnites	1,00	0,50	0,90	0,40	0,73	7,62	2,78
Erythroxylum deciduum	0,95	0,40	0,79	0,37	0,81	6,20	2,15
Erythroxylum suberosum	1,00	0,60	0,80	0,50	0,71	8,77	4,74
Eugenia dysenterica	5,00	5,00	2,00	1,50	0,73	6,88	3,47
Eugenia florida	0,90	0,77	0,71	0,54	0,73	8,26	3,46
Faramea hyacinthina	1,14	1,14	0,44	0,49	0,58	9,76	4,23
Ferdinandusa elliptica	3,20	1,60	1,40	0,50	0,65	14,02	9,87
Ficus goiana	0,45	0,50	0,10	0,10	0,41	5,46	2,46
Guapira graciliflora	1,50	1,00	1,20	0,60	0,46	9,56	4,04
Guapira noxia	2,50	0,80	0,80	0,60	0,49	12,57	6,78
Guarea guidonia	1,30	1,14	1,20	0,80	0,56	10,68	3,83
Guarea kunthiana	4,60	3,84	1,20	0,80	0,62	15,17	6,18
Guatteria sellowiana	1,20	0,70	0,80	0,50	0,54	12,08	3,24
Guazuma ulmifolia	1,68	1,93	0,26	0,18	0,52	9,88	4,42
Guettarda viburnoides	2,50	2,00	1,20	1,20	0,71	12,39	8,24
Hancornia speciosa	5,00	3,00	0,70	0,50	0,80	9,86	4,68
Handroanthus albus	30,00	2,50	3,00	1,00	1,02	14,58	6,70
Handroanthus impetiginosus	21,97	1,13	1,10	0,84	0,96	15,97	19,83
Handroanthus ochraceus	30,00	3,00	2,00	2,00	1,01	9,30	10,90
Handroanthus serratifolius	30,00	2,00	3,50	1,00	0,92	15,33	18,53
Heteropterys byrsonimifolia	18,37	0,70	0,99	4,08	0,92	7,86	4,74

Hirtella glandulosa	1,27	0,76	0,87	0,62	0,70	11,87	5,96
Hirtella martiana	2,20	1,30	1,50	0,80	0,97	8,79	3,19
Hymenaea courbaril	17,00	5,50	3,00	2,00	0,79	10,09	4,10
Hymenaea stigonocarpa	17,00	6,00	2,00	2,50	0,79	12,73	13,60
Hymenolobium heringerianum	5,34	1,48	5,79	1,46	0,80	4,94	1,69
Ilex conocarpa	1,20	1,20	0,80	0,70	0,52	10,20	4,10
Inga cylindrica	28,00	2,50	2,00	1,20	0,60	7,83	2,94
Inga edulis	32,37	2,15	2,15	1,13	0,76	11,52	4,85
Inga nobilis	10,57	3,14	1,92	1,15	0,56	13,11	5,03
Jacaranda caroba	6,37	3,83	1,60	0,40	0,41	11,37	5,18
Kielmeyera coriacea	15,00	4,00	5,00	3,00	0,61	15,38	4,57
Kielmeyera speciosa	11,00	4,50	5,00	4,00	0,65	13,27	5,21
Lafoensia pacari	8,00	5,30	2,00	1,00	0,70	11,13	6,04
Leptolobium dasycarpum	7,00	2,50	0,70	0,60	0,68	8,32	4,25
Lithraea molleoides	0,50	0,50	0,30	0,30	0,51	6,01	1,54
Luehea divaricata	0,84	0,72	0,50	0,30	0,56	10,98	5,63
Machaerium acutifolium	6,00	2,00	1,20	0,80	0,59	5,29	1,89
Machaerium hirtum	7,00	1,20	2,00	1,00	0,66	1,71	0,44
Machaerium opacum	8,00	0,50	1,00	1,00	0,80	6,51	2,93
Magonia pubescens	10,07	9,10	9,23	4,50	0,77	13,90	11,90
Matayba guianensis	1,60	1,60	1,00	0,70	0,82	9,63	3,48
Miconia albicans	0,50	0,50	0,50	0,50	0,61	8,81	3,76
Miconia burchellii	0,45	0,45	0,09	0,06	0,65	9,11	3,79
Miconia cuspidata	0,40	0,40	0,09	0,06	0,85	7,80	2,62
Miconia ferruginata	0,50	0,40	0,09	0,06	0,65	15,12	6,22

Miconia leucocarpa	0,30	0,30	0,09	0,06	0,60	8,25	4,50
Miconia rubiginosa	0,30	0,30	0,10	0,10	0,60	8,42	3,60
Mimosa claussenii	2,47	1,57	0,50	0,40	0,80	0,87	0,20
Mimosa hebecarpa	3,00	0,65	0,35	0,35	0,80	0,18	0,05
Monteverdia floribunda	1,00	0,80	0,80	0,60	0,75	8,02	3,46
Myrcia splendens	0,80	0,80	0,70	0,50	0,80	7,34	2,50
Myrcia tomentosa	0,80	0,80	0,30	0,30	0,80	9,75	3,23
Myrsine coriacea	0,40	0,30	0,20	0,10	0,54	8,15	2,40
Myrsine gardneriana	0,50	0,40	0,30	0,20	0,59	10,22	3,97
Myrsine guianensis	0,30	0,30	0,20	0,20	0,74	10,08	4,58
Myrsine parvifolia	5,00	4,00	0,30	0,35	0,71	7,91	3,54
Myrsine umbellata	0,50	0,40	0,30	0,20	0,56	9,73	3,80
Nectandra cissiflora	1,70	0,70	1,50	0,70	0,59	14,90	7,01
Neea theifera	1,50	0,80	0,40	0,30	0,68	8,48	4,51
Ocotea corymbosa	0,59	0,41	0,86	0,58	0,52	6,25	2,18
Ocotea spixiana	1,50	1,00	0,80	0,50	0,50	10,25	4,23
Ormosia arborea	4,08	2,44	1,19	1,15	0,70	18,63	14,77
Ouratea castaneifolia	1,20	1,00	0,60	0,40	0,77	12,13	4,05
Ouratea hexasperma	0,90	0,45	0,86	0,42	0,47	12,54	4,31
Palicourea rigida	1,00	0,80	0,80	0,40	0,55	19,69	15,86
Palicourea tetraphylla	0,46	0,46	-	-	0,55	16,14	5,14
Parkia platycephala	9,00	3,50	0,85	0,65	0,76	0,46	0,07
Peltophorum dubium	7,20	1,07	1,00	0,50	0,74	24,77	17,30
Pera glabrata	1,20	1,20	0,50	0,40	0,67	7,97	4,37

Physocalymma scaberrimum	0,50	0,50	0,41	0,40	0,85	10,13	5,59
Piptadenia gonoacantha	10,77	1,93	0,85	0,76	0,72	12,30	8,67
Piptocarpha macropoda	0,30	0,10	-	-	0,60	17,61	7,52
Piptocarpha rotundifolia	1,50	0,40	1,00	0,20	0,51	8,64	5,03
Plathymenia reticulata	15,00	2,00	0,70	1,00	0,49	16,00	6,00
Platonia insignis	8,00	7,60	4,00	2,50	0,70	10,64	5,92
Platycyamus regnellii	2,10	4,00	2,00	1,20	0,81	15,63	14,40
Platymiscium floribundum	7,00	3,00	3,00	1,20	0,90	10,28	5,38
Platypodium elegans	10,00	2,50	6,00	1,50	0,75	5,67	3,07
Plenckia populnea	5,50	0,80	-	-	0,53	7,72	5,25
Pouteria ramiflora	3,50	3,00	2,00	1,60	0,78	11,54	4,84
Pouteria torta	8,00	5,00	2,50	1,50	0,77	16,67	7,63
Protium altissimum	1,50	1,70	-	-	0,74	12,95	4,83
Protium heptaphyllum	1,37	0,67	0,88	0,60	0,63	23,90	18,93
Pseudobombax longiflorum	3,87	3,80	1,35	1,11	0,46	15,31	8,64
Pseudobombax tomentosum	27,00	10,00	0,70	0,60	0,34	25,56	18,23
Psidium laruotteanum	2,00	2,00	0,40	0,40	0,90	8,49	4,21
Psidium myrsinites	2,00	1,80	0,40	0,30	0,90	7,39	3,25
Psidium rufum	2,91	2,68	0,99	0,72	0,93	11,90	5,13
Pterodon emarginatus	6,40	3,63	0,97	0,46	0,91	14,27	6,20
Pterodon pubescens	6,12	3,84	-	-	0,73	3,15	1,07
Qualea dichotoma	2,50	1,50	1,50	0,50	0,70	10,31	5,44
Qualea grandiflora	12,00	5,00	3,50	1,50	0,63	11,97	4,37
Qualea multiflora	5,00	3,00	3,00	1,10	0,77	9,85	4,44

Qualea parviflora	5,00	2,70	3,00	1,00	0,63	7,89	3,53
Rhamnidium elaeocarpum	1,18	0,88	0,77	0,43	0,69	11,58	6,25
Roupala montana	4,00	1,50	2,60	1,20	0,73	13,60	6,17
Rudgea viburnoides	1,20	0,90	0,80	0,70	0,64	12,03	7,07
Salacia crassifolia	4,00	3,25	2,00	1,00	0,56	9,18	4,53
Salvertia convallariodora	6,00	3,00	3,00	1,00	0,65	18,88	11,11
Sapium glandulosum	0,90	1,00	0,80	0,50	0,41	14,00	5,00
Schinus terebinthifolia	0,50	0,50	0,40	0,40	0,46	14,75	6,97
Senegalia polyphylla	14,20	3,06	0,94	0,70	0,63	18,45	13,63
Simarouba amara	1,50	1,00	1,00	0,50	0,40	25,06	13,35
Siparuna guianensis	1,50	1,50	0,60	0,50	0,66	12,76	4,36
Siphoneugena densiflora	1,00	0,90	0,80	0,70	0,93	11,82	4,15
Solanum lycocarpum	15,00	15,00	0,70	0,50	0,28	12,27	6,06
Sterculia striata	17,00	6,00	2,00	1,00	0,52	16,00	25,00
Strychnos pseudoquina	2,24	2,15	1,62	1,41	0,65	10,77	5,76
Stryphnodendron adstringens	10,00	1,80	0,80	0,40	0,53	2,20	1,98
Stryphnodendron pulcherrimum	8,00	1,40	0,80	0,60	0,48	0,57	0,18
Styrax ferrugineus	0,95	0,60	0,77	0,50	0,34	11,22	6,39
Tabebuia aurea	16,00	2,00	2,29	1,73	0,76	12,64	5,93
Tabebuia roseoalba	22,67	0,83	1,08	4,60	0,76	13,45	16,58
Tachigali aurea	5,50	2,20	1,50	0,80	0,56	30,30	18,42
Tachigali subvelutina	8,00	1,80	1,50	0,50	0,77	20,69	17,44

Tachigali vulgaris	8,50	2,00	1,70	1,00	0,56	19,28	13,48
Tapirira guianensis	1,00	0,80	0,60	0,40	0,46	13,10	5,23
Tapirira obtusa	1,30	1,00	1,20	0,80	0,29	18,52	17,19
Terminalia argentea	5,00	1,50	1,50	0,50	0,80	11,80	5,15
Terminalia glabrescens	1,30	0,60	0,50	0,20	0,77	7,70	4,20
Tocoyena formosa	4,00	4,00	0,80	0,80	0,62	18,04	12,04
Trema micrantha	0,10	0,10	0,17	0,18	0,32	12,53	3,73
Vatairea macrocarpa	10,00	1,50	2,80	1,50	0,88	7,60	5,38
Virola sebifera	2,00	1,50	1,40	1,00	0,46	20,83	5,77
Vitex megapotamica	3,00	2,60	1,80	1,20	0,55	7,22	1,87
Vochysia elliptica	3,20	2,00	1,20	0,30	0,57	8,44	4,68
Vochysia rufa	5,00	2,50	3,00	1,20	0,47	12,74	5,21
Vochysia tucanorum	2,40	1,20	2,50	0,60	0,40	11,82	3,66
Xylopia aromatica	4,00	1,50	0,60	0,30	0,56	27,13	19,37
Xylopia emarginata	1,50	0,80	0,50	0,30	0,67	5,05	1,35
Xylopia sericea	2,50	2,00	0,70	0,40	0,57	7,22	1,87
Zanthoxylum rhoifolium	0,50	0,40	0,20	0,20	0,49	19,54	8,70
Zeyheria montana	8,00	8,00	5,00	0,50	0,77	12,58	4,26

Table S2. Diversity metrics, tree aboveground carbon stock, and cluster based on vegetation structure of each surveyed area.

Area	Plot	Cluster	Species Richness	Shannon Index	Simpson Index	Functional Richness	Functional Evenness	Functional Divergence	Phylogenetic Diversity	Standardized Phylogenetic Diversity	Mean Pairwise Distance	Standardized Mean Pairwise Distance	Mean Near Taxon Distance	Standardized Mean Near Taxon Distance	Aboveground Carbon Stock (Mg/ha)
Area 1	1	1	19	15,890	13,569	0,005	0,996	0,834	1731,166	0,188	227,011	1,625	142,386	0,017	0,021
Area 1	2	1	22	15,516	11,174	0,005	0,996	0,830	2080,179	1,266	219,187	0,883	139,643	0,187	0,041
Area 1	3	1	24	19,404	15,559	0,011	0,993	0,858	2004,171	-0,285	222,108	0,598	114,438	-0,854	0,018
Area 1	4	1	24	19,812	16,010	0,008	0,997	0,849	1982,205	-0,444	218,157	-0,125	125,546	-0,261	0,026
Area 2	5	1	22	18,410	15,474	0,007	0,995	0,897	1920,044	0,063	221,042	0,453	124,536	-0,488	0,019
Area 2	6	1	15	11,566	9,308	0,004	0,993	0,810	1282,865	-1,209	207,229	-0,118	143,875	-0,331	0,015
Area 2	7	1	14	10,911	8,654	0,007	0,988	0,825	1351,264	0,068	211,099	0,587	162,775	0,239	0,045
Area 3	8	2	12	5,975	4,148	0,007	0,991	0,808	1268,800	0,917	182,442	0,469	197,809	0,935	0,031
Area 3	9	2	23	13,633	10,968	0,012	0,995	0,865	2012,574	0,244	225,912	1,811	126,479	-0,238	0,145
Area 3	10	2	24	12,148	8,332	0,014	0,994	0,866	2065,963	0,155	220,635	1,798	144,902	0,485	0,137
Area 3	11	2	20	8,977	5,591	0,006	0,997	0,766	1734,978	-0,327	201,238	0,937	153,818	0,418	0,105
Area 3	12	2	28	16,767	11,548	0,016	0,996	0,851	2225,020	-0,447	221,631	1,166	150,505	1,100	0,133
Area 3	13	2	25	15,741	11,532	0,010	0,996	0,871	2133,624	0,215	214,469	0,121	139,536	0,445	0,094
Area 3	14	2	25	15,907	12,492	0,008	0,997	0,797	2052,425	-0,428	225,386	1,561	132,111	0,093	0,122
Area 3	15	2	20	13,417	11,098	0,006	0,996	0,892	1786,869	0,067	222,809	1,395	155,831	0,659	0,137
Area 3	16	2	25	14,341	10,473	0,008	0,997	0,850	2230,127	0,871	226,870	2,090	154,026	0,955	0,157
Area 4	17	2	16	10,944	8,960	0,005	0,993	0,812	1476,561	-0,172	214,994	0,908	128,847	-0,780	0,092
Area 4	18	1	25	16,583	12,287	0,007	0,997	0,843	2044,603	-0,426	221,848	1,101	107,892	-0,943	0,109
Area 4	19	2	17	11,497	9,757	0,004	0,994	0,733	1388,464	-1,462	220,752	1,306	114,374	-1,244	0,107
Area 4	20	2	23	14,023	10,395	0,010	0,995	0,899	2014,863	0,243	223,722	1,631	127,782	-0,235	0,149
Area 4	21	2	22	14,923	11,545	0,006	0,997	0,853	1944,678	0,323	223,561	1,440	162,619	1,138	0,173
Area 4	22	2	19	10,362	7,521	0,006	0,996	0,895	1830,497	0,971	215,904	1,429	166,923	0,877	0,192
Area 4	23	2	29	16,005	9,494	0,015	0,995	0,813	2342,749	-0,157	221,594	1,773	102,649	-0,765	0,068
Area 4	24	2	25	15,513	11,303	0,010	0,997	0,813	2153,822	0,325	222,467	1,314	141,497	0,497	0,174
Area 4	25	2	19	13,403	10,609	0,010	0,995	0,888	1839,086	1,084	217,343	0,788	133,502	-0,406	0,081
Area 5	26	3	8	2,819	1,792	0,003	0,992	0,829	789,037	-0,815	105,477	0,269	118,471	-1,183	0,025
Area 5	27	3	18	9,346	5,833	0,010	0,995	0,861	1846,206	1,729	203,493	1,026	158,473	0,488	0,022

Area 5	28	3	14	10,367	8,048	0,003	0,995	0,896	1403,088	0,635	216,064	1,370	139,612	-0,568	0,014
Area 5	29	3	19	13,616	9,976	0,007	0,995	0,804	1698,088	-0,069	215,157	0,710	109,413	-1,212	0,028
Area 5	30	3	18	12,055	8,528	0,006	0,995	0,770	1750,947	0,950	220,077	1,698	138,447	-0,249	0,025
Area 5	31	1	16	12,254	8,981	0,006	0,996	0,818	1358,545	-1,129	194,262	-1,783	101,248	-1,858	0,010
Area 5	32	1	17	14,322	12,374	0,009	0,995	0,852	1400,087	-1,418	195,971	-2,542	102,733	-1,868	0,012
Area 5	33	1	15	12,992	11,529	0,008	0,997	0,808	1420,442	0,037	208,123	-0,700	153,116	0,019	0,010
Area 5	34	1	11	8,281	6,126	0,006	0,992	0,920	1105,943	0,087	195,284	0,043	176,487	0,374	0,009
Area 5	35	1	13	10,882	9,328	0,005	0,993	0,868	1168,324	-0,912	195,050	-1,613	112,175	-1,697	0,012
Area 5	36	1	16	14,119	12,800	0,006	0,995	0,867	1300,587	-1,654	202,181	-1,858	107,304	-1,792	0,018
Area 5	37	1	16	13,982	12,165	0,009	0,996	0,818	1321,151	-1,562	204,469	-1,395	126,731	-1,001	0,014
Area 5	38	3	13	11,090	9,470	0,006	0,995	0,821	1075,878	-1,890	197,268	-1,301	113,188	-1,860	0,016
Area 6	39	3	16	10,071	6,891	0,007	0,995	0,823	1629,800	1,246	210,912	1,247	191,144	1,423	0,014
Area 6	40	3	17	11,158	8,154	0,006	0,995	0,858	1457,443	-0,910	216,242	1,304	127,800	-0,717	0,019
Area 6	41	1	17	10,590	7,450	0,008	0,994	0,788	1427,145	-1,169	183,709	-1,976	115,423	-1,147	0,059
Area 6	42	3	16	10,386	7,041	0,006	0,996	0,892	1358,453	-1,154	189,271	-1,202	94,657	-1,872	0,033
Area 6	43	1	11	3,814	2,231	0,004	0,993	0,898	992,856	-1,219	121,023	-0,864	137,519	-0,605	0,046
Area 6	44	1	11	7,132	5,444	0,003	0,993	0,791	1074,606	-0,334	192,929	0,216	138,598	-0,845	0,047
Area 6	45	3	9	4,689	3,542	0,003	0,994	0,843	1019,940	1,128	171,328	0,327	190,987	0,410	0,053
Area 6	46	1	15	8,244	5,763	0,007	0,995	0,869	1353,529	-0,546	197,394	0,454	145,925	-0,236	0,045
Area 6	47	3	13	8,356	6,230	0,007	0,995	0,827	1070,954	-1,810	190,269	-0,551	93,600	-2,084	0,030
Area 6	48	1	14	10,034	7,327	0,005	0,995	0,803	1270,116	-0,662	191,976	-1,173	107,589	-1,689	0,066
Area 6	49	1	11	8,296	6,494	0,003	0,993	0,918	974,979	-1,420	194,017	-0,350	161,701	-0,135	0,056
Area 6	50	1	14	10,218	8,092	0,005	0,994	0,852	1310,706	-0,272	206,995	0,292	152,187	-0,096	0,036
Area 6	51	3	18	11,845	8,710	0,006	0,995	0,869	1597,051	-0,264	205,652	-0,110	116,126	-0,985	0,041
Area 6	52	3	14	9,169	6,761	0,006	0,995	0,773	1395,291	0,555	200,542	0,104	173,406	0,564	0,050
Area 6	53	3	13	8,359	6,519	0,006	0,994	0,819	1278,883	0,232	197,477	0,058	126,072	-1,055	0,050
Area 6	54	3	20	14,329	10,843	0,007	0,995	0,795	1580,493	-1,533	203,855	-0,987	102,109	-1,549	0,046
Area 6	55	3	19	12,440	8,783	0,008	0,996	0,883	1529,921	-1,412	199,749	-0,843	89,799	-1,816	0,051
Area 6	56	3	15	9,786	7,051	0,007	0,995	0,859	1340,731	-0,730	202,293	0,169	109,765	-1,437	0,058
Area 6	57	1	15	11,681	9,475	0,005	0,994	0,846	1173,341	-2,262	190,865	-2,245	90,470	-2,353	0,020
Area 6	58	1	16	10,840	7,111	0,008	0,996	0,830	1357,015	-1,158	177,191	-2,625	87,406	-2,254	0,016

Area 6	59	3	10	7,865	6,545	0,005	0,994	0,843	1001,312	-0,120	197,446	-0,066	183,758	0,442	0,006
Area 6	60	1	15	12,093	10,169	0,008	0,995	0,864	1166,879	-2,268	199,943	-1,206	108,809	-1,807	0,021
Area 6	61	1	12	8,934	7,188	0,006	0,993	0,859	1129,584	-0,553	201,051	0,056	138,821	-0,779	0,020
Area 6	62	1	14	9,807	6,723	0,005	0,994	0,793	1267,566	-0,739	188,091	-1,138	93,669	-2,128	0,020
Area 7	63	1	25	19,820	16,653	0,009	0,996	0,825	2209,870	0,601	222,494	0,526	153,230	1,160	0,049
Area 7	64	3	16	13,272	11,504	0,014	0,991	0,721	1510,877	0,142	209,450	-0,489	150,579	0,038	0,013
Area 7	65	3	11	9,139	7,692	0,009	0,987	0,692	1111,876	0,105	203,391	0,081	188,209	0,735	0,014
Area 7	66	3	12	7,727	5,565	0,006	0,994	0,790	1021,709	-1,666	171,416	-1,747	90,906	-2,118	0,018
Area 7	67	3	8	5,751	4,676	0,001	0,988	0,887	792,533	-0,688	162,070	-1,731	104,405	-2,227	0,014
Area 7	68	3	4	3,075	2,636	0,000	0,971	0,694	498,099	0,809	150,181	0,362	237,604	0,730	0,007
Area 7	69	3	7	4,743	3,636	0,004	0,977	0,689	709,986	-0,755	161,495	-0,555	157,212	-0,803	0,009
Area 7	70	3	13	11,184	9,587	0,002	0,994	0,757	975,586	-2,848	175,645	-3,963	74,227	-3,347	0,009
Area 7	71	3	9	7,329	6,416	0,002	0,992	0,760	872,183	-0,747	189,325	-0,810	151,305	-0,794	0,010
Area 7	72	3	9	8,073	7,734	0,004	0,987	0,816	930,686	0,022	202,446	-0,037	150,728	-0,799	0,009
Area 8	73	1	30	15,301	10,042	0,009	0,997	0,893	2375,858	-0,309	205,156	-0,613	81,436	-1,646	0,209
Area 8	74	1	27	15,367	10,946	0,010	0,996	0,917	2202,842	-0,279	209,720	-0,285	120,121	-0,268	0,297
Area 8	75	1	17	9,704	6,601	0,005	0,995	0,804	1472,725	-0,754	192,755	-0,606	108,324	-1,246	0,130
Area 8	76	1	18	13,591	11,043	0,006	0,996	0,873	1590,075	-0,368	222,272	1,303	108,151	-1,490	0,066
Area 8	77	1	13	7,315	4,690	0,006	0,994	0,849	1198,559	-0,573	193,584	0,897	167,724	0,218	0,100
Area 9	78	3	8	7,293	6,721	0,003	0,993	0,760	979,119	1,883	217,734	1,926	241,868	1,942	0,010
Area 9	79	3	8	7,862	7,714	0,004	0,986	0,909	871,209	0,352	211,797	0,918	198,139	0,567	0,007
Area 9	80	3	10	8,585	7,410	0,008	0,992	0,768	1173,992	1,831	211,281	0,976	217,003	1,534	0,007
Area 9	81	3	8	7,038	6,259	0,007	0,993	0,786	945,815	1,412	204,342	0,782	226,576	1,478	0,005
Area 9	82	3	9	8,492	8,100	0,004	0,987	0,918	928,820	-0,057	213,379	0,969	194,272	0,706	0,006
Area 9	83	3	11	10,311	9,757	0,004	0,992	0,868	1146,543	0,513	215,506	0,702	182,131	0,533	0,007
Area 9	84	3	8	6,274	5,120	0,003	0,992	0,804	731,649	-1,420	185,797	-0,201	164,413	-0,490	0,006
Area 9	85	3	10	5,583	3,798	0,006	0,993	0,826	908,754	-1,308	186,175	1,206	181,177	0,303	0,009
Area 9	86	3	7	5,612	4,765	0,002	0,990	0,807	839,180	1,302	203,663	1,646	239,932	1,511	0,006
Area 9	87	3	12	9,874	8,000	0,007	0,993	0,772	1162,283	-0,202	212,680	0,925	192,036	1,017	0,005
Area 9	88	3	13	11,487	10,000	0,004	0,993	0,791	1123,665	-1,315	212,508	0,275	111,833	-1,759	0,006
Area 9	89	3	10	10,000	10,000	0,005	0,990	0,788	1090,715	0,830	217,875	0,972	187,283	0,575	0,004

Area 9	90	3	7	5,133	3,920	0,002	0,990	0,807	839,180	1,308	194,557	1,763	245,681	1,620	0,005
Area 9	91	3	12	9,874	8,000	0,007	0,993	0,772	1162,283	-0,188	212,680	1,003	192,036	1,047	0,006
Area 9	92	3	14	11,465	9,587	0,008	0,995	0,837	1448,157	1,022	213,642	0,497	184,896	1,105	0,021
Area 9	93	3	14	11,555	10,125	0,009	0,994	0,844	1531,551	1,885	225,895	1,947	199,644	1,638	0,014
Area 9	94	3	16	12,706	10,526	0,009	0,993	0,812	1404,259	-0,772	210,619	-0,105	141,768	-0,309	0,011
Area 9	95	3	10	7,840	6,119	0,004	0,991	0,865	1061,322	0,517	206,652	1,115	196,744	0,843	0,006
Area 9	96	3	7	6,518	6,149	0,002	0,989	0,781	814,621	0,898	206,376	0,999	219,282	0,998	0,005
Area 10	97	3	19	16,298	13,928	0,017	0,991	0,781	1662,343	-0,365	218,448	0,323	139,050	-0,125	0,015
Area 10	98	3	15	12,333	10,294	0,013	0,992	0,830	1459,697	0,441	210,501	-0,033	150,440	-0,102	0,006
Area 10	99	3	14	12,184	10,522	0,010	0,989	0,746	1284,054	-0,514	193,091	-2,262	138,581	-0,660	0,003
Area 10	100	3	13	8,110	5,091	0,011	0,989	0,724	1468,371	2,126	192,798	0,554	199,829	1,150	0,008
Area 10	101	3	12	9,970	8,345	0,011	0,990	0,801	1198,730	0,122	208,830	0,389	186,866	0,895	0,005
Area 10	102	3	9	8,151	7,348	0,008	0,991	0,862	1057,840	1,573	211,491	1,007	217,541	1,400	0,002
Area 10	103	3	13	11,592	10,383	0,008	0,986	0,809	1393,092	1,344	218,201	0,915	193,991	1,415	0,007
Area 10	104	3	9	7,671	6,688	0,005	0,987	0,815	901,789	-0,368	192,413	-0,572	165,582	-0,282	0,003
Area 10	105	3	13	9,075	6,427	0,007	0,993	0,811	1335,306	0,812	189,348	-0,866	162,349	0,110	0,008
Area 10	106	3	12	10,790	9,757	0,007	0,994	0,803	1251,597	0,682	206,528	-0,296	181,424	0,735	0,006
Area 10	107	3	11	8,327	6,579	0,005	0,994	0,838	1038,933	-0,704	193,259	-0,455	168,146	0,016	0,005
Area 10	108	3	14	7,938	4,481	0,004	0,996	0,791	1211,076	-1,183	177,827	-0,383	157,310	0,037	0,013
Area 10	109	3	12	5,492	2,941	0,006	0,994	0,797	1164,196	-0,202	160,112	0,647	210,619	1,076	0,007
Area 10	110	3	8	5,263	3,658	0,002	0,991	0,766	741,414	-1,418	147,056	-1,907	141,776	-0,934	0,005
Area 10	111	3	18	13,491	10,240	0,010	0,994	0,806	1715,862	0,631	203,094	-0,903	148,601	0,177	0,015
Area 10	112	3	7	5,243	4,046	0,003	0,993	0,838	741,531	-0,210	179,186	0,282	204,217	0,454	0,003
Area 11	113	1	12	11,368	10,714	0,009	0,994	0,796	1274,945	0,970	216,743	0,665	185,786	0,967	0,011
Area 11	114	2	9	5,493	3,903	0,003	0,995	0,774	993,208	0,781	191,649	1,469	232,774	1,523	0,040
Area 11	115	1	13	11,536	9,966	0,006	0,993	0,754	1240,591	-0,211	208,701	-0,184	151,652	-0,272	0,033

Area 11	116	1	7	6,598	6,250	0,003	0,991	0,746	833,630	1,194	211,919	1,480	230,394	1,357	0,008
Area 11	117	2	13	9,771	7,053	0,006	0,994	0,749	1261,160	-0,003	214,005	1,585	184,642	0,849	0,020
Area 11	118	3	5	4,353	3,846	0,000	0,989	0,706	559,885	-0,077	184,063	0,835	204,517	0,124	0,009
Area 11	119	3	7	5,858	4,840	0,001	0,993	0,682	676,550	-1,268	195,345	0,878	199,582	0,416	0,011
Area 11	120	3	10	8,743	7,538	0,003	0,995	0,802	909,448	-1,234	208,814	0,676	176,435	0,169	0,014
Area 11	121	3	9	7,521	6,422	0,003	0,994	0,724	959,594	0,375	211,969	1,510	206,341	0,976	0,015
Area 11	122	3	8	6,586	5,452	0,001	0,994	0,762	826,151	-0,262	205,357	1,352	210,751	0,984	0,011
Area 11	123	3	7	5,858	4,840	0,001	0,991	0,737	681,004	-1,183	198,545	1,204	189,107	0,070	0,010
Area 12	124	2	10	8,225	7,127	0,004	0,991	0,788	884,707	-1,612	184,317	-1,635	129,614	-1,354	0,043
Area 13	125	2	8	7,429	6,882	0,008	0,982	0,869	786,067	-0,785	196,786	-0,306	158,860	-0,604	0,034
Area 13	126	2	14	11,602	10,000	0,008	0,992	0,789	1226,535	-1,020	205,183	-0,585	147,434	-0,347	0,051
Area 13	127	2	9	7,434	6,618	0,006	0,990	0,815	850,036	-0,958	185,162	-1,335	155,675	-0,620	0,052
Area 13	128	3	4	3,057	2,656	0,001	0,998	0,916	495,218	0,701	152,778	0,423	240,904	0,811	0,008
Area 13	129	3	5	4,389	3,930	0,001	0,990	0,802	470,904	-1,861	138,611	-2,634	86,936	-2,941	0,006
Area 13	130	3	5	4,642	4,400	0,001	0,992	0,873	503,134	-1,311	159,479	-1,684	128,874	-1,897	0,015
Area 13	131	3	9	6,137	4,364	0,004	0,991	0,799	908,055	-0,312	180,410	0,037	169,532	-0,132	0,017
Area 13	132	1	13	10,853	9,449	0,007	0,994	0,774	1123,460	-1,385	199,803	-1,104	122,356	-1,322	0,035
Area 13	133	2	6	4,720	3,947	0,004	0,990	0,788	556,778	-1,832	165,370	-0,615	130,009	-1,713	0,018
Area 13	134	1	12	11,082	10,286	0,009	0,992	0,831	1088,257	-0,948	199,442	-1,368	142,603	-0,789	0,013
Area 13	135	1	14	12,415	11,215	0,010	0,991	0,800	1329,106	-0,098	206,099	-0,763	142,479	-0,521	0,015
Area 13	136	2	8	6,856	5,828	0,006	0,988	0,822	916,553	0,978	202,874	0,967	216,557	1,115	0,042
Area 14	137	3	13	9,215	7,049	0,007	0,994	0,786	1174,150	-0,858	204,731	0,552	172,472	0,405	0,018
Area 14	138	3	14	11,821	10,333	0,009	0,994	0,832	1465,620	1,275	214,390	0,456	183,811	1,159	0,025
Area 14	139	3	18	13,018	9,025	0,013	0,995	0,819	1879,990	2,067	210,175	0,306	141,724	-0,145	0,026

Area 14	140	3	6	4,860	3,857	0,001	0,990	0,759	724,629	1,080	180,349	0,607	229,970	1,005	0,011
Area 14	141	3	10	9,076	8,167	0,004	0,995	0,786	1015,737	0,003	206,485	0,228	167,237	-0,074	0,009
Area 14	142	3	10	7,061	5,521	0,005	0,994	0,819	904,644	-1,300	181,703	-0,880	130,675	-1,138	0,014
Area 14	143	3	19	14,444	11,441	0,010	0,997	0,856	1565,911	-1,220	192,537	-2,821	92,974	-2,026	0,039
Area 14	144	1	19	13,160	9,000	0,011	0,995	0,796	1692,316	-0,084	199,901	-0,919	133,837	-0,324	0,036
Area 14	145	3	21	12,216	7,943	0,011	0,995	0,874	1616,961	-1,650	203,235	-0,076	96,820	-1,485	0,020
Area 14	146	3	9	7,585	6,429	0,004	0,993	0,831	881,077	-0,649	179,737	-1,565	133,354	-1,353	0,013
Area 14	147	3	15	10,847	8,100	0,011	0,993	0,831	1243,228	-1,572	190,085	-1,778	104,588	-1,726	0,021
Area 15	148	2	19	14,252	11,441	0,006	0,996	0,856	1965,634	2,082	219,511	0,897	171,974	1,294	0,038
Area 15	149	2	21	16,610	13,071	0,007	0,996	0,823	1903,607	0,427	223,203	1,145	152,957	0,736	0,042
Area 16	150	2	15	11,408	9,219	0,007	0,995	0,815	1544,250	1,255	206,565	-0,200	161,920	0,323	0,042
Area 16	151	2	12	9,257	7,577	0,009	0,994	0,884	1309,755	1,323	216,899	1,566	190,198	0,936	0,106
Area 16	152	2	14	10,746	8,813	0,004	0,994	0,788	1384,441	0,388	202,774	-0,453	147,576	-0,283	0,051
Area 16	153	2	16	10,537	7,811	0,009	0,995	0,863	1621,899	1,228	219,924	1,930	195,110	1,587	0,097
Area 16	154	2	14	10,286	8,654	0,008	0,994	0,775	1308,331	-0,300	217,182	1,255	141,472	-0,463	0,070
Area 16	155	2	16	9,297	6,378	0,006	0,994	0,812	1477,900	-0,152	205,884	0,941	114,331	-1,146	0,029
Area 17	156	1	11	10,009	9,000	0,006	0,992	0,922	1175,335	0,849	218,070	1,262	197,601	1,159	0,015
Area 17	157	1	10	8,234	7,000	0,006	0,992	0,916	1045,011	0,352	211,743	1,157	197,914	0,917	0,012
Area 17	158	2	7	5,329	4,083	0,004	0,992	0,826	707,007	-0,837	155,092	-1,875	149,393	-1,096	0,110
Area 17	159	2	9	8,549	8,067	0,005	0,993	0,828	868,574	-0,833	205,501	0,108	170,196	-0,134	0,057
Area 17	160	1	9	7,288	5,918	0,005	0,993	0,829	978,240	0,621	182,918	-1,137	159,462	-0,482	0,007
Area 17	161	1	8	5,639	4,000	0,004	0,992	0,845	839,605	-0,039	171,358	-0,379	160,747	-0,470	0,008
Area 18	162	3	12	10,901	10,000	0,011	0,988	0,772	1181,873	0,035	203,114	-0,695	151,767	-0,405	0,014
Area 18	163	3	19	16,200	13,762	0,021	0,989	0,778	1655,286	-0,469	213,644	-0,393	146,654	0,227	0,017

Area 18	164	3	20	17,476	15,338	0,022	0,988	0,784	1703,272	-0,610	212,472	-0,900	133,268	-0,280	0,013
Area 18	165	1	14	12,588	11,255	0,011	0,989	0,767	1244,979	-0,915	202,030	-1,427	132,758	-0,930	0,008
Area 18	166	1	10	8,683	7,737	0,009	0,986	0,803	1000,253	-0,215	201,417	-0,208	159,332	-0,413	0,007
Area 19	167	1	22	14,759	10,217	0,007	0,995	0,826	2108,619	1,400	210,872	0,031	169,969	1,387	0,004

Table S3. Result of the model averaging of the Linear Mixed Model between *Cerrado* tree aboveground carbon stock, diversity metrics and functional traits community weighted. CWM: community weighted mean, LL: Leaf Length, FRic: Functional Richness, FEve: Functional Evenness, SL: Seed Length, WD: Wood density, FL: fruit length, ses: standard effect size, PD: Phylogenetic Diversity, Sp_Rich: Species richness, MPD: Mean Pairwise Distance, FW: Fruit Width, SW: Seed Width, MNTD: Mean Near Taxon Distance, FDiv: Functional Divergence.

A

	Estimate	**Std. Error**	**Adjusted SE**	**Z value**	**Pr(>|z|)**	
(Intercept)	2.673.918	0.151547	0.153902	17.374	< 2E-16	***
cwm_fw_cm	0.041280	0.050134	0.050446	0.818	0.41318	
MPD	-0.206253	0.063772	0.064662	3.190	0.00142	**
sp.rich	0.590674	0.096971	0.098278	6.010	< 2E-16	***
ses.pd	0.080238	0.053893	0.054392	1.475	0.14016	
cwm_fl_cm	-0.013974	0.039018	0.039235	0.356	0.72172	
cwm_wd_sba	0.019765	0.047304	0.047604	0.415	0.67799	
cwm_sl_cm	0.006858	0.024160	0.024307	0.282	0.77784	
feve	0.005419	0.022099	0.022278	0.243	0.80781	
fric	-0.005952	0.028896	0.029163	0.204	0.83828	
cwm_ll_cm	-0.001685	0.013796	0.013946	0.121	0.90380	

B

	Estimate	**Std. Error**	**Adjusted SE**	**Z value**	**Pr(>|z|)**	
(Intercept)	2.995.987	0.261376	0.268907	11.141	<2e-16	***
fric	-0.326163	0.210494	0.214089	1.523	0.128	
sp.rich	0.475481	0.205907	0.209129	2.274	0.023	*
ses.mntd	0.101854	0.133349	0.134585	0.757	0.449	
ses.pd	-0.024487	0.082048	0.082803	0.296	0.767	
cwm_ll_cm	-0.071067	0.135087	0.136431	0.521	0.602	
feve	-0.056679	0.141640	0.143303	0.396	0.692	
cwm_sw_cm	0.019908	0.078161	0.079081	0.252	0.801	
cwm_fw_cm	0.026647	0.095549	0.096756	0.275	0.783	
cwm_fl_cm	0.013901	0.052617	0.053282	0.261	0.794	
mpd_ab	-0.002712	0.022718	0.023108	0.117	0.907	

C

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	392.154	0.09749	0.10144	38.657	2,00E-16	***
cwm_wood density	-0.52594	0.11170	0.11593	4.537	5.7e-06	***
fdiv	0.15210	0.12648	0.12809	1.187	0.235	
feve	0.06462	0.10902	0.11034	0.586	0.558	
ses.mntd	0.04624	0.10456	0.10573	0.437	0.662	
ses.pd	-0.14668	0.16551	0.16689	0.879	0.379	
ses.mpd	0.07209	0.10072	0.10204	0.706	0.480	
cwm_ll_cm	0.04615	0.09364	0.09495	0.486	0.627	

4. Chapter 3 - Abiotic attributes outperform biodiversity in driving carbon storage across an environmental gradient in Brazilian tropical forest

4.1. Abstract

Tropical forests are globally recognized for their pivotal role in regulating ecosystem processes, supporting biodiversity and ecosystem services. Thus, understanding how the biotic and abiotic factors drive ecosystem functioning, mainly carbon stock, is crucial for effective conservation and climate adaptation strategies. The main objective of this study is to investigate how abiotic and biotic factors interact to influence ecosystem functioning, specifically tree aboveground carbon stock, across an environmental gradient in Brazilian tropical forests. We addressed two fundamental questions: 1) What is the pattern of resource use strategies in Tropical Forests along a climatic gradient? 2) How do abiotic and biotic attributes drive AGC in Tropical Forests along a climatic gradient? The main analysis performed a Piecewise Structural Equation Modeling to understand how tree aboveground carbon stock is affected by abiotic and biotic factors; how diversity is affected by abiotic factors; and how wood density is affected by abiotic and biotic factors. Therefore, the results showed a gradient environment between the forest, most represented by temperature, and no difference in resource use strategies between forests. Additionally, maximum temperature and stem structural diversity are the main drivers of the ecosystems, showing a positive and direct effect on tree aboveground carbon stock, and community weighted mean of wood density positively by sum of bases and negatively by species richness.

Keywords: Resource use strategy, Cloud Forest, Dry Forest, Acquisitive, Conservative.

4.2. Introduction

Over the past decade, studies on Biodiversity-Ecosystem Functioning (BEF) have grown significantly (Van Der Plas 2019), driven by their relevance in addressing and mitigating climate change. BEF research focuses on understanding the relationship between biodiversity indices and ecosystem functioning, which underpins critical ecosystem services such as carbon sequestration, biomass production and stability, litter decomposition, pollination, and more (Loreau et al. 2001; Hooper et al. 2005; Cardinale et al. 2011; Balvanera et al. 2014; Tilman et al. 2014). The BEF relationship is driven by multiple factors, including biotic drivers (e.g., vegetation attributes such as species richness, structural diversity, competition, and facilitation) and abiotic factors (e.g., soil fertility, texture, and climatic conditions like annual precipitation and temperature). These biotic and abiotic drivers often interact, jointly influencing the BEF relationship (Van Der Sande et al. 2017). By examining these interactions, the BEF approach provides critical insights into how ecosystems respond to climate change, making it a valuable tool for addressing the ecological consequences of climate change across diverse environments (Prado-Junior et al. 2016; Poorter et al. 2017; Van Der Sande et al. 2017; Poorter et al. 2019).

Regarding biotic drivers, they are largely determined by plant species' functional traits (Violle et al. 2007), which influence the BEF relationship through varying resource-use strategies. These strategies exist along a spectrum, ranging from acquisitive traits (i.e. rapid resource acquisition and high growth rates) to conservative traits (i.e. resource conservation and resilience under limiting conditions) (Lavorel and Garnier 2002; Violle et al. 2007). These strategies reflect how individuals allocate resources (e.g., nutrients, water, and light) to survive and reproduce across environmental gradients (Lavorel and Garnier 2002; Violle et al. 2007). Functional traits are measured at the individual level, however, they enable the classification and comparison of entire plant communities (Violle et al. 2007). For example, plant communities in harsh environments, such as dry and warm areas, typically consist of species with conservative traits that enhance survival under challenging abiotic conditions. In contrast, communities in more favorable environments often include species with acquisitive traits that optimize resource acquisition and growth (Poorter et al. 2019). These different functional composition in the communities affect directly on the ecosystem services, such as carbon storage, that can be driven by the dominant species (Grime 1998) or by diversity through resource portioning (Tilman 2001).

The drivers shaping ecosystem functioning often shift depending on the scale of study. At local and regional scales, biotic attributes, such as species composition and diversity, are the primary determinants of ecosystem services (Loreau et al. 2001; Pan et al. 2011). In contrast, at larger scales, such as national or global, abiotic attributes emerge as the dominant drivers of ecosystem services (Loreau et al. 2001). Among these abiotic factors, precipitation, temperature and soil characteristics are particularly important. For example, annual precipitation can positively influence vegetation carbon storage, whereas altitude and mean annual temperature can have negative effects (Zhao and Zhou 2006). Additionally, soil acidity can restrict plant growth (Gazol et al. 2022), thereby negatively affecting carbon storage. Similarly, soil fertility plays a key role in determining vegetation growth, as fertile soils support the development of more robust vegetation compared to less fertile ones (Bueno et al. 2018). These drivers and their relationship with ecosystem services can also vary depending on the ecosystems being considered.

BEF studies have predominantly focused on certain ecosystems due to their complexity and significance in providing ecosystem services (Van Der Plas 2019). Tropical forests, for instance, are widely recognized as the planet's largest carbon sinks, playing a crucial role in mitigating climate change (Pan et al. 2011). For example, Brazilian tropical forests encompass a variety of forest types, ranging from lowland forests to high-altitude ecosystems. Atlantic Cloud Forests is an example that occurs in the mountains at higher altitudes. These forests are characterized by unique and often endemic species adapted to specific environmental conditions, including significant temperature fluctuations, low temperatures, high humidity condensation, elevated soil moisture, and soils rich in organic matter (Bruijnzeel et al. 2011). In contrast, Dry Forests occurs in drier and warm regions, and present plants adapted to these environmental constrains. In Brazil the most known Dry Forest is the Caatinga biome, however, in Amazon region there are scattered fragments of Dry Forest, occurring on shallow soils related to outcrops of rocks derived from iron formations, granite and sandstone. Nevertheless, the BEF relationship may differ between dry forests and humid forests, due to different vegetation communities shaped by the intrinsic environmental characteristics, different forest structure, and others. Thus, ecosystem services (e.g. carbon storage) can be driven by different process and attributes.

The main objective of the study is to investigate how abiotic and biotic factors interact to influence ecosystem functioning, specifically tree aboveground carbon stock, across an environmental gradient in Brazilian tropical forests. Therefore, we addressed two mains questions: 1) What is the pattern of resource use strategies in tropical forests along a climatic gradient? 2) How do abiotic and biotic attributes drive AGC in tropical forests along a climatic gradient? We hypothesize that based on the continuum between resource acquisition (fast return and low energy cost) and conservation (slow return and high energy cost), we expect that wet forests present a community of plant species with acquisitive traits compared to dry forests, which are composed of more conservative ones. The mass ratio hypothesis (based on functional composition) and structural diversity could play a more significant role in dry forests, as functional trait composition (e.g., drought resistance traits) might be more critical in determining aboveground biomass stock than resource availability. Thus, we expect that across forests, the abiotic attributes (e.g., soil fertility, climate, and water availability) have a positive and direct effect on biotic (species richness and stem structural diversity) and an indirect and positive effect on AGC.

4.3. Material and Methods

Study area and forest plots selection

Data were used from a survey of Cloud and Dry Forests across Brazil. The Cloud Forests are located in the southeastern region of Brazil, while the Dry Forests are found in the northern part of the country (Fig. 1).

Cloud Forest

The data is from a survey conducted in the Mantiqueira Mountain Range (Serra da Mantiqueira), located in the Southeastern Brazil. The Mantiqueira Mountain Range covers parts of Minas Gerais, Rio de Janeiro, São Paulo and Espírito Santo states, and it is considered one of the highest mountain range in the east of South America, achieving 2.892 m (Gonzaga and Menini-Neto, 2017). The soil is composed predominantly of red-yellow ferralsols, red-yellow acrisols and rock outcrops.

It was selected seven cloud forests sites along the Meridional Mantiqueira: Morro do Careca in Serra dos Marins; Mata do Brejo da Lapa in Itatiaia National Park; Mata do Santo Agostinho in Serra do Papagaio State Park; and Setentrional Mantiqueira: Mata do Pico do Grama in Serra do Brigadeiro State Park; Mata das Macieiras in Caparaó National Park; forest close to the visitors center in Ibitipoca State Park and Mata da Cachoeira do Chapadão in RPPN Chapadão da Serra Negra. The areas were classified as Cloud Forests based on their microclimatic characteristics, which are largely influenced by altitude. These include low temperatures, high precipitation with frequent cloud cover even during the driest seasons, low insolation, frost, and strong winds (Bruijnzeel et al. 2011). Besides, it was selected sites with different topography, soil, climate variables and elevational quotas (gradient from 1057 m to 2325 m a.s.l.), trying to encompass high environmental heterogeneity among the areas.

In each site, were sampled ten plots (20×20 m). From each plot, the individuals with the diameter at breast height (1.30m from the soil) ≥ 5.0 cm were identified to species level, according to APG IV classifications (The Angiosperm Phylogeny Group et al. 2016).

Dry Forest

The climate of the study area corresponds to humid tropical ("Aw") type in the Köppen system, with a well-defined marked dry season between May and October (average precipitation < 60 mm in the driest months), and a rainy season between November and April. Average monthly temperatures range between 19 and 31°C. The data is from a survey conducted in the National Forest of Carajás (Amazon), located in the North of Brazil, in the southeastern of Pará State, Brazil. The National Forest of Carajás is composed by a environments mosaic due to different phytogeographic conditions, 95% of forests, 3% of ferruginous campo rupestre – canga, and 2 % by deciduous forest (in the middle of seasonal semi-deciduous forest and dense rain forest surrounding), and dry forests (Schaefer et al. 2009). Importantly, the DFs in Carajás are embedded in a distinct vegetation matrix (Amazonian Domain) having a differential climate compared with typical Seasonal (Dry) Forests from elsewhere in Brazil. They are different pedoenvironments that range from ferruginous canga outcrops to Oxisols, whose phytophysiological variations range from perennial to forests ombrophilous.

Thus, it was selected four forest sites: 1) "Águas Claras I", with nine plots, 2) "Águas Claras II" with 12 plots; 3) Mid Proterozoic Carajás Granite, with 10 plots; and 4) Você escreveu quthe Xingu Arquean Complex, with nine plots. In total, 40 plots were surveyed (20 m × 20 m = 400 m^2) in the study area. Within each plot, all trees having a diameter at breast height (DBH) ≥ 5.0 cm were identified to the species level, according to APG IV classifications (The Angiosperm Phylogeny Group et al. 2016).

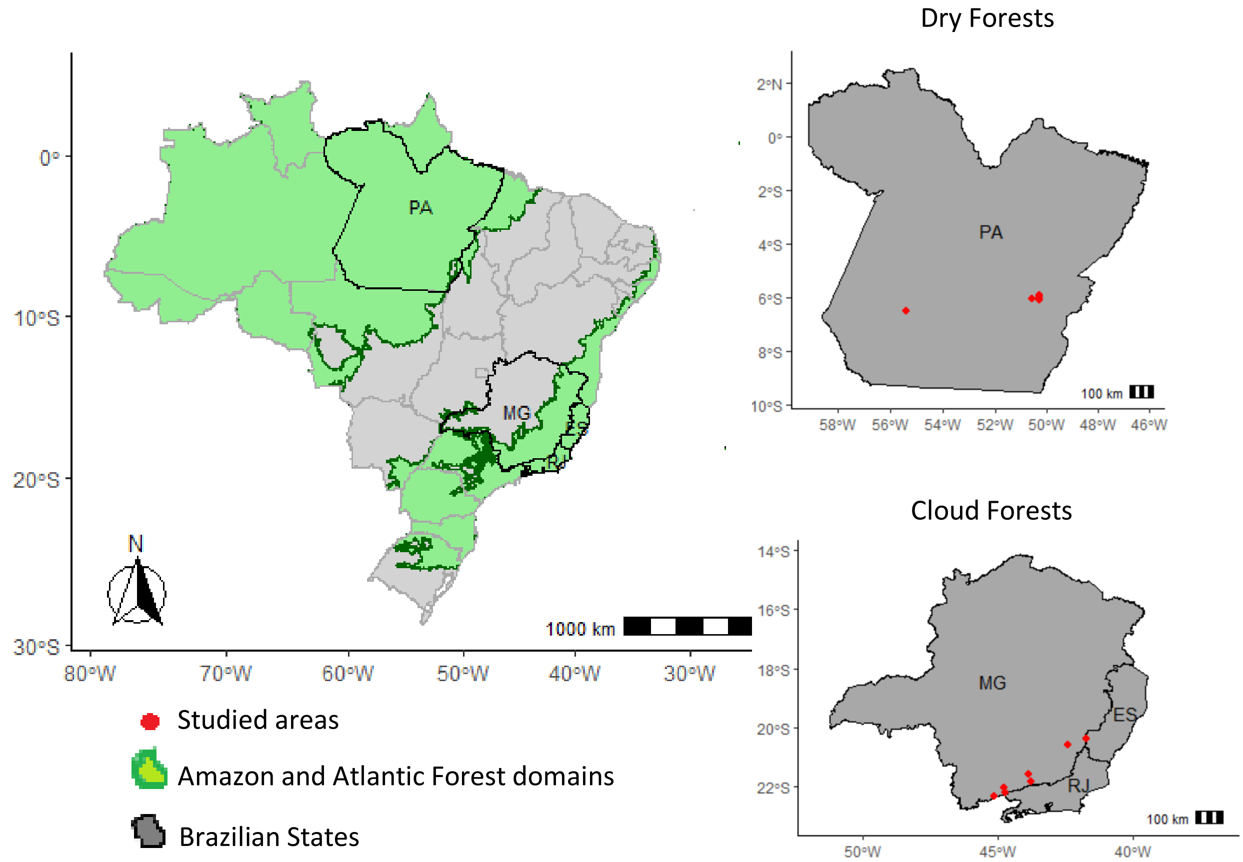

Figure 1. Map of the sampled locations in the Amazon Dry Forests (four areas) and Atlantic Cloud Forests (seven areas). PA = Pará State, MG = Minas Gerais State, RJ = Rio de Janeiro State, ES = Espírito Santo State.

Abiotic variables

We used sum of exchangeable bases (SB) as an indicator of soil fertility (Huston 2012; Poorter et al. 2017; Ali et al. 2019). The SB is composed of the sum of cations Ca2+, Mg2+, K+, and Na+, in cmolc/dm3. The soil sampling was slightly different for each forest type: i) Cloud forest: it was collected five topsoil samples (0 to 20 cm of depth, without the leaf litter) from the corners and center of each plot to obtain a composite sample for each plot (Donagemma et al. 2011), and for ii) Dry forest: it was collected three topsoil samples (0 to 10 cm of depth, without the leaf litter) from the corners and center of each plot to obtain a composite sample for each plot (Donagemma et al. 2011).

We initially accessed a diverse range of climatic variables and selected the final set based on a Spearman correlation matrix (Fig. S1), prioritizing biologically meaningful variables while ensuring a comprehensive representation of climatic variability; thus, we used maximum temperature (representing temperature variation), annual precipitation (capturing precipitation patterns), climatic water deficit (reflecting the interaction between soil water availability, plant responses, and temperature), and sum of bases (indicating soil fertility); to obtain these variables, we used the "geodata" package in R (R Core Team 2019) to download data from CHELSA-TraCE21k TraCE21k (Karger et al. 2023) at a minimum resolution of 30 arcseconds (~1 km² at the equator), a dataset derived from downscaling TraCE-21k data using the CHELSA V1.2 algorithm ("Climatologies at high resolution for the earth's land surface areas"); finally, we used the "*terra*" package to extract values for each specific geographic location corresponding to the forest types.

Biotic variables

We calculated the species richness of each plot, summing up the number of species present. Furthermore, we accessed species wood density through the Global Wood Density Database, virtual herbaria, and literature (Zanne et al. 2009; Lorenzi 1992, 2000, 2009). Additionally, we calculated the community weighted mean of wood density (CWM_WD) weighting by the species abundance in the community of each plot, using the packages "tidyr" and "dplyr" of R software.

For the vegetation structure, we used a metric called stem structural diversity (SSD), considering diameter at breast height (DBH) and height (Zhai et al. 2022). This metric was calculated similarly to functional dispersion (Laliberté and Legendre 2010). SSD measures the average distance of each individual in a sampling plot from the centroid of all individuals, where the centroid is defined in a two-dimensional space based on DBH and height.

We calculated the tree aboveground carbon stock (AGC) for each plot, summing up the values of each tree and quantifying based on the carbon stock per hectare. To estimate carbon stock of individual trees based on DBH and height measurements, we used a specific allometric equations (Chave et al. 2014) and multiplied for 0.5, assuming that 50% of biomass is carbon (Thomas and Martin 2012). For the measurements, we extrapolated the AGC values to a per-hectare basis.

$$AGB = 0.0673 * (\mathrm{WD} * (\mathrm{DBH})^2 * \mathrm{H})^{0.976}$$

$$AGC = AGB * 0.5$$

Whereas: AGB: aboveground biomass (kg); WD: wood density (g/cm³); DBH: diameter at breast height (cm), H: tree height (m), AGC: aboveground carbon stock.

Statistical analyses

Environmental gradient

Principal Component Analysis (PCA) was performed to reduce the dimensionality of the data and identify the environmental gradient and the main patterns of variation in the climatic, soil and diversity variables. PCA was conducted using the “prcomp” function from the “base” R package (R Core Team, 2019), which applies the decomposition of the covariance or correlation matrix of the original data. Prior to applying PCA, the data were standardized to ensure that all variables had a mean of zero and a standard deviation of one, using the “scale” function in R.

Species composition

Non-Metric Multidimensional Scaling (NMDS) was applied to the Bray-Curtis dissimilarity matrix to visualize the relationships between samples in a lower-dimensional space. The “metaMDS” function from the vegan package was used with 100 iterations and a maximum of 500 optimization attempts. The Bray-Curtis dissimilarity index was used to assess community differences between samples, calculated based on species abundance. A Bray-Curtis dissimilarity matrix was generated using the “vegdist” function from the vegan package in R.

Tree aboveground carbon stock

T test was used to compare the log-transformed AGC between Cloud and Dry Forests. Before performing the test, AGC was log transformed to improve the normality of the distribution. Assumptions of normality and homoscedasticity were checked using the “qqp” and “leveneTest” function, respectively, of the of the “car” package.

Community weighted mean of wood density

The Mann-Whitney-Wilcoxon test was used to compare the Community Weighted Mean of Wood Density (CWM_WD) between Cloud and Dry Forests. This non-parametric test was chosen as it does not require the assumption of normality in the data distribution. The analysis was performed in R using the “wilcox.test” function, specifying the two groups (cloud and dry forests) as the independent variable and the CWM wood density as the dependent variable. A significance level of 0.05 was applied to assess the results.

Structural Equation Modeling

We used Piecewise Structural Equation Modeling (pSEM) to examine the process involved in the resource use strategy of the two forests and to understand how biotic and abiotic attributes influence aboveground carbon (AGC), using the selected variables (Fig. S1). This method allows for the modular adjustment of structural models, enabling the independent evaluation of each equation within the model. Analyses were performed using the "piecewiseSEM" and "nlme" packages in the R software was used (R Core Team 2019), incorporating three Linear Mixed Models (LMMs), including areas as random effect due to spatial autocorrelation (Table 1). Special correlation was tested using "mantel" function from the "vegan" package in the R software was used (R Core Team 2019).

Table 1. Response and predictor variables, and the three Linear Mixed Models of Piecewise Structural Equation Modeling.

Models	Dependent variables	Independents variables
Model 1	Species richness	Stem structural diversity, Maximum temperature, Sum of bases, Annual precipitation
Model 2	AGC	Species richness, Stem structural diversity, Sum of bases, Annual precipitation, Climatic water deficit, Maximum temperature, Community weighted mean of wood density
Model 3	CWD_WD	Species richness, Stem structural diversity, Sum of bases, Climatic water deficit, Annual precipitation, Maximum temperature

Model fitting and evaluation were based on maximum likelihood estimation, and global model adequacy was assessed using Fisher's C-test. All variables were log transformed and standardized (z-scores) to facilitate the interpretation of effect coefficients and ensure comparability among variables. Results were interpreted based on the coefficient of determination (Conditional R^2) for each individual equation and the direct, indirect, and total effects within the system.

4.4. Results

Environmental gradient

In the three PCAs , the first two axes explained more than 65% of the total data variation (soil, climatic, and diversity. Fig. S3). In the soil-related PCA (Fig. S3 B), PC1 explained 37.5% and PC2 27.6% of the variance Cloud Forests are placed in more acid areas, whereas Dry Forests are placed in more fertile areas in more clayey soils (Table S1 A). Regarding the climate-related PCA (Fig. S3A), PC1 explained 58.3% of the variance, while PC2 accounted for 27.6%; Cloud Forests were associated with a higher annual temperature range, whereas Dry Forests exhibited higher maximum and annual mean temperatures (Table S1B). Finally, based on diversity-related PCA (Fig. S3 C), PC1 explained 41.6% and PC2 30.4% of the variance, however, forest types have no clear separation, which the variables were differently correlated to each axis (Table S1 C).

Species composition

We found 219 tree species in Cloud Forest, and 311 in Dry Forest, represented by 82 families (Table S2). There were only eight species shared between the two forest types: *Aspidosperma parvifolium, Esenbeckia grandiflora, Myrcia splendens, Protium heptaphyllum, Prunus myrtifolia, Roupala brasiliensis, Roupala montana,* and *Vitex polygama*. The NMDS results (Fig. S4) also confirmed it, since there was a very slightly overlap between the ellipses, and the NMDS stress value was 0.107, indicating a good fit.

Tree aboveground carbon stock

The total AGC across all Cloud Forest plots was 14977.28 tons, with individual plot values ranging from 15.13 to 632.90 tons. In contrast, the total aboveground carbon stock in the Dry Forest was 157.1139 tons, with plot values ranging from 44.44 to 632.90 tons. Based on tons per hectare, there was difference in AGC between Dry and Cloud Forest (T = 4.28, DF = 108, p-value < 0.001), at a level of 5% of significance, which Cloud Forest showed mean values (2664 ± 1889) not different from Dry Forest (4699 ± 3395) (Fig. 2).

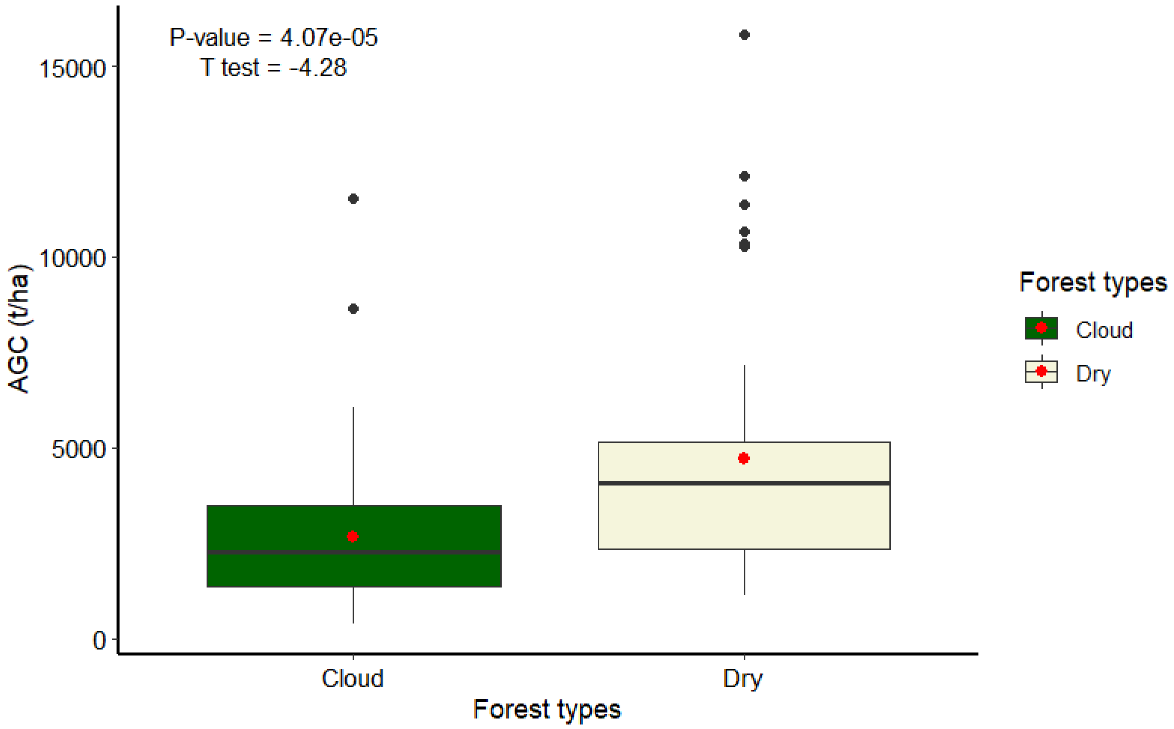

Figure 2. Comparison of aboveground carbon stock (AGC) among forest types (T-test, $P < 0.05$). Red dots represent the mean.

Community weighted mean of wood density

The results showed no differences in CWM of wood density between the two forest types (W = 1299.50, p-value = 0.5343), which Cloud Forest (0.66 ± 0.04) showed lower values than Dry Forest (0.65 ± 0.08) (Fig. 3).

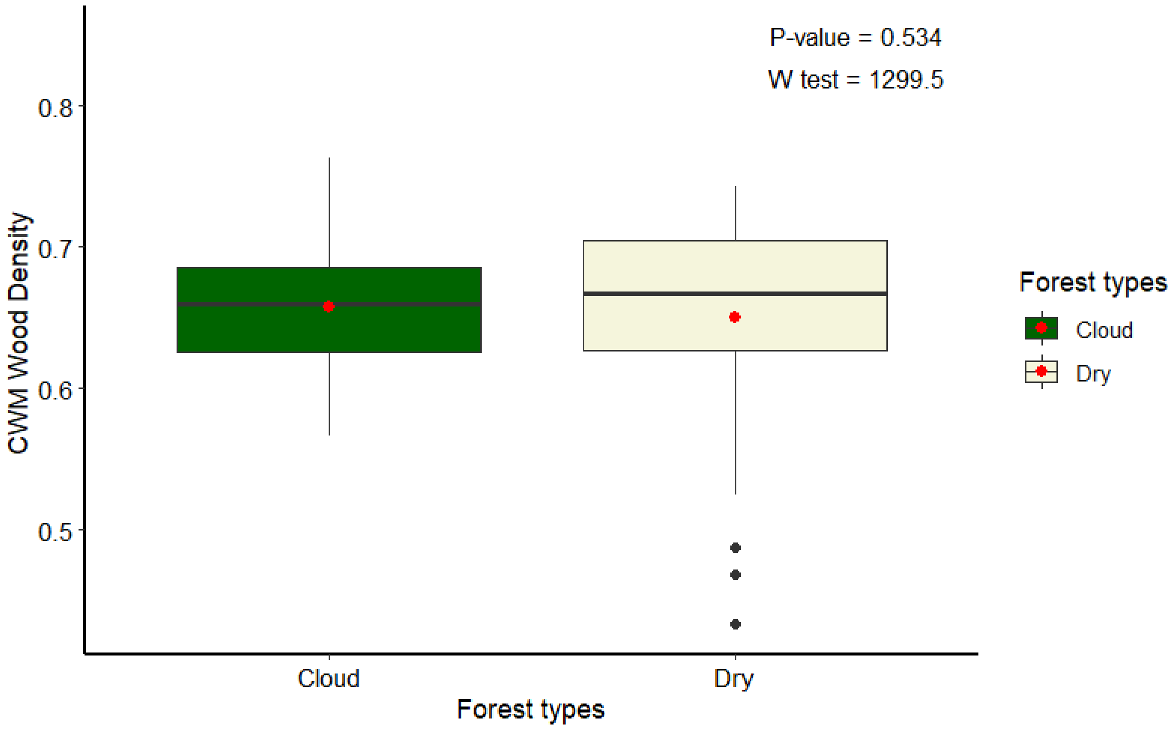

Figure 3. Comparison of community weighted mean of wood density (AGC) among forest types. Red dots represent the mean.

Relationship between abiotic, biotic variables and aboveground carbon stock

Piecewise Structural equation models (pSEM) were constructed to analyze: i) the effects (direct and indirect) of the selected variables (Table 1) (based on a Spearman correlation matrix) on CWM_WD to understand how is the process of resource use strategy in the two forests and the effects in the AGC, ii) the effects on species richness, and iii) the effects of all selected variables on AGC. The results (Fig. 4) based on Fisher's test (C = 2.451, df = 2, p-value = 0.294) the model presented a good fit. We observed only direct effects on the response variables, which CWM_WD was directly positively influenced by sum of bases (0.450, p-value > 0.001) and directly negatively with species richness (-0.203, p-value= 0.03), and AGC was influenced directly and positively by stem structural diversity (0.525, p-value < 0.001), and by maximum temperature (0.334, p-value= 0.048) (Fig. 4).

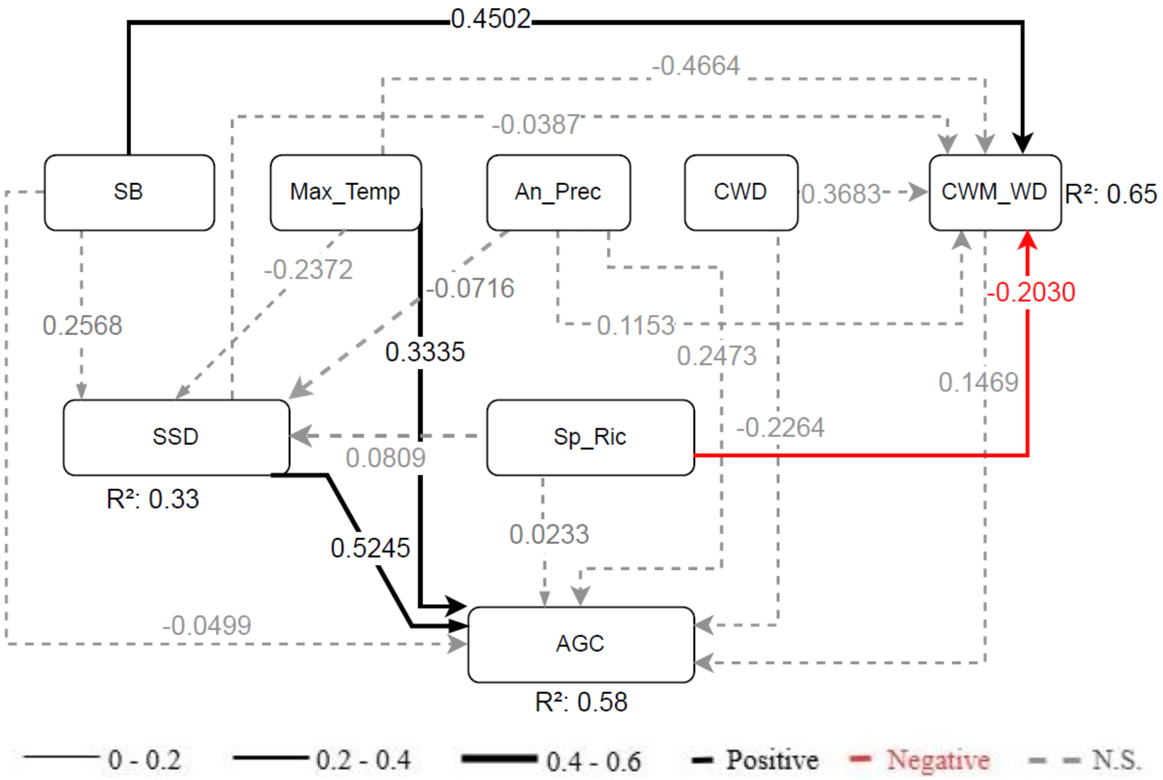

Figure 4. Piecewise Structural Equation modeling representing: i) how tree aboveground carbon stock (AGC) is affected by abiotic and biotic factors, ii) how diversity (species richness) is affected by abiotic factors, and iii) how wood density is affected by abiotic and biotic factors. SB: sum of bases; Max_temp: maximum temperature; An_prec: annual precipitation; CWD: climatic water deficit; CWD_WD: community weighted mean of wood density; Sp_richness: species richness; SSD: stem structural diversity; AGC: tree aboveground carbon stock; Black arrows: positive relationship; Red arrow: negative relationship; Solid lines: statistically significant results ($p < 0.05$); Dashed lines: nonsignificant results ($p > 0.05$). The thickness of the lines represent the relationship power. The values associated to the line means the coefficient value for each relationship, and R² represents the variance in Y-axis linearly explained by X-axis.

4.5. Discussion

Despite there are two contrasting forest types, Cloud and Dry Forests, we considered an environmental gradient, since our results showed a clear pattern of abiotic (climatic and soil) gradient. Based on the aboveground carbon stock Dry Forests presented higher mean values compared to Cloud Forests, and no clear separation in resource use strategies between the two forests, since there was no difference in community weighted mean of wood density. Finally, there was not any effect on diversity metrics, however, there was a positive and direct effect of soil fertility on wood density and, positive and direct effect of maximum temperature and stem structural diversity on aboveground carbon stock (AGC).

There was a clear environmental gradient within the areas, whereas the Cloud Forest showed more acidity soil with high levels of silty and organic matters, that is a characteristic of high levels of leaching and the influence of low temperatures combined with humidity (Jarvis and Mulligan 2011).

The observed difference in species composition between the two forests was expected, given that they are situated in contrasting environments that filter different species; nevertheless, nine of the 521 species were found in both areas. This result, suggest that these species can be more generalists and occur in different environments and altitudes. It is crucial to gain a deeper understanding of these generalist species, especially in the context of ongoing climate change (Van der Putten et al. 2010), as they can play a significant role in restoration programs.

The environmental differences between the forests were reflected in the variation in AGC. In high-altitude environments, factors such as shallow and acidic soils can restrict tree growth (Gazol et al. 2022), whereas the conditions in the studied Dry Forest, including higher soil fertility, may have favored tree growth. Our results corroborates with studies showing values for carbon stock ranging from around 100 t/ha (Girardin et al. 2014) up to 384.16 t/ha (Alvarez et al. 2012), in Cloud Forests. However, for Dry Forest, the results found in our research are higher than other studies that found a range from 19 to 67.3 t/ha of carbon for Dry Forest (Skutsch and Ba 2010; Aguiar et al. 2014), but corroborates with Tiessen et al. (1998) that found approximately the same values.

Based on resource use strategies, harsh environments select species with conservative characteristics, such as high wood density (Poorter et al. 2019), to deal with high temperatures and high levels of disturbance. However, in our study, there was no difference between forests. Variations in vegetation structure facilitate resource partitioning, which in turn enables the coexistence of a high number of species. This coexistence is driven by niche complementarity, where species occupy distinct niches, allowing them to coexist (Tilman et al. 2014). There is a difference on the effects of biodiversity in the ecosystem functioning when considering the different spatial scales (Loreau et al. 2001). For instance, at local scale, the effects of biotic attributes can be more prominent than abiotic ones, however, considering regional and large spatial scales, abiotic (e.g. soil fertility, climate, water availability) attributes can be more important than biotic ones (Loreau et al. 2001). Our study corroborates with Loreau et al. (2001), as there was a positive relationship between maximum temperature and AGC, additionally the stem structural diversity also showed a positive relationship.

4.6. Conclusion

Despite the environmental differences between forests there was no difference in resource use strategies, based on community weighted mean of wood density.

There is difference in tree aboveground carbon stock between Cloud and Dry Forests, whereas Dry Forests higher values compared to Dry ones.

In a regional scale the most important driver of tree aboveground carbon stock is maximum temperature and stem structural diversity, and the community weighted mean of wood density is driven positively by soil fertility and negatively by species richness.

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4.8. Supplementary Information

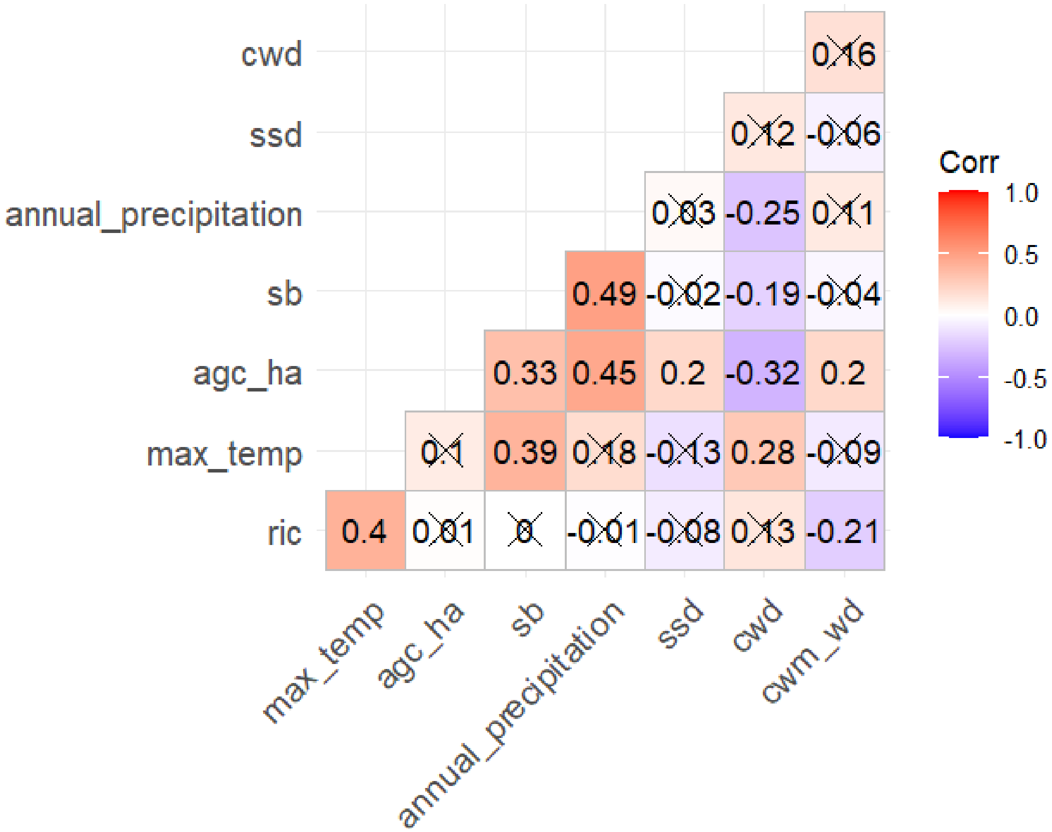

Figure S1. Spearman correlation matrix. sb = Sum of bases, max_temp = maximum temperature, ric = species richness, cwm_wd = community weighted mean of wood density, agc_ha = tree aboveground carbon stock per hectare, cwd = climatic water deficit, ssd = stem structural diversity, annual_precipitation = annual precipitation. The “X” in the cells means that the correlation was not significant at a level of 5%. The colors represent the intensity and the direction of the correlation, which light colors are weak and dark are strong, and purple means negative and red positive correlations.

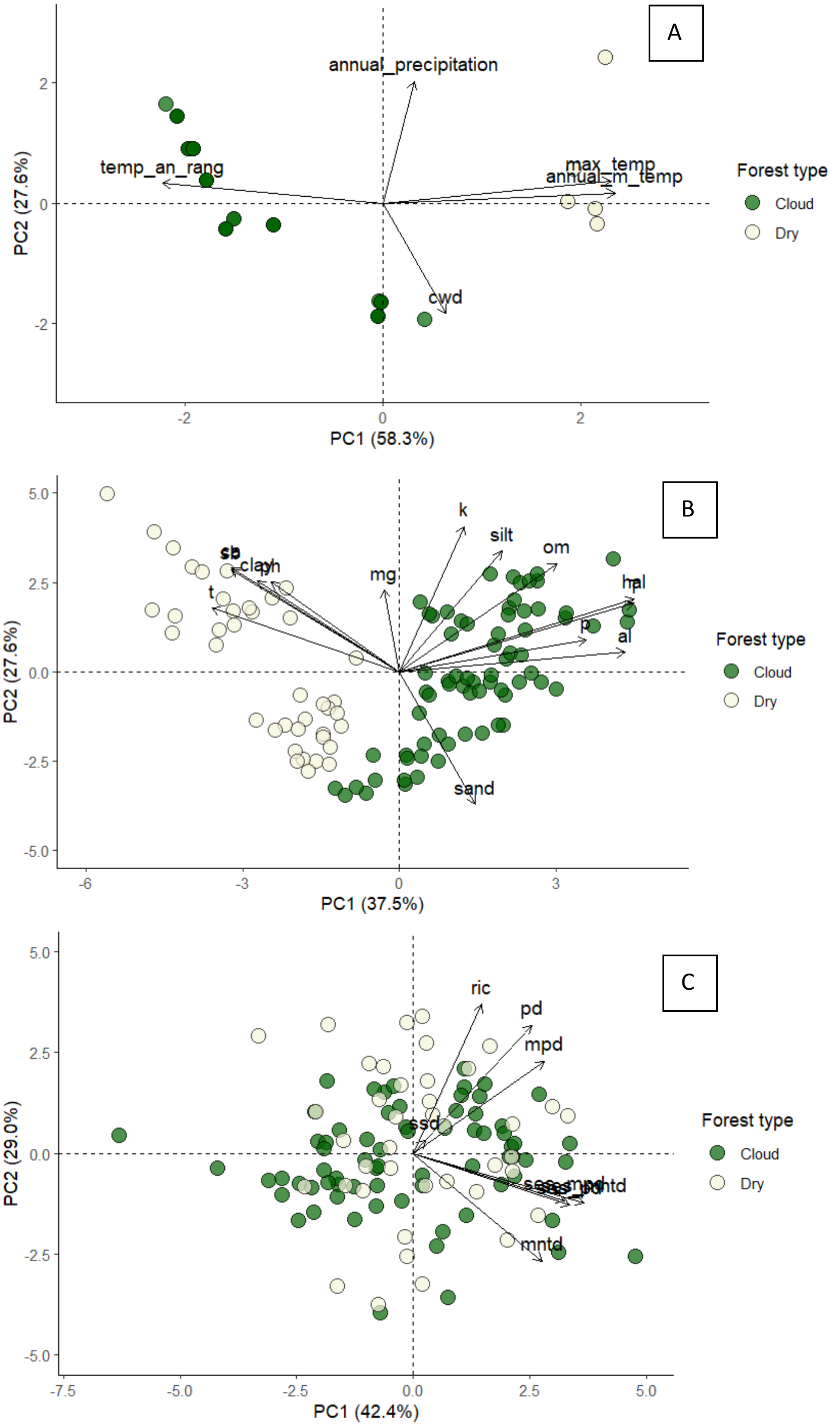

Figure S3. Principal component analysis (PCA) for climatic, soil and diversity variables. In this plot, the points represent the observations (sample units), while the arrows indicate the original variables. The plot was adjusted to highlight the first two principal components (PC1 and PC2), which explained the majority of the variance in the data. The arrows represent the climatic (A), soil (B), and diversity (C) variables. Green points: Cloud Forests, Biege points: Dry Forests.

Table S1. Correlation of soil, climate, and diversity variables with PCA axes 1 and 2, along with associated p-values. Significant correlations are indicated by p-values < 0.05. Table A: Soil-related PCA; Table B: Climate-related PCA; Table C: Diversity-related PCA.

PC1		A
Soil Variables	**Correlation**	**p.value**
H+Al	0.8849880	1,21E-31
T	0.8842430	1,68E-31
Al	0.8491362	1,03E-25
p	0.7056138	7,50E-12
om	0.5930976	8,66E-06
Silt	0.3875985	2,87E+01
Sand	0.2850017	2,55E+03
k	0.2438147	1,03E+04
pH	-0.4847148	8,05E-02
Clay	-0.5349263	1,74E-03
SB	-0.6330805	1,16E-07
Ca	-0.6336695	1,09E-07
t	-0.7052546	7,92E-12

PC2		
Soil Variables	**Correlation**	**p.value**
k	0.7992669	1,25E-19
Silt	0.6631671	2,94E-09
om	0.5953906	6,87E-06
Ca	0.5743131	5,38E-05
SB	0.5614257	1,77E-04
Clay	0.4984242	3,01E-02
pH	0.4936783	4,25E-02
Mg	0.4500353	8,11E-01
H+Al	0.4015461	1,38E+01
T	0.3764384	5,05E+01
t	0.3487179	1,89E+02
Sand	-0.7308410	1,27E-13

PC1		B
ClimateVariables	**Correlation**	**p.value**
Annual mean temperature	0.9923119	7,71E-94
Maximum temperature	0.9744597	6,91E-66
CWD	0.2690429	4,48E+03
Temperature annual range	-0.9430722	1,88E-47

PC2

ClimateVariables	Correlation	p.value
Annual precipitation	0.8552009	1,33E-26
CWD	-0.7744950	3,26E-17

PC1 C

Diversity Variables	Correlation	p.value
Ses.MNTD	0.8738867	1,29E-29
Ses.PD	0.8033577	4,61E-20
Ses.MPD	0.7759786	2,38E-17
MPD	0.6696715	1,26E-09
MNTD	0.6617749	3,52E-09
PD	0.6048543	2,60E-06
Species richness	0.3516484	1,65E+02

PC2

Diversity Variables	Correlation	p.value
Species richness	0.8820302	4,40E-31
PD	0.7592320	7,16E-16
MPD	0.5438890	8,22E-04
SSD	-0.2800537	3,04E+03
ses.MPD	-0.2916485	1,99E+03
ses.MNTD	-0.3044091	1,22E+03
ses.PD	-0.6375022	6,96E-08
MNTD	0.8820302	4,40E-31

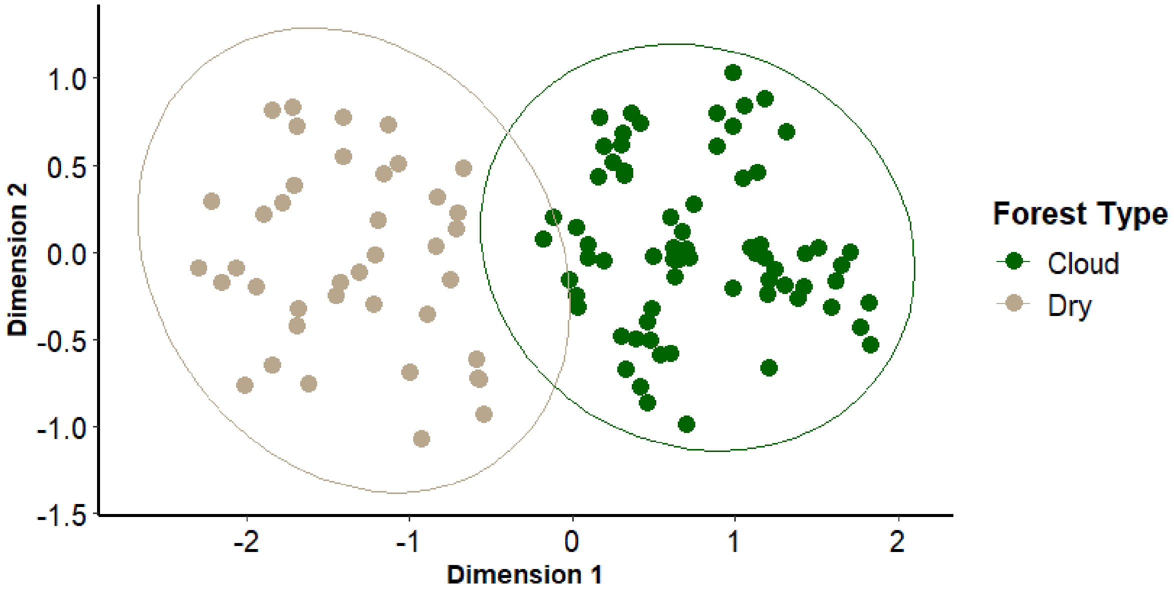

Figure S4. Non-Metric Multidimensional Scaling (NMDS) result. The adequacy of the NMDS was based on the stress value, which reflects the quality of it. The ellipses representing the confidence interval (95%) showed that the composition of species in the two forests. Green points: Cloud Forests, Biege points: Dry Forests.

Table S2. List of families and species with their associated forest types.

Families and Species	Forest Type
Achariaceae	
Lindackeria paludosa	Dry
Anacardiaceae	
Astronium gracile	Dry
Astronium lecointei	Dry
Myracrodruon fraxinifolium	Dry
Spondias mombin	Dry
Tapirira amazonica	Dry
Tapirira guianensis	Dry
Tapirira obtusa	Cloud
Thyrsodium paraense	Dry
Thyrsodium spruceanum	Dry
Annonaceae	
Annona cacans	Cloud
Annona emarginata	Cloud
Annona montana	Dry
Cymbopetalum euneurum	Dry
Duguetia cadaverica	Dry
Duguetia flagellaris	Dry
Duguetia stelechantha	Dry
Guatteria australis	Cloud
Guatteria foliosa	Dry
Guatteria olivacea	Dry
Guatteria pohliana	Cloud
Guatteria polyantha	Cloud
Guatteria sellowiana	Cloud
Rollinia insignis	Dry
Xylopia polyantha	Dry
Apocynaceae	
Aspidosperma araracanga	Dry
Aspidosperma macrophyllum	Dry
Aspidosperma multiflorum	Dry
Aspidosperma nitidum	Dry
Aspidosperma olivaceum	Cloud
Aspidosperma parvifolium	Cloud, Dry
Aspidosperma subincanum	Dry
Couma guianensis	Dry
Couma utilis	Dry
Himatanthus sucuuba	Dry
Rauvolfia sprucei	Dry
Tabernaemontana angulata	Dry

Tabernaemontana muricata	Dry
Aquifoliaceae	
Ilex paraguariensis	Cloud
Ilex theezans	Cloud
Araliaceae	
Schefflera calva	Cloud
Schefflera morototoni	Dry
Schefflera vinosa	Cloud
Arecaceae	
Astrocaryum aculeatum	Dry
Astrocaryum gynacanthum	Dry
Attalea maripa	Dry
Euterpe edulis	Cloud
Oenocarpus bacaba	Dry
Oenocarpus distichus	Dry
Syagrus comosa	Dry
Syagrus oleracea	Dry
Asteraceae	
Baccharis oblongifolia	Cloud
Eremanthus erythropappus	Cloud
Eremanthus incanus	Cloud
Moquiniastrum polymorphum	Cloud
Piptocarpha macropoda	Cloud
Piptocarpha regnellii	Cloud
Symphyopappus compressus	Cloud
Vernonanthura discolor	Cloud
Bignoniaceae	
Handroanthus impetiginosum	Dry
Handroanthus vellosoi	Cloud
Jacaranda brasiliana	Dry
Jacaranda copaia	Dry
Jacaranda puberula	Cloud
Tabebuia ochracea	Dry
Tabebuia roseoalba	Dry
Tabebuia serratifolia	Dry
Bixaceae	Dry
Cochlospermum orinocense	Dry
Boraginaceae	
Cordia exaltata	Dry
Cordia hirta	Dry
Cordia naidophila	Dry
Cordia nodosa	Dry
Burseraceae	
Crepidospermum rhoifolium	Dry

Protium apiculatum	Dry
Protium aracouchini	Dry
Protium elegans	Dry
Protium guianense	Dry
Protium heptaphyllum	Cloud, Dry
Protium nitidifolium	Dry
Protium nitidum	Dry
Protium pilosissimum	Dry
Protium robustum	Dry
Protium rubrum	Dry
Protium spruceanum	Dry
Protium subserratum	Dry
Protium tenuifolium	Dry
Tetragastris altissima	Dry
Tetragastris panamensis	Dry
Trattinnickia burserifolia	Dry
Trattinnickia panamensis	Dry
Calophylaceae	
Kielmeyera membranacea	Cloud
Cardiopteridaceae	
Citronella paniculata	Cloud
Caricaceae	
Jacaratia spinosa	Dry
Celastraceae	
Cheiloclinium cognatum	Dry
Maytenus evonymoides	Cloud
Maytenus gonoclada	Cloud
Maytenus guyanensis	Dry
Maytenus robusta	Cloud
Monteverdia gonoclada	Cloud
Chrysobalanaceae	
Couepia venosa	Cloud
Hirtella bicornis	Dry
Hirtella hispidula	Dry
Hirtella racemosa	Dry
Licania hypoleuca	Dry
Licania octandra	Dry
Licania sprucei	Dry
Clethraceae	
Clethra scabra	Cloud
Clusiaceae	
Calophyllum brasiliense	Dry
Caraipa densifolia	Dry
Clusia criuva	Cloud

Clusia weddelliana	Dry
Garcinia madruno	Dry
Symphonia globulifera	Dry
Combretaceae	
Buchenavia congesta	Dry
Buchenavia grandis	Dry
Buchenavia parvifolia	Dry
Buchenavia unifolia	Dry
Connaraceae	
Connarus perrottetii	Dry
Crhysobalanaceae	
Hirtella hebeclada	Cloud
Cunnoniaceae	
Weinmannia paulliniifolia	Cloud
Weinmannia pinnata	Cloud
Cunoniaceae	
Lamanonia ternata	Cloud
Cyatheaceae	
Cyathea corcovadensis	Cloud
Ebenaceae	
Diospyros cavalcantei	Dry
Elaeocarpaceae	
Sloanea guianensis	Cloud
Sloanea hirsuta	Cloud
Sloanea nitida	Dry
Sloanea pubescens	Dry
Sloanea schomburgkii	Dry
Erythroxylaceae	
Erythroxylum carajense	Dry
Erythroxylum citrifolium	Dry
Erythroxylum macrophyllum	Dry
Erythroxylum nelson	Dry
Erythroxylum pelleterianum	Cloud
Escalloniaceae	
Escallonia bifida	Cloud
Euphorbiaceae	
Alchornea glandulosa	Cloud
Alchornea triplinervia	Cloud
Aparisthmium cordatum	Dry
Croton alchorneicarpus	Cloud
Croton cajucara	Dry
Croton urucurana	Dry
Glycydendron amazonicum	Dry
Mabea angularis	Dry

Maprounea guianensis	Dry
Sapium biglandulosum	Dry
Sapium glandulatum	Dry
Tetrorchidium parvulum	Cloud
Fabaceae	
Abarema cochleata	Dry
Abarema mataybifolia	Dry
Acacia polyphylla	Dry
Anadenanthera rigida	Dry
Andira fraxinifolia	Cloud
Bauhinia macrostachya	Dry
Bauhinia pulchella	Dry
Bauhinia ungulata	Dry
Bowdichia virgilioides	Dry
Cassia leandrii	Dry
Cenostigma tocantinum	Dry
Chamaecrista itambana	Cloud
Chloroleucon acacioides	Dry
Copaifera duckei	Dry
Copaifera martii	Dry
Copaifera multijuga	Dry
Dalbergia foliolosa	Cloud
Dialium guianense	Dry
Dicorynia paraensis	Dry
Diplotropis purpurea	Dry
Dipteryx odorata	Dry
Dipteryx polyphylla	Dry
Enterolobium contortisiliquum	Dry
Erythrina ocraceae	Dry
Hymenaea courbaril	Dry
Hymenaea intermedia	Dry
Hymenaea parvifolia	Dry
Inga alba	Dry
Inga blanchetiana	Cloud
Inga cayennensis	Dry
Inga gracilifolia	Dry
Inga grandiflora	Dry
Inga huberi	Dry
Inga lateriflora	Dry
Inga laurina	Dry
Inga longiflora	Dry
Inga macrophylla	Dry
Inga marginata	Dry

Inga panamensis	Dry
Inga paraensis	Dry
Inga rubiginosa	Dry
Inga sellowiana	Cloud
Inga stipularis	Dry
Inga thibaudiana	Dry
Inga umbratica	Dry
Machaerium aculeatum	Dry
Machaerium brasiliense	Cloud
Mimosa acutistipula	Dry
Ormosia altimontana	Cloud
Ormosia paraensis	Dry
Parapiptadenia rigida	Dry
Parkia multijuga	Dry
Parkia platycephala	Dry
Piptadenia rigida	Dry
Piptadenia suaveolens	Dry
Platymiscium duckei	Dry
Platymiscium paraense	Dry
Pseudopiptadenia psilostachya	Dry
Pterocarpus officinalis	Dry
Pterocarpus rohrii	Dry
Pterodon emarginatus	Dry
Senna macranthera	Cloud
Stryphnodendron guianense	Dry
Stryphnodendron racemiferum	Dry
Swartzia apetala	Cloud
Swartzia arumateuana	Dry
Swartzia corrugata	Dry
Tachigali melanocarpa	Dry
Tachigali myrmecophila	Dry
Goupiaceae	
Goupia glabra	Dry
Humiriaceae	
Endopleura uchi	Dry
Sacoglottis guianensis	Dry
Sacoglottis mattogrossensis	Dry
Vantanea guianensis	Dry
Hypericaceae	
Vismia brasiliensis	Cloud
Vismia guianensis	Cloud
Vismia parviflora	Cloud

Icacinaceae	
Emmotum nitens	Dry
Lacistemataceae	
Lacistema aggregatum	Dry
Lamiaceae	
Hyptidendron asperrimum	Cloud
Vitex polygama	Cloud, Dry
Vitex sellowiana	Cloud
Vitex triflora	Dry
Lauraceae	
Aniba canelilla	Dry
Aniba firmula	Cloud
Aniba guianensis	Dry
Beilschmiedia taubertiana	Cloud
Cinnamomum glaziovii	Cloud
Endlicheria paniculata	Cloud
Licaria canella	Dry
Mezilaurus duckei	Dry
Nectandra lanceolata	Cloud
Nectandra oppositifolia	Cloud
Ocotea aciphylla	Cloud
Ocotea amazonica	Dry
Ocotea bicolor	Cloud
Ocotea caudata	Dry
Ocotea corymbosa	Cloud
Ocotea daphnifolia	Cloud
Ocotea dispersa	Cloud
Ocotea divaricata	Cloud
Ocotea ferrea	Dry
Ocotea laxa	Cloud
Ocotea longifolia	Dry
Ocotea matogrossensis	Dry
Ocotea minor	Dry
Ocotea nutans	Cloud
Ocotea odorifera	Cloud
Ocotea olivacea	Dry
Ocotea oppositifolia	Cloud
Ocotea pulchella	Cloud
Ocotea tabacifolia	Dry
Ocotea tristis	Cloud
Persea major	Cloud
Persea microphylla	Cloud
Persea rufotomentosa	Cloud
Persea venosa	Cloud

Rhodostemonodaphne grandis	Dry
Systemonodaphne geminiflora	Dry
Lecythidaceae	
Eschweilera coriacea	Dry
Eschweilera grandiflora	Dry
Eschweilera nana	Dry
Eschweilera pedicellata	Dry
Eschweilera truncata	Dry
Lecythis zabucajo	Dry
Malpighiaceae	
Byrsonima crispa	Dry
Byrsonima incarnata	Dry
Byrsonima variabilis	Cloud
Malpiguiaceae	
Byrsonima ligustrifolia	Cloud
Malvaceae	
Apeiba echinata	Dry
Bombacopsis nervosa	Dry
Ceiba pentandra	Dry
Eriotheca globosa	Dry
Guazuma ulmifolia	Dry
Helicteres sacarolha	Dry
Lueheopsis rosea	Dry
Pachira endecaphylla	Cloud
Pachira globosa	Dry
Pachira spectabilis	Dry
Pseudobombax longiflorum	Cloud
Rhodognaphalopsis duckei	Dry
Sterculia excelsa	Dry
Theobroma speciosum	Dry
Melastomataceae	
Huberia glazioviana	Cloud
Huberia nettoana	Cloud
Leandra aurea	Cloud
Leandra salicina	Cloud
Leandra secunda	Dry
Miconia budlejoides	Cloud
Miconia chartacea	Cloud
Miconia cinnamomifolia	Cloud
Miconia cubatanensis	Cloud
Miconia cuspidata	Dry
Miconia holosericea	Dry
Miconia latecrenata	Cloud
Miconia lepidota	Cloud

Miconia mellina	Cloud
Miconia pusilliflora	Cloud
Miconia pyrifolia	Dry
Miconia sellowiana	Cloud
Miconia spichigeri	Dry
Miconia tetraspermoides	Dry
Mouriri angulicosta	Dry
Mouriri dimorphandra	Dry
Mouriri ficoides	Dry
Mouriri grandiflora	Dry
Mouriri huberi	Dry
Mouriri nigra	Dry
Meliaceae	
Cabralea canjerana	Cloud
Cedrela fissilis	Dry
Cedrela odorata	Dry
Guarea silvatica	Dry
Trichilia catigua	Cloud
Trichilia emarginata	Cloud
Trichilia micrantha	Dry
Trichilia pallida	Dry
Menispermaceae	
Abuta grandifolia	Dry
Abuta guianensis	Dry
Monimiaceae	
Macropeplus dentatus	Cloud
Macropeplus ligustrinus	Cloud
Mollinedia gilgiana	Cloud
Mollinedia schottiana	Cloud
Moraceae	
Bagassa guianensis	Dry
Batocarpus amazonicus	Dry
Brosimum acutifolium	Dry
Brosimum gaudichaudii	Dry
Brosimum guianense	Dry
Brosimum longifolium	Dry
Brosimum rubescens	Dry
Clarisia ilicifolia	Dry
Clarisia racemosa	Dry
Ficus guianensis	Dry
Ficus mexiae	Cloud
Ficus obtusifolia	Dry
Ficus obtusiuscula	Cloud
Ficus organensis	Cloud

Helicostylis tomentosa	Dry
Helicostylis turbinata	Dry
Maclura tinctoria	Dry
Maquira guianensis	Dry
Maquira sclerophylla	Dry
Perebea mollis	Dry
Sorocea bonplandii	Cloud
Sorocea guilleminiana	Dry
Sorocea ilicifolia	Dry
Myristicaceae	
Virola calophylla	Dry
Virola michelii	Dry
Myrtaceae	
Blepharocalyx salicifolius	Cloud
Calyptranthes tricona	Cloud
Calyptranthes widgreniana	Cloud
Campomanesia laurifolia	Cloud
Eugenia brasiliensis	Cloud
Eugenia cerasiflora	Cloud
Eugenia florida	Cloud
Eugenia handroi	Cloud
Eugenia involucrata	Cloud
Eugenia ligustrina	Cloud
Eugenia longipedunculata	Cloud
Eugenia moonioides	Cloud
Eugenia nutans	Cloud
Myrceugenia alpigena	Cloud
Myrceugenia bracteosa	Cloud
Myrceugenia cuculata	Cloud
Myrceugenia miersiana	Cloud
Myrceugenia myrcioides	Cloud
Myrceugenia ovalifolia	Cloud
Myrceugenia regnelliana	Cloud
Myrcia amazonica	Cloud
Myrcia anacardiifolia	Cloud
Myrcia anceps	Cloud
Myrcia coelosepala	Cloud
Myrcia eriocalyx	Cloud
Myrcia guianensis	Cloud, Dry
Myrcia hartwegiana	Cloud
Myrcia laruotteana	Cloud
Myrcia laxiflora	Cloud
Myrcia montana	Cloud
Myrcia pubipetala	Cloud

Myrcia retorta	Cloud
Myrcia splendens	Cloud, Dry
Myrcia subcordata	Cloud
Myrcia subverticillaris	Cloud
Myrcia vauthiereana	Cloud
Myrcia venulosa	Cloud
Myrciaria floribunda	Cloud
Myrciaria tenella	Cloud
Pimenta pseudocaryophyllus	Cloud
Psidium cattleyanum	Cloud
Siphoneugena crassifolia	Cloud
Siphoneugena densiflora	Cloud
Siphoneugena dussii	Cloud
Siphoneugena kuhlmannii	Cloud
Myrtaceae	
Calycolpus goetheanus	Dry
Calyptranthes crebra	Dry
Eugenia cupulata	Dry
Eugenia patrisii	Dry
Eugenia punicifolia	Dry
Myrcia cuprea	Dry
Myrcia fenestrata	Dry
Myrcia flavescens	Dry
Myrcia magnoliifolia	Dry
Myrcia multiflora	Dry
Myrcia rufipila	Dry
Myrcia tomentosa	Dry
Nyctaginaceae	
Guapira ferruginea	Dry
Guapira opposita	Cloud
Neea floribunda	Dry
Neea oppositifolia	Dry
Neea ovalifolia	Dry
Neea robusta	Dry
Ochnaceae	
Ouratea semiserrata	Cloud
Olacaceae	
Dulacia candida	Dry
Heisteria silvianii	Cloud
Minquartia guianensis	Dry
Opiliaceae	
Agonandra brasiliensis	Dry
Pentaphylacaceae	
Ternstroemia brasiliensis	Cloud

Peraceae	
Pera glabrata	Cloud
Phyllanthaceae	
Margaritaria nobilis	Dry
Piperaceae	
Piper aduncum	Dry
Piper arboreum	Cloud
Podocarpaceae	
Podocarpus sellowii	Cloud
Primulaceae	
Cybianthus coriaceus	Cloud
Cybianthus peruvianus	Cloud
Myrsine coriacea	Cloud
Myrsine gardneriana	Cloud
Myrsine glazioviana	Cloud
Myrsine lancifolia	Cloud
Myrsine umbellata	Cloud
Myrsine venosa	Cloud
Proteaceae	
Euplassa itatiaiae	Cloud
Euplassa semicostata	Cloud
Panopsis multiflora	Cloud
Roupala brasiliensis	Cloud, Dry
Roupala montana	Cloud, Dry
Putranjivaceae	
Drypetes variabilis	Dry
Quiinaceae	
Lacunaria jenmanii	Dry
Quiina glaziovii	Cloud
Rhamnaceae	
Rhamnus sphaerosperma	Cloud
Ziziphus itacaiunensis	Dry
Rosaceae	
Prunus brasiliensis	Cloud
Prunus myrtifolia	Cloud, Dry
Rubiaceae	
Alibertia claviflora	Dry
Alibertia guianensis	Dry
Alibertia myrciifolia	Dry
Amaioua intermedia	Cloud
Bathysa cuspidata	Cloud
Chimarrhis turbinata	Dry
Chomelia pohliana	Dry
Chomelia tenuiflora	Dry

Cordiera concolor	Cloud
Duroia gransabanensis	Dry
Faramea filipes	Dry
Faramea nigrescens	Cloud
Faramea torquata	Dry
Ferdinandusa goudotiana	Dry
Hillia parasitica	Cloud
Isertia	Dry
Palicourea corymbifera	Dry
Palicourea guianensis	Dry
Posoqueria latifolia	Cloud
Psychotria vellosiana	Cloud
Schizocalyx cuspidatus	Cloud
Warszewiczia schwackei	Dry
Rutaceae	
Conchocarpus pilocarpoides	Dry
Galipea jasminiflora	Dry
Metrodorea flavida	Dry
Neoraputia paraensis	Dry
Zanthoxylum rhodoxylum	Dry
Zanthoxylum rhoifolium	Dry
Zanthoxylum riedelianum	Dry
Rutaceeae	
Esenbeckia grandiflora	Cloud, Dry
Sabiaceae	
Meliosma sellowii	Cloud
Salicaceae	
Azara uruguayensis	Cloud
Banara guianensis	Dry
Casearia arborea	Dry
Casearia javitensis	Dry
Casearia pitumba	Dry
Casearia sylvestris	Cloud
Xylosma pseudosalzmanii	Cloud
Sapindaceae	
Allophylus edulis	Cloud
Allophylus sericeus	Cloud
Cupania ludowigii	Cloud
Cupania oblongifolia	Cloud
Cupania scrobiculata	Dry
Cupania vernalis	Cloud
Cupania zanthoxyloides	Cloud
Matayba arborescens	Dry
Matayba elegans	Dry

Matayba guianensis	Dry
Matayba inelegans	Dry
Matayba marginata	Cloud
Porocystis toulicioides	Dry
Talisia allenii	Dry
Toulicia pulvinata	Dry
Toulicia vera-luciana	Dry
Vouarana guianensis	Dry
Sapotaceae	
Chrysophyllum colombianum	Dry
Chrysophyllum pomiferum	Dry
Chrysophyllum sparsiflorum	Dry
Ecclinusa guianensis	Dry
Micropholis casiquiarensis	Dry
Micropholis guyanensis	Dry
Pouteria brevipes	Dry
Pouteria caimito	Dry
Pouteria elegans	Dry
Pouteria fimbriata	Dry
Pouteria grandiflora	Dry
Pouteria guianensis	Dry
Pouteria hispida	Dry
Pouteria latianthera	Dry
Pouteria multiflora	Dry
Pouteria parviflora	Dry
Pouteria petiolata	Dry
Pouteria rostrata	Dry
Pouteria vernicosa	Dry
Simaroubaceae	
Simaba polyphylla	Dry
Simarouba amara	Dry
Siparunaceae	
Siparuna amazonica	Dry
Siparuna glycycarpa	Dry
Siparuna guianensis	Dry
Solanaceae	
Aureliana brasiliana	Cloud
Solandra grandiflora	Cloud
Solanum argenteum	Cloud
Solanum bullatum	Cloud
Solanum cinnamomeum	Cloud
Solanum pseudoquina	Cloud
Solanum schlechtendalianum	Dry
Styracaceae	

Styrax discolor	Dry
Styrax pohlii	Cloud
Symplocaceae	
Symplocos celastrinea	Cloud
Symplocos falcata	Cloud
Symplocos insignis	Cloud
Symplocos microstyla	Cloud
Symplocos oblongifolia	Cloud
Symplocos pentandra	Cloud
Symplocos revoluta	Cloud
Theaceae	
Gordonia fruticosa	Dry
Thymelaeaceae	
Daphnopsis coriacea	Cloud
Ulmaceae	
Ampelocera edentula	Dry
Urticaceae	
Cecropia distachya	Dry
Cecropia latiloba	Dry
Cecropia ulei	Dry
Pourouma guianensis	Dry
Verbenaceae	
Lippia grandis	Dry
Violaceae	
Rinorea macrocarpa	Dry
Rinorea racemosa	Dry
Vochysiaceae	
Callisthene minor	Dry
Erisma uncinatum	Dry
Qualea paraensis	Dry
Qualea rosea	Dry
Vochysia magnifica	Cloud
Vochysia maxima	Dry
Vochysia saldanhana	Cloud
Winteraceae	
Drimys brasiliensis	Cloud

5. General Conclusion

This thesis explores the relationships between biodiversity-ecosystem functioning, focusing on biotic attributes, such as taxonomic, structural, functional and phylogenetic diversity; abiotic attributes, such as soil fertility, precipitation and temperature, and its relationship with tree aboveground carbon stock in tropical ecosystems, ranging from the Cerrado to Forests along environmental gradients. Collectively, the findings emphasize the importance of these attributes, both at local, regional and national scales, in understanding carbon storage patterns and the ecological processes shaping these ecosystems.

In the Cerrado, the results reveal that different vegetation types form a mosaic primarily defined by vegetation structure, while species composition exhibits significant phenotypic variability. This plasticity allows the same species to occur across distinct vegetation types, suggesting a high adaptive capacity to local environmental variations and highlighting the need for further studies on intra- and interspecific variation in functional traits.

Moreover, vegetation structure is closely linked to species dominance and aboveground carbon stocks. Taller vegetation types rely heavily on dominant species to drive carbon storage, whereas smaller vegetation types show a stronger positive association between species richness and carbon stocks. These patterns can indicate that distinct ecological processes, shape communities.

In tropical forests, resource use strategies did not differ significantly between Cloud and Dry Forests. At a regional scale, maximum temperature and stem structural diversity is the primary driver of aboveground carbon stocks, underscoring the predominant influence of abiotic and biotic factors on ecosystem processes.

Overall, this thesis demonstrates that the interplay between biotic and abiotic factors shapes biodiversity, vegetation structure, and ecosystem functioning at both local and regional scales. These findings contribute to a deeper understanding of the dynamics of tropical ecosystems and provide insights for conservation and management strategies, highlighting the critical role of functional traits, vegetation structure, and environmental factors in maintaining ecosystem services.