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Tese de Doutorado

A sinfonia da biodiversidade na Mata Atlântica: unindo diferentes facetas para entender os mecanismos de coexistência e distribuição de espécies arbóreas

The symphony of biodiversity in the Atlantic Forest: bringing together different facets to understand the mechanisms of coexistence and distribution of tree species

JOICE KLIPEL

Porto Alegre, setembro de 2023.

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Resumo

A Mata Atlântica, uma das florestas mais biodiversas do mundo, assemelha-se a uma sinfonia, onde diversos elementos interagem harmoniosamente para criar uma complexa totalidade. Estes elementos abrangem não apenas a riqueza de espécies, mas também a diversidade funcional e filogenética. Nesta tese, exploramos os padrões de crescimento, coexistência e distribuição de espécies arbóreas ao longo dos gradientes ambientais na região sul da Mata Atlântica. Utilizamos abordagens funcionais e filogenéticas, e examinamos atributos menos convencionais, como a área da copa das árvores. A pesquisa foi desenvolvida em várias escalas, desde a perspectiva individual (capítulo 1) até as interações locais (capítulo 2) e influências regionais (capítulos 3 e 4). As principais conclusões destacam a forte influência da área da copa das árvores e da estrutura das copas, em nível de comunidade, no crescimento das árvores. Além disso, ressaltamos a relevância das interações bióticas locais no crescimento individual das árvores. Por fim, ao analisar a variação dos atributos funcionais e das relações filogenéticas em comunidades distribuídas em gradientes climáticos, como temperatura e pluviosidade, e gradientes espaciais, como altitude e a transição entre ambientes campestres e florestais, obtivemos uma visão abrangente da distribuição das espécies lenhosas, com a variação dos atributos funcionais das plantas desempenhando um papel coordenador fundamental. Esta tese foi construída na interseção entre a teoria de montagem de comunidades, as florestas e a biodiversidade.

Palavras-chave: Atributos Funcionais, árvores, crescimento, biodiversidade, ecologia de comunidades, florestas, filogenia, Mata Atlântica, região subtropical

Abstract

The Atlantic Forest, one of the world's most biodiverse forests, compares a symphony where various elements interact harmoniously to create a complex whole. These elements encompass not only species richness but also functional and phylogenetic diversity. In this thesis, we explored tree species' growth, coexistence, and distribution patterns across environmental gradients in the southern region of the Atlantic Forest. We employed functional and phylogenetic approaches and examined unconventional traits such as tree canopy areas. The research was conducted at multiple scales, from the individual perspective (Chapter 1) to local interactions (Chapter 2) and regional influences (Chapters 3 and 4). The main findings underscore the strong influence of tree canopy area and canopy structure at the community level on tree growth. Additionally, we emphasize the relevance of local biotic interactions in individual tree growth. Finally, we gained a comprehensive understanding of woody species distribution by analyzing the variation in functional traits and phylogenetic relationships in communities distributed across climatic gradients, such as temperature and rainfall, and spatial gradients, such as altitude and the transition between grassland and forest environments. Functional trait variation in plants played a central coordinating role. This thesis was constructed at the intersection of community assembly theory, forests, and biodiversity.

Keywords: Atlantic Forest, biodiversity, community ecology, forests**,** functional traits, growth, phylogeny, subtropical region, trees

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Introdução geral

Uma sinfonia representa uma composição musical de estrutura complexa, frequentemente constituída por seções individuais que abrangem uma variedade de temas e ritmos distintos, os quais se entrelaçam harmoniosamente para formar uma narrativa completa. Ao pensar sobre este conceito, percebo que "sinfonia" se revela um termo extremamente apropriado para aludir à biodiversidade da Mata Atlântica.

Um dos objetivos mais antigos dos ecólogos é elucidar os processos que geram e mantêm a biodiversidade. Frequentemente, a biodiversidade é associada apenas à riqueza de espécies, enquanto outros componentes são menos comuns. Biodiversidade também se refere a um conceito multifacetado que envolve diferentes componentes como diversidade de espécies (número de espécies), diversidade funcional (diferença nas características morfológicas, fisiológicas e/ou fenológicas entre espécies) e diversidade filogenética (diversidade de relações evolutivas entre as espécies) (Pavoine & Bonsall, 2011). Nesse sentido, a biodiversidade da Mata Atlântica pode ser entendida como uma verdadeira sinfonia da natureza, em que cada componente da diversidade contribui para a composição do todo.

Para compreender a biodiversidade das florestas atlânticas, frequentemente nos deparamos com a necessidade de examinar as comunidades florestais tanto em uma escala local quanto em uma escala macroecológica. Em escalas menores, somos capazes de captar nuances e interações específicas entre as espécies ou indivíduos que habitam essas florestas. Essa observação nos permite entender como as comunidades se formam, interagem e evoluem em resposta a fatores locais. Por outro lado, ao ampliar nossa perspectiva para uma escala macroecológica, ganhamos uma visão panorâmica das tendências e padrões que se manifestam em um contexto mais amplo. Isso nos ajuda a entender as conexões entre diferentes ecossistemas e a compreender como fatores globais podem influenciar a biodiversidade.

Portanto, esta tese foi elaborada com base em conhecimentos prévios que abrangem uma ampla gama de escalas, desde as mais locais, como no caso do meu trabalho de conclusão de curso (Klipel et al., 2021), até as mais abrangentes, como no caso da minha dissertação (Klipel et al., 2022). Essa abordagem entrelaça uma série de conceitos que abarcam a estruturação de comunidades, o ecossistema florestal e a biodiversidade. Integrar esses conceitos pode enriquecer nossa compreensão sobre as florestas atlânticas além de nos ajudar a tomar medidas em prol da conservação desses ecossistemas vitais e do manejo sustentável.

Teorias ecológicas: partitura das comunidades florestais

A estruturação das comunidades é governada por quatro processos fundamentais: seleção, deriva, especiação e dispersão (Vellend, 2010). A seleção se refere às diferenças determinísticas de aptidão entre indivíduos de distintas espécies. Existem três formas de seleção: constante, denso-dependência e variação espacial/temporal. A denso-dependência é o principal modelo teórico na ecologia de comunidades (Hille Ris Lambers et al., 2002; Vellend, 2010; Wright, 2002), onde a aptidão individual em uma determinada espécie depende, pelo menos em parte, da densidade da própria espécie, assim como das densidades das outras espécies. Dessa forma, a denso-dependência beneficia as espécies quando operam em densidades baixas, permitindo uma coexistência estável. Por outro lado, a deriva ecológica abrange processos estocásticos que moldam a densidade e a coexistência ao longo do tempo e do espaço, influenciados por nascimentos, mortes e produção de descendentes. Enquanto isso, a especiação representa a formação de novas espécies, e a dispersão engloba o deslocamento de organismos pelo espaço, influenciando a dinâmica das comunidades com base em fatores como tamanho, conectividade e composição.

Esses processos de estruturação das comunidades operam a partir de um conjunto regional de espécies, das quais apenas algumas conseguem atravessar os filtros bióticos e abióticos para estabelecer comunidades locais. Localmente, as interações competitivas contribuem para a coexistência das espécies (Chesson, 2000), a qual é direcionada por dois principais mecanismos: equalizadores e estabilizadores (HilleRisLambers et al., 2012). Os mecanismos equalizadores estão relacionados à equivalência de *fitness* entre as espécies, enquanto os estabilizadores tendem a atenuar a competição interespecífica das espécies, através da diferença de nichos e/ou partição de recursos. Quando as diferenças de nicho são mais influentes do que as diferenças de *fitness*, promovem-se a coexistência e a diversidade durante a formação da comunidade (Levine & HilleRisLambers, 2009). Isso evita a exclusão competitiva de competidores menos aptos por competidores mais aptos. Nesse sentido, a competição emerge como um filtro determinante para o sucesso ecológico e evolutivo. Modelos complexos de coexistência em comunidades ricas em espécies continuam desafiando a ciência, entretanto, os mecanismos que emergem em sistemas com mais de dois competidores provavelmente desempenham um papel preponderante na manutenção da diversidade (Levine et al., 2017).

A ecologia funcional se concentra no estudo das funções dos organismos dentro de ecossistemas. Ela se preocupa em entender como os organismos interagem com seu ambiente e desempenham papéis específicos na manutenção da estrutura e funcionamento dos ecossistemas e tem sido muito utilizada para o entendimento dos mecanismos de estruturação das comunidades. De acordo com Violle et al. (2007), um atributo é definido como 'qualquer característica morfológica, fisiológica ou fenológica mensurável em nível individual, desde a célula até o organismo como um todo'. Para que um atributo seja funcional, ele deve 'afetar o *fitness* (de um indivíduo) de forma indireta por meio de seus efeitos no crescimento, reprodução e sobrevivência'. A referência ao *fitness* é crucial para determinar a funcionalidade de um atributo (Poorter et al., 2008; Shipley et al., 2016). Os mecanismos de coexistência impactam a dinâmica de estruturação e composição das comunidades (Levine et al., 2017), afetando a variação na amplitude e no valor médio dos atributos funcionais e, consequentemente, os *trade-offs* das espécies presentes. Por exemplo, o *trade-off* entre crescimento e mortalidade, onde espécies com menor taxa de crescimento geralmente são mais longevas (Wright et al., 2010).

Portanto, a coexistência de espécies dentro das comunidades e a ordenação de espécies ao longo de gradientes ambientais são reguladas pelo grau de similaridade das adaptações das espécies. Nesse contexto, não apenas abordagens funcionais, mas também filogenéticas, desempenham um papel crucial na investigação dessas hipóteses. As relações filogenéticas entre espécies coexistentes em uma comunidade podem fornecer *insights* sobre a intensidade competitiva e as diferenças históricas e evolutivas entre as espécies (Castillo et al., 2010; Kunstler et al., 2012). A coexistência de espécies que possuem características ecológicas distintas é resultado da seleção de espécies evolutivamente divergentes, que ocorre a partir de um pool maior de espécies (Vellend, 2010). Essas divergências podem ser resultado tanto de pressões seletivas do passado quanto de influências contemporâneas (Diniz-Filho et al., 2011; Gerhold et al., 2015). Além disso, essas divergências podem emergir por meio de processos neutros. Portanto, a coexistência de espécies é moldada por uma interação complexa entre pressões seletivas, fatores filogenéticos e funcionais e processos neutros, todos desempenhando papéis intrincados na formação das comunidades ecológicas.

Diversidades funcionais e filogenéticas: elementos diferentes que se sincronizam na melodia

Embora muitos estudos utilizem a diversidade filogenética como substituto da funcional, é crucial reconhecer que ambas as formas de diversidade oferecem informações diferentes embora complementares sobre as diferenças ecológicas e evolutivas das espécies (Webb et al., 2002). Enquanto os atributos funcionais fornecem informações sobre as diferenças ecológicas entre as espécies (diversidade) e suas exigências de habitat (estado do atributo) (HilleRisLambers et al., 2012), as relações filogenéticas nos permite compreender as restrições evolutivas e biogeográficas mais profundas na distribuição regional das espécies (de Bello et al., 2017; Gerhold et al., 2015). Integrar essas duas perspectivas enriquece nossa compreensão da complexidade subjacente à coexistência e à dinâmica das comunidades ecológicas.

Ritmo sustentável: manutenção da diversidade das comunidades florestais em harmonia

Para organismos sésseis de vida longa, como as árvores, acredita-se que as interações com os vizinhos próximos tenham um papel crítico em influenciar o desempenho individual das plantas (por exemplo, crescimento) e, assim, estruturar a composição e a diversidade das comunidades (Levine, 2016). A disponibilidade de recursos para um indivíduo de árvore depende fortemente das árvores vizinhas, tornando as interações entre árvores cruciais para o crescimento individual (Britton et al., 2023; Coomes & Allen, 2007). Além disso, essas interações têm o potencial de se expandir, dando origem a padrões emergentes em nível de comunidade (Hart et al., 2016; Uriarte et al., 2010; Webb et al., 2002). Por exemplo, fatores como a cobertura da copa e o porte das árvores vizinhas, bem como as semelhanças nos atributos funcionais e a relação filogenética entre as árvores que interagem, podem ter um impacto direto na disponibilidade de recursos (Castillo et al., 2010; Kunstler et al., 2012). Dessa forma, a habilidade de uma árvore em competir com seus vizinhos desempenha um papel fundamental em determinar quão bem ela será capaz de crescer.

A relação entre o crescimento relativo das árvores e seus atributos funcionais têm sido alvo de extensas investigações na literatura (Scalon et al., 2022; Visser et al., 2016). Atributos funcionais como características das folhas, altura e densidade da madeira são amplamente explorados e demonstraram ser bons indicadores do crescimento arbóreo, embora isso sempre leve em consideração o contexto das coletas de dados e as condições ambientais locais. No entanto, existem atributos menos convencionais que também podem ser preditores eficazes do crescimento das árvores, como a área da copa, bem como atributos que combinam a área da copa com características das folhas. Esses aspectos ainda requerem maior atenção e investigação para uma compreensão mais completa de sua contribuição para o crescimento das árvores. Em uma perspectiva mais ampla a nível de comunidade, interações bióticas locais também exercem um papel crucial ao influenciar o desempenho individual, moldando os fenótipos individuais das árvores. Nesse contexto, analisar a dissimilaridade dos atributos funcionais entre árvores individuais e suas vizinhas pode ampliar nossa compreensão sobre como as interações no ambiente local afetam a taxa de crescimento das árvores (Mahaut et al., 2023), tanto em nível individual quanto de comunidade. Essa análise torna-se ainda mais relevante considerando que espécies com diferentes necessidades de recursos ou habitats tendem a possuir valores distintos em seus atributos funcionais, o que pode resultar em uma competição menos intensa em comparação com espécies que compartilham atributos semelhantes (Adler et al., 2013). Da mesma forma, a dissimilaridade filogenética entre árvores que coexistem é prevista para facilitar a partilha de recursos e diminuir a suscetibilidade a ataques de inimigos naturais (Castillo et al., 2010; Uriarte et al., 2010; Yue et al., 2022). Isso viabiliza que as espécies coexistam em nichos ecológicos distintos, evitando a competição direta e permitindo uma convivência mais harmoniosa (Chen et al., 2016).

Do "dó" ao "si": gradientes ambientais e sua influência na distribuição das plantas

Investigar a variação dos atributos funcionais e das relações filogenéticas em comunidades também representa uma abordagem poderosa para obter *insights* abrangentes sobre a distribuição das espécies em comunidades de plantas ao longo de gradientes ambientais (Cornwell & Ackerly, 2009; De Bello et al., 2006). Isto baseia-se na ideia de que as assembleias de espécies são o resultado de filtros que determinam a presença e a ausência de espécies, bem como a dominância de algumas (Keddy, 1992). Enquanto o pool de espécies disponível determina o conjunto de espécies que potencialmente podem se dispersar para um local, mecanismos subsequentes de seleção de espécies por condições abióticas (por exemplo, temperatura e pluviosidade) e bióticas (por exemplo, competição e facilitação) são influenciados pelos atributos funcionais das espécies e pelas interações filogenéticas, que por sua vez afetam os processos demográficos das plantas (dispersão, crescimento, sobrevivência e reprodução) (Keddy, 1992; McGill et al., 2007). A diferenciação entre a aptidão dos indivíduos – seja por mecanismos associados a diferenças de *fitness* ou de nicho, altera as taxas demográficas das populações, que por sua vez influenciam a estrutura de abundância das espécies e a dinâmica das comunidades.

Estudos anteriores em sua maioria avaliaram como um único componente da biodiversidade varia em comunidades vegetais ao longo de gradientes ambientais. Por exemplo, componentes de diversidade taxonômica (Condit et al., 2013), funcional (Carboni et al., 2014) ou filogenética (Rezende et al., 2017). No entanto, poucos estudos quantificaram simultaneamente múltiplos aspectos da biodiversidade em comunidades (Dainese et al., 2015; De Bello et al., 2006; Luo et al., 2019). Em especial, ainda existe pouca evidência de que diferentes medidas de biodiversidade responderão de maneira semelhante a gradientes ambientais comuns (Bello et al., 2013; Pavoine & Bonsall, 2011). Assim, ao combinarmos as abordagens funcionais e filogenéticas na diferenciação das espécies, podemos obter uma compreensão mais abrangente sobre a composição de espécies, estratégias ecológicas e história evolutiva nas comunidades ao longo de gradientes ambientais, que englobam tanto gradientes climáticos (como temperatura e pluviosidade) quanto espaciais (como altitude e a transição entre ambientes campestres e florestais).

A combinação de abordagens funcionais e filogenéticas na diferenciação das espécies tem sido encorajada, embora não esteja claro se esses componentes da biodiversidade são redundantes ou complementares (Cadotte & Tucker, 2017). De fato, atributos funcionais e filogenia frequentemente estão relacionados uma vez que atributos estão submetidos à evolução (Webb et al., 2002) e podem fornecer informações não independentes. Em geral, a possível sobreposição de informações entre estruturas filogenéticas e funcionais depende da força do sinal filogenético que os atributos possuem (Cadotte & Tucker, 2017; Dainese et al., 2015). Com base nessa suposição, espécies intimamente relacionadas deveriam compartilhar mais similaridades funcionais do que aquelas distantes, seguindo o conceito de conservação de nicho ecológico (Wiens et al., 2010).

Entretanto, regras de montagem em diferentes comunidades podem levar a padrões distintos entre as estruturas funcionais e filogenéticas, e a possível falta de independência entre essas estruturas pode mascarar os múltiplos processos de montagem que atuam nas comunidades. Padrões de convergência e divergência nas estruturas funcionais e filogenéticas podem surgir de processos diferentes, e esses padrões podem estar apenas parcialmente ou não relacionados entre si. Portanto, ao separar a estrutura filogenética da estrutura funcional, é potencialmente possível diferenciar os padrões e os possíveis impulsionadores tanto dos componentes evolutivos quanto ecológicos, incluindo a evolução adaptativa mais recente, dentro de grupos de espécies (de Bello et al., 2017; Diniz-Filho et al., 2011).

Além disso, os padrões de distribuição de espécies lenhosas em ambientes contrastantes, como no caso de paisagens com mosaicos de campo e floresta, podem estar intrinsecamente ligados a estratégias adaptativas para ocorrência em um ou ambos os habitats. Portanto, ao avaliar a composição das espécies lenhosas entre esses habitats, a primeira impressão pode erroneamente sugerir que não existem diferenças, visto que apenas a taxonomia está sendo considerada. Entretanto, uma análise mais profunda revela que as estratégias adaptativas das espécies, seja para um único habitat ou para ambos, podem estar diretamente relacionadas às suas histórias evolutivas e/ou atributos funcionais, que podem variar entre as diferentes espécies ou em escala individual (Cadotte et al., 2010; Cornwell &

Ackerly, 2009). Consequentemente, integrar informações funcionais em diferentes escalas ecológicas pode oferecer percepções valiosas sobre a adaptação de espécies lenhosas em habitats contrastantes (Cornwell & Ackerly, 2009). Isso é especialmente importante para compreender os processos de avanço da vegetação lenhosa que vêm ocorrendo devido às mudanças climáticas, favorecendo o crescimento de árvores em vez de gramíneas em muitos ecossistemas abertos em todo o mundo (Bond, 2008), principalmente em regiões pouco estudadas, como o sul do Brasil (Overbeck et al., 2007).

Esta tese se estrutura em quatro capítulos que abrangem a montagem da comunidade, os atributos funcionais e a filogenia, com o objetivo de compreender o crescimento e a distribuição de árvores ao longo dos gradientes ambientais nas florestas subtropicais da Mata Atlântica:

Capítulo 1: The role of tree crown on the performance of trees in individual and community levels

Objetivos: Neste estudo, abordamos as seguintes questões: qual é o método ideal para calcular o tamanho da copa em florestas subtropicais brasileiras? Ao multiplicar o tamanho da copa pelo massa foliar (e.x. LMA) há melhoria no ajuste dos modelos de crescimento das árvores em comparação com modelos sem o LMA? Existe uma correlação entre o aumento do empacotamento das copas das árvores e um maior crescimento relativo médio em nível de comunidade?

Capítulo 2: The effect of neighbor species' traits on tree growth in subtropical moist forests depend on relative individual height and performance

Objetivos: Neste estudo, investigamos simultaneamente a influência da similaridade funcional, do índice de aglomeração local e da estrutura funcional e filogenética da comunidade no crescimento individual das árvores. Utilizamos duas abordagens para explorar esses fatores: quantificando a força da interação ao medir a influência de indivíduos vizinhos na taxa de crescimento das árvores focais e examinando o efeito da estrutura da comunidade no crescimento individual das árvores.

Capítulo 3: Variability in leaf traits reveals contrasting strategies between forest and grassland woody communities across southern Brazil

Objetivos: Nós objetivas comparar as mudanças na diversidade funcional, na diversidade filogenética (diversidade filogenética com tamanho de efeito padronizado) e na composição funcional (média ponderada da comunidade) das espécies lenhosas entre florestas e campos; avaliar se as espécies lenhosas especialistas em florestas, especialistas em campos e generalistas possuem estratégias ecológicas distintas em termos de características de suas folhas; e avaliar as mudanças nas características das folhas de espécies lenhosas com populações que ocorrem em ambos os habitats (ou seja, espécies generalistas).

Capítulo 4: How do distinct facets of tree diversity and community assembly respond to environmental variables in the subtropical Atlantic Forest?

Objetivos: Este estudo tem como objetivo avaliar as variações na biodiversidade das comunidades arbóreas ao longo de gradientes ambientais nas florestas subtropicais do sul do Brasil. O estudo considera a riqueza de espécies, a diversidade funcional e filogenética, bem como a composição de atributos da comunidade. Consideramos informações específicas de atributos para a diversidade funcional, refletindo a evolução adaptativa recente, em contraste com as restrições filogenéticas mais profundas na diversidade funcional.

A seguir, cada um dos capítulos é apresentado no formato de artigo científico, seguindo as regras de formatação correspondente à revista que será ou foi submetido.

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Capítulo 1

Chapter 1

The role of tree crown on the performance of trees in individual and community levels

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The role of tree crown on the performance of trees in individual and community levels

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Highlights

- Crown area is a good predictor of individual tree growth rate
- Integrating leaf mass area to crown area improve individual growth models
- Higher canopy packing improves tree community performance in terms of overall growth

Abstract

Functional traits offer insights into plant performance. However, linking traits to individual tree performance requires considering the overall phenotypic context and utilizing traits measured at the individual level. Furthermore, trees can adjust their crown shapes and sizes at the community level to optimize canopy space utilization, enhancing the community-level growth rate. In this study, we assessed the crown area of 1032 individual trees, a simple trait measured at the individual level, to test trait-growth relationships. The observed crown area, measured as an ellipse, and total photosynthetic mass positively impacted tree growth rates. Importantly, this impact was not solely based on leaf mass (LMA). This implies that LMA's predictive power could improve by integrating leaf-level traits with whole-plant allocation to leaf area. Additionally, our study found that increased canopy packing levels raised the community-level growth rate within our plots. This structural indicator is vital for forest communities, facilitating denser tree arrangements and efficient light interception in the forest. We highlight the importance of considering crown size as a critical variable to be measured during fieldwork for floristic inventories and in studies focused on tree performance.

Keywords: Canopy size, canopy space, crown architecture, crown volume, leaf mass area, relative growth

1. Introduction

Examining whether functional traits predict ecological functions is crucial for advancing trait-based ecology (Shipley et al., 2016). This trait-based ecological approach aims to generalize and predict ecological phenomena across various organizational and spatial scales, irrespective of taxonomy. By employing functional traits, it facilitates the integration and scaling of processes from the individual and species level to community and ecosystem levels (Shipley et al. 2016; Chacón-Labella et al., 2023). Functional traits are any characteristics of an organism's phenotype, including morphological, physiological, or phenological traits, that directly or indirectly impact the individual's fitness through performance components such as growth, reproduction, and/or survival (Violle et al., 2007). Furthermore, functional traits mediate the interactions between phenotype and environment, thus impacting local biotic interactions and ecosystem processes. However, their relationships with individual performance are seldom tested in field studies (Poorter et al., 2018) and given the common occurrence of non-functional phenotypic characteristics (Volaire et al., 2020), empirical testing is essential.

Specific leaf area, wood density, and seed mass are widely known examples of functional traits (Westoby, 1998) that affect plant performance and ecosystem processes (e.g., Lebrija-Trejos et al., 2016; Poorter et al., 2019; Wright et al., 2004). However, they have been also found to be weak predictors of growth rates, as for young trees on a global scale (Paine et al., 2015), indicating a stronger dependence on the local environment and growth-trait relationships. The limited predictability of demographic rates can be attributed, in part, to the utilization of alone functional traits without considering the overall phenotypic context of the individual (Yang et al., 2018). In trees, which are large and long-lived organisms, the expected relationships between traits and performance, when considering organ-level trade-offs such as the leaf economic spectrum (Wright et al., 2004), can become unclear, weak or absent without considering the context of the individual. To address this, Rubio et al. (2021) integrated leaf dry mass per area (measured at the organ level, hereafter LMA) with crown size of tree individuals (representing the total photosynthetic mass at the whole-plant level) to capture the information about total allocation at the individual level (Rubio et al., 2021). This approach, incorporating functional traits from both leaf and crown levels, can better predict tree species variation in growth rates compared to using these traits alone (Li et al., 2017).

In forest ecosystems, the distribution of tree crowns within forest canopies significantly influences light interception and microclimatic conditions in the understory. This distribution renders canopy structure, or canopy packing, a vital indicator of competitiveness among neighboring trees (Thorpe et al., 2010; Vieilledent et al., 2010) that may impact resource use and productivity. Studies have proposed that different species with complementary architectural and physiological traits tend to form denser groupings (Longuetaud et al., 2013). That is, an increase in functional diversity leads to enhanced canopy packing over time, a pattern observed in a set of tropical and temperate forests (Zheng et al., 2022). The capacity of trees to adjust their crown shapes and sizes in response to shifts in the local environment is crucial for species-rich forests to optimize canopy space utilization (Jucker et al., 2015), which may reduce light competition (Longuetaud et al., 2013) and increase growth rates at the community level.

The tree crown size consists of branches and leaves extending from the main trunk and is often measured in terms of area and volume through vertical and horizontal extensions. Both crown area and volume involve measurements based on various geometric shapes (e.g., circle, cylinder, ellipse, ellipsoid) and which shape is the most effective predictor of tree performance varies among species and ecosystems (Franceschi et al., 2022). Larger crown sizes are generally linked to increased tree growth as they enable greater light capture (Li et al., 2017), which turn the crown architecture a promising trait in predicting individual growth rates. However, the relationship between crown size and growth lacks overall empirical tests with field data (Iida & Swenson, 2020). Research in tropical forests has revealed that crown depth and diameter traits respond to environmental gradients (Shenkin et al., 2020) and recent studies have shown tree strategies related with crown. For instance, on a global scale, crown depth and diameter covary with tree height, influencing the ability to compete for space and trade-offs between maximizing light interception and costs with mechanical damage in tree architecture (Maynard et al., 2022). In subtropical forests, shorter trees with wider crowns tend to have heavier wood density, indicating a link with other important functional traits and a conservative strategy (Yang & Swenson, 2023).

This study aims to contribute with a more comprehensive understanding of functional traits and tree performance relationships, by exploring the tree crown characteristics (individual size and canopy packing) with growth rates at individual and community levels (Figure 1). By evaluating the importance of considering the crown as a key functional trait influencing tree and community growth performance, we aim to provide insights into forest dynamics and structure. More specifically, we address the following questions: 1) what is the optimal method for calculating crown size in subtropical Brazilian forests? 2) Does integrating crown size with LMA enhance model fits for tree growth compared to models with isolated traits (i.e., either crown or LMA)? 3) Does increased canopy packing correlate with higher mean relative growth at the community level?

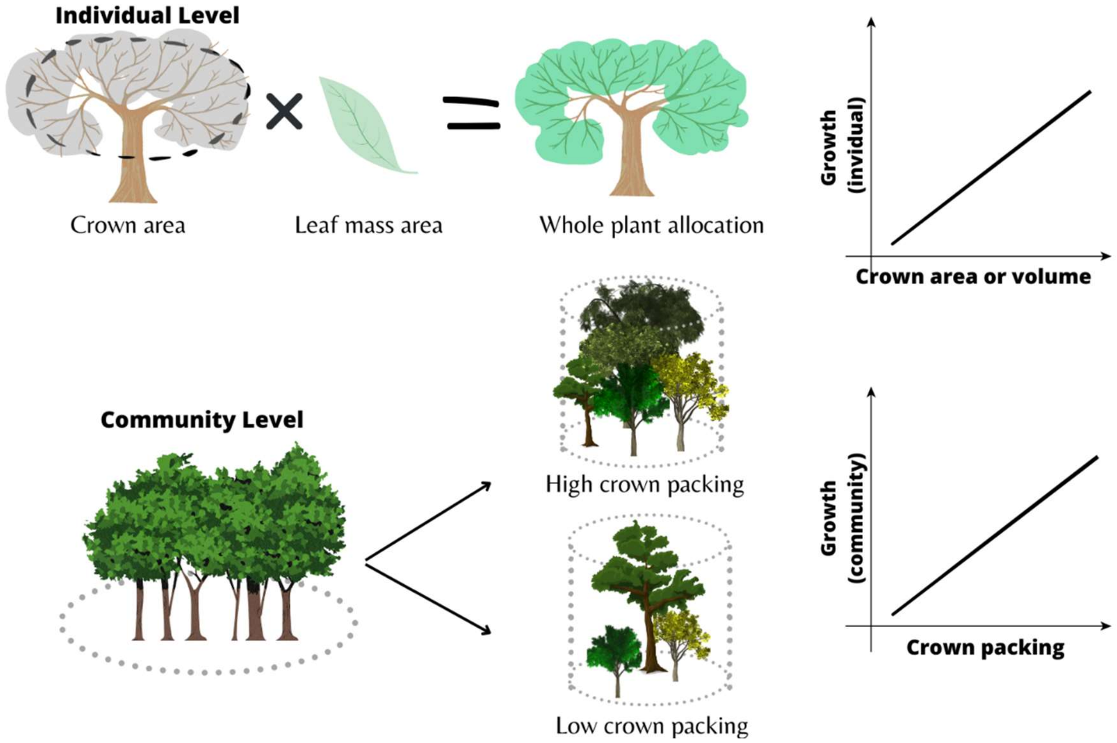

Figure 1: Schematic representation integrating crown area data collection at individual and community levels. This integration includes leaf mass area measurements with crown (whole plant allocation) and accommodates diverse canopy packing densities (community level). We show varying canopy packing and expected relationships between these structural traits with individual tree growth or community growth as a whole.

2. Material and Methods

2.1 Study area

This study was conducted in long-term forest plots located in the subtropical Atlantic Forest in southern Brazil (LERSAF project: Long-term Ecological Research in Subtropical Atlantic Forest). It comprises Araucaria Forest and Atlantic Moist Forest across an elevation variation of 320-930 meters. The climate in Araucaria Forest is humid subtropical, with temperate summers (the Cfb Köppen's climate classification) and in Atlantic Moist Forest is humid subtropical with hot summers (the Cfa Köppen's classification) (Alvares et al., 2013).

Tree and forest community data used in this study were obtained from nine permanent plots in old-growth forests within protected areas distributed across four localities: the Pró-Mata Private Natural Reserve (29º26'S and 50º14'W), Aparados da Serra National Park (29º07' to 29º15'S and 50º01' to 50º10'W), Reserva Biológica da Serra Geral (29°37'S and 50°11' W), and Forqueta (29°33'S and 50°12' W). The forest inventories have been conducted approximately every five years since 2014, following the RAINFOR protocols (Phillips et al., 2001). In each permanent plot we used data from 12-100 m² subplots (here considered as a community, where every individual tree with ≥ 5 cm of diameter at breast height (DBH, measured at 1.3 m from the ground) is tagged with a unique number, identified at the species level, and monitored through the time. Besides DBH measurement, individual height, crown diameter sizes, and crown depth were measured with laser and diametric tapes.

2.2 Data sets

The annual growth rate (AGR) was measured for all trees in the subplots using the basal area calculated from the DBH measurement in two censuses (2014 and 2019) (eq. 1):

Eq. 1:

$$AGR = (Basal\ area_{t+1} - Basal\ area_{t}) / _{time}$$

where *t* is the time interval between both censuses. Negative values were excluded due to potential factors such as stem contraction, measurement inaccuracy, or breakage. Also, only living individuals who were present in both surveys were taken into account. To determine the community-level growth rate, we considered the same formula but based on the sum of all individuals' basal areas present in the subplot in both censuses.

In the second census, crown diameter and depth were measured for all surviving trees using laser tape. The diameter was measured in two cardinal directions: North-South (d1) and East-West (d2). Crown depth was determined by the length between the base of the crown and the total height of the tree. The base of the crown was determined as the bifurcation point of the lowest branch of the tree's living crown. These measures were used to calculate crown area and volume. The crown area was determined in two ways: as an ellipse with two diameters (i.e, d1 and d2); and, as a circle with the crown largest diameter only. The crown volume was calculated by multiplying the canopy area by the depth of the canopy, employing formulas for both a cylinder and an ellipsoid for the calculation.

Leaf dry mass per area (LMA, g/cm^2) was used to represent a leaf functional trait broadly considered in trait-based studies. It was calculated from its inverse relationship with specific leaf area (SLA, cm^2/g), which average values per species were obtained from field measurements on individuals distributed across study sites (at least five individuals per species), currently stored in the Plant Ecology Lab database (available in the TRY Plant Trait Database; Kattge et al., 2020). LMA is a key functional trait of the leaf economic spectrum, posively related with leaf lifespan and photosynthetic rate (Wright et al., 2004). In addition, it also scales more easily to the whole-plant level via measurement of total photosynthetic mass (Yang et al., 2018).

To assess question 2, we integrated the leaf trait value (LMA of the species) with the crown individual measurements by multiplying both values. This may indicate the total photosynthetic mass (Mp) in terms of area and volume. To calculate Mp, we followed a similar approach to Rubio et al. (2021). However, instead of estimating crown size using allometric models, we relied on actual field measurements of each tree.

To assess question 3, we defined the canopy packing for each community using equation (eq. 2), which correlates the proportion of aboveground space available to trees with the space occupied by the canopy (Jucker et al., 2015). Canopy packing values range between 0 (no canopy) and 1 (fully occupied space):

Eq. 2:

$$Canopy\ packing = \frac{\sum CV}{Community\ area\ x\ [H_{\max j} - (H - CD)_{\min j}]}$$

where ΣCV represents the sum of crown volumes (CV) for all trees within a plot, which is equivalent to the total canopy volume. The area of each community is consistently 100 m^2 (our subplots), while *Hmaxj* and *(H−CD)minj* denote the maximum tree height (Hmax) and the height of the lowest live branch (minimum value of all trees for individual's height, H, and crown depth, CD, difference) within a site *j*, respectively.

2.3 Statistical analyses

Firstly, we used linear mixed-effect models to investigate the most suitable shape to represent the effect of crown size (i.e., ellipse, circle, cylinder, and ellipsoid) on tree growth rate (question 1). The models included species as a random variable, allowing us to use the conditional and marginal coefficients of determination (i.e.., R^{2}c and R^{2}m, respectively) to select the best variable.

Secondly, we used linear mixed-effect models to evaluate the impact of crown size, Mp, and LMA on individual tree AGR (question 2). Species were also included as a random variable in the models. The logarithmic value of AGR was used as the response variable, and separate models were constructed using the best predictor associated with crown measurement (the answer of question 1), the LMA alone, and the integrated value between crown and LMA (i.e., Mp) as potential predictors. We determined the best fits using the

Akaike Information Criterion (AIC). To establish a better comparison between predictors at different measurement units, we standardized these variables to zero mean and unit variance (Schielzeth, 2010).

Finally, we used linear mixed-effect models to evaluate the impact of canopy packing on community-level growth rate (question 3). The four localities were included as a random variable in the models to account for differences in forest type and environmental conditions. We used the 'lme' function in the "nlme" R package (Pinheiro et al., 2023). All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020).

3. Results

Our sample comprised 1032 tree individuals of 123 species belonging to 41 botanical families. The average growth of individuals was 0.0006 $cm^2/ha.yr^{-1}$ (or 6.91 $cm^2.y^{-1}$), with a standardized deviation 0.001 $cm^2/ha.yr^{-1}$ (or 14.54 $cm^2.y^{-1}$), a maximum value of 0.02 $cm^2/ha.yr^{-1}$ (or 259.22 $cm^2.y^{-1}$), and a minimum of 1.33e-09 $cm^2/ha.\ yr^{-1}$ (or 0.13 $cm^2.y^{-1}$).

Our analyses indicated that the model utilizing the ellipse shape as the crown size measurement demonstrated the best fit for our tree species (Table 1). These findings suggest that using an ellipse to measure the crown of individual trees is the most appropriate way to investigate their influence on individual tree growth for subtropical Atlantic forests (Figure 2a and Table 1).

Crown area significantly impacted tree growth. Trees exhibiting larger crown areas demonstrated higher AGR (Figure 2a and Table 2). The same pattern was found for Mp and AGR (Figure 2b and Table 2) but integrating the leaf functional trait (an organ-level trait here scaled to species as an averaged trait) into the individual crown area value did not increase AGR explanation, on the contrary, crown area alone showed a better explanation. Moreover, LMA alone was found to be statistically insignificant (Figure 2c and Table 2). Our results are similar considering individuals with DBH > 10 cm (see Material Supplementary Table 1 and 2).

Finally, we found a positive association between community-level growth rate and canopy packing ($R^2m = 0.32$, $R^2c = 0.51$, coefficient = 2.40, std. error = 0.33, p-value < 0.001) (Figure 3).

Table 1: Linear mixed-effect models with annual growth rate (AGR) and individual metrics of crown area (ellipse and circle) and volume (cylinder and ellipsoid) of individual trees in subtropical Atlantic forests. The table shows the model's standardized coefficients, Akaike's value (AICc), ΔAIC (AICi - AICmin), and Akaike weights (wi). Models are ordered from the lower AICc value, showing the model with the best goodness of fit and a higher probability of being the best model. Moreover, the table shows the models with marginal R^2 (R^2m, related to fixed effect - crown size metrics) and conditional (R^2c, random effects - species identity). All models are significant ($p < 0.01$).

Crown Models	Coefficient	AICc	ΔAIC	*wi*	R^2m	R^2c
AGR ~ Ellipse	1.00	3220.5	0.00	0.79	0.18	0.33
AGR ~ Circle	0.98	3223.2	2.73	0.20	0.18	0.32
AGR ~ Cylinder	0.96	3263.2	42.78	0.00	0.15	0.30
AGR ~ Ellipsoid	0.98	3273.7	53.21	0.00	0.14	0.30

Table 2: The table shows tested models aiming to determine the best predictor for annual tree growth (AGR) of individual trees in subtropical Atlantic forests. These models incorporate crown area (ellipse), total photosynthetic mass (Mp), and leaf mass per area (LMA). For each model, we provide standardized coefficients, Akaike's value (AICc), ΔAIC (AICi - AICmin), and Akaike weights (wi). Lower AICc value indicates the model with the best fit and higher likelihood of being superior. The table also presents models with marginal R^2 (R^2m) related to fixed effects (functional traits) and conditional R^2 (R^2c) accounting for random effects (species identity). Significant models are denoted with an asterisk (*).

Growth Models	Coefficient	AICc	ΔAIC	wi	R^2m	R^2c
AGR ~ Ellipse	0.57	3220.5	0	1	0.18	0.32*
AGR ~ Mp	0.55	3242.5	24.23	0	0.17	0.31*
AGR ~ LMA	0.13	3431.5	210.5	0	0.01	0.24

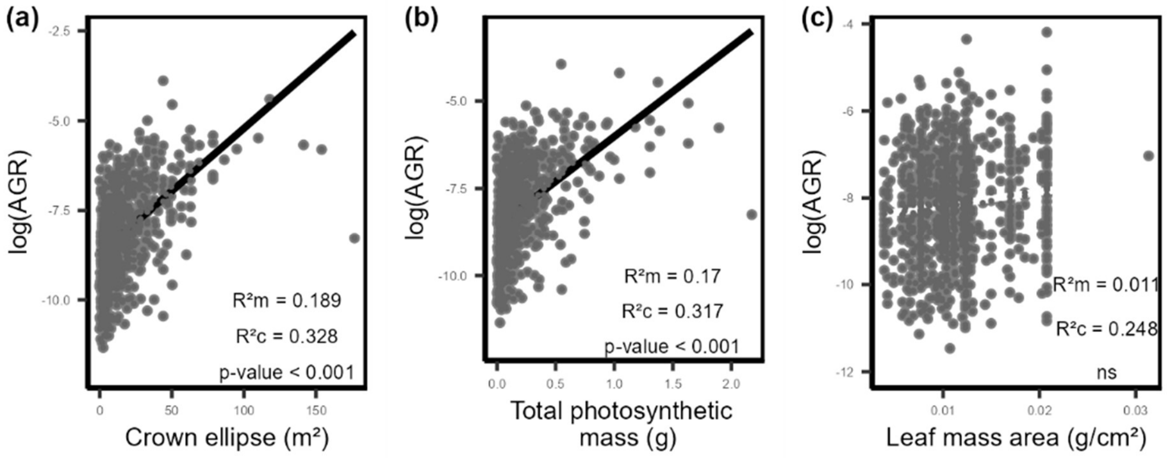

Figure 2: Relationship between annual growth rate (AGR) and Crown Area- ellipse (a), Total Photosynthetic Mass (b) and Leaf Mass Area (c). ns = non-significative (p-value > 0.01).

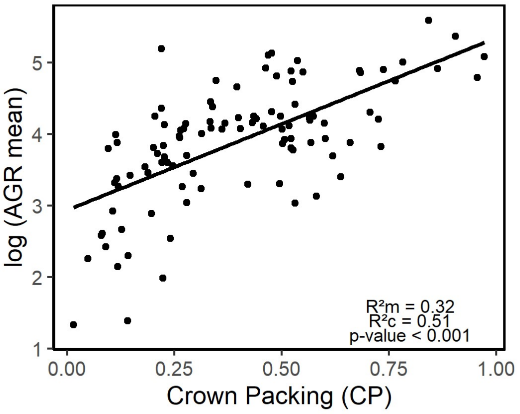

Figure 3: Relationship between community-level growth rate (AGR mean) and canopy packing (CP) in subtropical Atlantic forests.

4. Discussion

A significant challenge in tree ecology studies is identifying plant functional traits as reliable predictors of tree growth and performance. Many of these traits have proven to be poor predictors, raising questions about their functional significance (Paine et al., 2015; Poorter et al., 2008). The limited success of traits in determining individual tree performance may stem from insufficient consideration of the overall phenotypic context of the individual that explains performance and the underlying functional processes (e.g., photosynthesis), as most studies are based on the use of traits measured at individuals but scaled (averaged) to the species level (Iida & Swenson, 2020; Yang et al., 2021).

Here, we evaluated the effectiveness of crown area, a simple trait measured at the individual level, in testing the trait-growth relationships of trees. We found that the crown area quantified as an ellipse and the total photosynthetic mass (i.e., Mp) positively influenced the tree's growth rate, not being predictable solely based on leaf mass (i.e., LMA). This implies that LMA, which often fails to predict tree performance (Yang et al., 2018), could be a stronger predictor by integrating leaf-level traits with whole plant allocation to leaf area. However, the similarity in performance between growth models involving crown area and those incorporating total photosynthetic mass indicates that excluding LMA and solely measuring crown area could be sufficient for growth models in this forest, as also observed by Rubio et al. (2021).

The use of functional traits, such as here for the LMA, in species mean trait level may fail to predict tree performance since the values are based on the organ-level and the intraspecific variation is not being considered. This may be crucial as observed in studies focusing on the understanding of community assembly at local scales, which depends critically on intraspecific trait variation (Klipel et al., 2023; Yang et al., 2021). However, collecting local functional traits, even those that are considered soft traits ("easy" measured traits), becomes challenging when operating within highly diverse forests. On the other hand, measuring the crown size could be relatively easily included in forest census, as individual tree height is currently adopted in most studies. Comparing our models of crown area and total tree-level photosynthetic mass (Mp), we highlight the importance of considering crown size as a critical variable to be measured in floristic inventories and in studies focused on tree performance once it can act as a surrogate for total leaf area and light interception.

Light represents a crucial resource for plants and becomes limited in closed forests, influencing their recruitment, growth, and survival (Matsuo et al., 2021; Uriarte et al., 2018). Forest canopies establish vertical and horizontal light gradients shaped by the forest's structural components such as tree height, crown size (length, width, depth), and foliage distribution within the crowns. Then, trees that vary in height and crown sizes can complement the forest canopy, and intercepting light across the vertical and horizontal gradient likely enhances both individual and community growth through light niche partitioning (Matsuo et al., 2021). In addition to forest structure attributes, functional traits related to light interception, such as leaf economics spectrum, are highly related to growth (Liu et al., 2016; Modolo et al., 2021). As expected, we found a positive correlation between total photosynthetic mass, crown area, and individual growth. Trees with larger crowns deployed for light interception exhibited faster individual growth rates as this trait is closely related to canopy light interception and overall allocation for resource capture (Rubio et al., 2021). It is also important to note that individuals with larger canopies and a greater investment in structure (more biomass) at the expense of leaf area (smaller leaf size) experience greater growth. But this becomes evident from a canopy area of approximately 50 m, as there is a trade-off between increased self-shading with a very voluminous canopy, and, consequently, photosynthesis is not optimized. This suggests that trees with conservative attributes can enhance their performance by increasing the size of their canopies.

Furthermore, the crown's structure and canopy composition impact local environmental conditions within the forest (Pretzsch, 2014), particularly regarding light and precipitation interception. This interaction between structure, environment, and growth is pivotal in driving population and community dynamics since it relates to light interception, energy capture through photosynthesis, and resource utilization efficiency

(Grams & Andersen, 2007). Within the community context, different trees may exhibit varying crown sizes and heights to adapt the canopy in response to competition for light among neighboring trees (Thorpe et al., 2010; Vieilledent et al., 2010). Trees capable of adjusting their crowns (i.e., intraspecific variation in crown morphology) to encourage canopy space filling at the community level can amplify the overall forest performance. By supporting this hypothesis, we found that elevated levels of canopy packing increased the community-level growth rate within our local community plots. This structural indicator seems essential for forest communities, facilitating denser tree arrangement and efficient light interception in the forest (Pretzsch, 2014), partitioning this crucial resource. Consequently, such crown complementarity contributes to improved individual and community growth over time.

5. Conclusion

Our study indicates that crown area, represented as an ellipse and integrated as total tree-level photosynthetic mass (Mp), positively influences annual tree growth rates. Notably, this influence is much less dependent on leaf mass per area (LMA) than on crown area per se. Trees with larger crowns and with more leaf mass per area deployed for light interception, but at the same time supporting long leaf lifespan, tend to have faster individual growth rates. Together, these traits are closely related to canopy light interception but also to efficiently maintaining their leaves in the long term. Additionally, the formation of structurally compartmentalized and larger canopies by trees can also enhance light interception at the community level, thereby increasing tree community productivity. Recognizing the significance of incorporating crown measurements into studies and fieldwork enhances our understanding of tree growth dynamics and ecosystem performance.

CRediT authorship contribution statement

Joice Klipel: Conceptualization, Formal analysis, Software, Writing – original draft, Data curation, Investigation, Methodology. **Davi da Cunha Morales:** Conceptualization, Formal analysis, Software, Writing – original draft, Data curation, Investigation, Methodology. **Kauane Maiara Bordin:** Data curation, Writing – review & editing. **Rayana Caroline Picolotto:** Writing – review & editing. **Rodrigo Scarton Bergamin:** Supervision, Writing – review & editing. **Sandra Cristina Müller:** Supervision, Writing – review & editing.

Declaration of Competing Interest

None.

Data availability

All the data used for analysis in this study can be found in the supplementary material.

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Supplementary Material

Table 1: Linear models were employed to assess the annual growth rate (AGR) in relation to crown area (both ellipse and circle) and volume (both cylinder and ellipsoid). The analysis focused on individuals with a DBH of 10 cm or more. The table presents standardized coefficients, Akaike's information criterion (AICc), ΔAIC (AICi - AICmin), and Akaike weights (*wi*) for each model. Lower AICc values are underlined, indicating the model with the best fit and a higher likelihood of being the optimal choice. Moreover, the table shows the models with marginal R^2 (R^2m, related to fixed effect) and conditional (R^2c, random effects, i.e., species).

Growth Model	Coefficient	AICc	ΔAIC	*wi*	R^2m	R^2c
AGR ~ Ellipse	0.40	1684.9	0	0.696	0.11	0.30
AGR ~ Circle	0.40	1686.6	1.71	0.296	0.11	0.29
AGR ~ Ellipsoid	0.39	1694.1	9.23	0.007	0.10	0.29
AGR ~ Cylinder	0.36	1699.2	14.32	0.001	0.09	0.29

Table 2: The table shows tested models aiming to determine the best predictor for annual tree growth (AGR) considering individuals with a DBH of 10 cm or more. These models incorporate crown area (CA-ellipse), total photosynthetic mass (Mp), and leaf mass per area (LMA). For each model, we provide standardized coefficients, Akaike's value (AICc), ΔAIC (AICi - AICmin), and Akaike weights (*wi*). Lower AICc values are highlighted, indicating the model with the best fit and higher likelihood of being superior. The table also presents models with marginal R^2 (R^2m) related to fixed effects (habitat type) and conditional R^2 (R^2c) accounting for random effects (species). Significant models ($p < 0.01$) are denoted with an asterisk (*).

Growth Models	Coefficient	AICc	ΔAIC	*wi*	R^2m	R^2c
AGR ~ CA	0.40	1684.9	0	0.971	0.11	0.30*
AGR ~ Mp	0.39	1691.9	7.05	0.29	0.10	0.316*
AGR ~ LMA	0.02	1756.4	71.54	0.00	0.0004	0.286

Table 3: List of 123 species of 1032 individuals with DBH equal to or greater than 5 cm. Growth is the mean variation in basal area between individuals of a species; The crown area is the area of the average ellipse of individuals of a species; LMA is average leaf mass (1/SLA) of the species; Mp is the mean total photosynthetic mass of individuals of the species; Abundance is the number of individuals of each species. The standard deviation is shown in parentheses.

Specie	Mean Growth ($cm^2/ha.y^{-1}$)	Mean Crown area (ellipse, m^2)	Mean LMA	Mean Mp	Number of Individuals
Actinostemon concolor	0.00011 (0)	8.20892 (7.089)	0.00989	0.08115 (0.07)	26
Aegiphila integrifolia	0.00012 (NA)	2.35619 (NA)	0.01640	0.03863 (NA)	1
Aiouea saligna	5e-05 (NA)	1.5708 (NA)	0.01450	0.02277 (NA)	1
Alchornea triplinervia	0.00569 (0.011)	36.04978 (20.25)	0.01103	0.39906 (0.26)	5
Annona neosericea	0.00056 (NA)	28.27433 (NA)	0.00858	0.24271 (NA)	1
Araucaria angustifolia	0.00151 (0.001)	24.13426 (31.348)	0.01230	0.29686 (0.386)	61
Blepharocalyx salicifolius	0.00023 (0)	8.63938 (1.111)	0.00809	0.06987 (0.009)	2
Brosimum glaziovii	0.00017 (NA)	7.06858 (NA)	0.01233	0.08718 (NA)	1
Cabralea canjerana	0.00122 (0.001)	25.13274 (17.953)	0.00637	0.16165 (0.118)	14
Calyptranthes concinna	0.00015 (0)	15.55088 (15.027)	0.01193	0.18559 (0.179)	5
Calyptranthes grandifolia	0.00061 (0.001)	16.54223 (12.106)	0.01035	0.17122 (0.125)	9
Campomanesia xanthocarpa	0.00084 (0.001)	18.06416 (8.261)	0.00649	0.11719 (0.054)	5
Casearia decandra	0.00027 (0)	10.55864 (9.803)	0.00578	0.06108 (0.057)	19
Casearia obliqua	8e-05 (NA)	0.7854 (NA)	0.00726	0.0057 (NA)	1
Casearia sylvestris	0.00039 (0)	18.58776 (9.978)	0.00697	0.1292 (0.068)	15
Cecropia glaziovii	0.00402 (NA)	37.69911 (NA)	0.00620	0.23386 (NA)	1
Cedrela fissilis	0.0013 (NA)	27.48894 (NA)	0.00510	0.14033 (NA)	1
Cestrum intermedium	0.00064 (NA)	2.35619 (NA)	0.00454	0.01069 (NA)	1
Chrysophyllum inornatum	0.00037 (0)	21.43892 (13.743)	0.01039	0.22267 (0.143)	16
Chrysophyllum viride	0.00021 (NA)	23.75829 (NA)	0.00835	0.19849 (NA)	1
Cinnamomum amoenum	0.00049 (NA)	4.71239 (NA)	0.01202	0.05663 (NA)	1
Cinnamomum glaziovii	0.00159 (0.002)	15.38071 (22.509)	0.01293	0.19963 (0.279)	6
Clethra scabra	0.00174 (NA)	18.84956 (NA)	0.01560	0.29404 (NA)	1
Cordia trichotoma	0.00125 (0.001)	26.04904 (10.685)	0.00673	0.17532 (0.072)	3
Coussapoa microcarpa	0.00839 (0.011)	64.40265 (75.529)	0.01164	0.74995 (0.88)	2
Croton macrobothrys	0.00202 (NA)	62.83185 (NA)	0.00524	0.32948 (NA)	1
Cryptocarya aschersoniana	0.00027 (0)	2.74889 (0.555)	0.01125	0.03093 (0.006)	2
Cupania vernalis	0.0012 (NA)	30.78761 (NA)	0.00778	0.23962 (NA)	1
Daphnopsis fasciculata	0.00032 (0)	5.58581 (3.351)	0.01282	0.07159 (0.043)	29
Drimys angustifolia	0.00084 (0.001)	7.37783 (6.243)	0.00923	0.06811 (0.058)	16
Drimys brasiliensis	0.00021 (0)	6.401 (4.012)	0.01293	0.08276 (0.052)	4
Endlicheria paniculata	0.00049 (0.001)	20.51853 (19.953)	0.00807	0.16565 (0.161)	4
Esenbeckia grandiflora	0.00041 (0.001)	15.70796 (4.443)	0.01437	0.22568 (0.064)	2
Eugenia handroi	6e-04 (0.001)	17.07208 (15.975)	0.01304	0.22262 (0.208)	19
Eugenia multicostata	0.0016 (0.002)	19.63495 (15.189)	0.01072	0.21041 (0.163)	5

Eugenia oeidocarpa	0.00023 (0)	10.112 (6.414)	0.01009	0.10204 (0.065)	6
Eugenia rostrifolia	0.003 (0.004)	15.31526 (17.216)	0.01183	0.18112 (0.204)	2
Eugenia subterminalis	0.00038 (0)	13.19544 (7.003)	0.01105	0.14583 (0.077)	21
Eugenia uruguayensis	0.00027 (0)	22.77655 (16.236)	0.01078	0.24545 (0.175)	4
Eugenia verticillata	0.00016 (0)	9.29388 (5.558)	0.00953	0.08857 (0.053)	3
Euterpe edulis	0.00025 (0)	11.30299 (5.797)	0.00769	0.08696 (0.045)	99
Faramea montevidensis	0.00053 (NA)	32.98672 (NA)	0.00820	0.27043 (NA)	1
Ficus adhatodifolia	0.00192 (0.002)	33.37942 (10.946)	0.01044	0.34846 (0.114)	3
Garcinia gardneriana	0.00038 (0.001)	16.66166 (14.206)	0.01230	0.20497 (0.175)	7
Guapira opposita	0.00018 (0)	6.61043 (8.49)	0.00660	0.04362 (0.056)	6
Hennecartia omphalandra	0.00065 (0.001)	20.78851 (16.293)	0.00647	0.13448 (0.105)	8
Hieronyma alchorneoides	0.00335 (0.003)	50.31457 (34.258)	0.01186	0.59685 (0.406)	8
Hirtella hebeclada	0.00046 (0)	21.94206 (16.67)	0.01598	0.35067 (0.266)	4
Ilex dumosa	0.00102 (NA)	4.71239 (NA)	0.03134	0.14769 (NA)	1
Ilex microdonta	0.00088 (0.001)	18.88056 (13.995)	0.01695	0.32001 (0.237)	38
Ilex paraguariensis	0.00037 (0)	17.46398 (12.872)	0.01704	0.29764 (0.219)	12
Inga lentiscifolia	3e-05 (NA)	6.28319 (NA)	0.00711	0.04469 (NA)	1
Inga marginata	0.00057 (0.001)	14.92257 (13.962)	0.00842	0.12571 (0.118)	4
Inga virescens	0.00058 (NA)	11.78097 (NA)	0.00763	0.08988 (NA)	1
Lamanonia ternata	0.00254 (0.004)	21.62299 (14.671)	0.00751	0.16246 (0.11)	8
Laplacea acutifolia	0.00108 (0.001)	17.01101 (27.093)	0.01240	0.21098 (0.336)	11
Lonchocarpus cultratus	0.00142 (0.002)	15.70796 (19.11)	0.00563	0.08849 (0.108)	3
Machaerium stipitatum	4e-05 (NA)	1.5708 (NA)	0.00737	0.01158 (NA)	1
Matayba elaeagnoides	2e-04 (0)	29.45243 (24.991)	0.00803	0.23638 (0.201)	2
Matayba intermedia	2e-04 (NA)	25.52544 (NA)	0.01698	0.4333 (NA)	1
Maytenus evonymoides	2e-05 (NA)	0.3927 (NA)	0.00891	0.0035 (NA)	1
Meliosma sellowii	0.00041 (0)	9.70528 (8.057)	0.00629	0.06106 (0.051)	7
Miconia cinerascens	0.00026 (NA)	1.76715 (NA)	0.01617	0.02858 (NA)	1
Mimosa scabrella	0.00578 (0)	37.69911 (6.664)	0.00605	0.22805 (0.04)	2
Mollinedia schottiana	0.00022 (0)	5.1869 (2.452)	0.00423	0.02194 (0.01)	12
Mollinedia triflora	7e-05 (0)	10.99557 (9.539)	0.00487	0.05355 (0.046)	5
Muellera campestris	0.00383 (NA)	23.56194 (NA)	0.00612	0.14425 (NA)	1
Myrceugenia euosma	0.00154 (0.002)	17.29943 (14.315)	0.01256	0.21733 (0.18)	19
Myrceugenia mesomischa	0.00027 (0)	11.31464 (9.779)	0.00862	0.09752 (0.084)	16
Myrceugenia miersiana	0.00028 (0)	11.31104 (7.048)	0.00989	0.1119 (0.07)	30
Myrceugenia myrcioides	0.00033 (0)	6.48664 (6.231)	0.01035	0.06717 (0.065)	58
Myrceugenia oxysepala	0.00014 (0)	6.43045 (5.179)	0.00814	0.05233 (0.042)	4
Myrcia guianensis	0.00045 (0)	13.15542 (15.395)	0.01849	0.24326 (0.285)	8
Myrcia lajeana	0.00027 (0)	16.10066 (9.006)	0.01071	0.17238 (0.096)	6
Myrcia oligantha	0.00014 (0)	9.27752 (6.904)	0.01199	0.11122 (0.083)	8
Myrcia pubipetala	0.00035 (0)	16.19884 (23.735)	0.01202	0.19473 (0.285)	6
Myrcia retorta	8e-04 (0.002)	13.92349 (18.656)	0.02077	0.28921 (0.388)	68
Myrcia tijucensis	0.00028 (0)	8.56084 (8.948)	0.00700	0.0599 (0.063)	5
Myrciaria floribunda	0.00044 (0.001)	29.95733 (27.17)	0.00954	0.28571 (0.259)	7
Myrrhinium atropurpureum	0.00011 (NA)	14.13717 (NA)	0.01249	0.17662 (NA)	1
Myrsine coriacea	0.00092 (0.001)	10.35744 (15.105)	0.00888	0.09196 (0.134)	4

Myrsine guianensis	0.00023 (0)	1.86532 (1.527)	0.01329	0.02478 (0.02)	2
Myrsine lorentziana	0.00028 (0)	6.97041 (7.839)	0.01138	0.07932 (0.089)	8
Nectandra grandiflora	0.00019 (0)	5.30144 (3.716)	0.01786	0.09467 (0.066)	12
Nectandra oppositifolia	0.00114 (0.002)	16.49336 (16.661)	0.01667	0.27499 (0.278)	2
Nectandra puberula	0.00014 (NA)	12.56637 (NA)	0.01218	0.1531 (NA)	1
Ocotea bicolor	8e-04 (0.001)	14.75722 (16.641)	0.01499	0.22125 (0.249)	19
Ocotea elegans	0.00043 (0.001)	6.68897 (4.445)	0.01124	0.07517 (0.05)	9
Ocotea porosa	0.00082 (0.001)	25.06318 (14.486)	0.01119	0.28039 (0.162)	7
Ocotea pulchella	0.00016 (NA)	2.35619 (NA)	0.01185	0.02792 (NA)	1
Ocotea silvestris	1e-04 (0)	11.84642 (13.734)	0.00944	0.11187 (0.13)	3
Pachystroma longifolium	0.00059 (0.001)	17.82854 (16.037)	0.01366	0.24357 (0.219)	5
Piptocarpha angustifolia	0.00431 (NA)	62.83185 (NA)	0.01101	0.69192 (NA)	1
Piptocarpha axillaris	0.00144 (0.001)	12.33075 (8.729)	0.02028	0.25001 (0.177)	13
Pisonia zapallo	0.00027 (NA)	3.53429 (NA)	0.00610	0.02157 (NA)	1
Plinia pseudodichasiantha	3e-05 (NA)	5.89049 (NA)	0.00921	0.05423 (NA)	1
Podocarpus lambertii	0.00042 (0.001)	11.51917 (8.061)	0.01228	0.1415 (0.099)	3
Posoqueria latifolia	9e-05 (NA)	4.71239 (NA)	0.01845	0.08696 (NA)	1
Prunus myrtifolia	0.00088 (0.001)	8.44303 (9.909)	0.01051	0.08872 (0.104)	3
Prunus subcoriacea	0.00012 (NA)	21.20575 (NA)	0.01079	0.22876 (NA)	1
Pseudobombax grandiflorum	8e-04 (0.001)	23.56194 (13.329)	0.01071	0.25233 (0.143)	2
Psidium longipetiolatum	1e-04 (NA)	2.94524 (NA)	0.01794	0.05285 (NA)	1
Psychotria suterella	0.00017 (0)	10.91922 (4.768)	0.00390	0.04257 (0.019)	18
Rollinia rugulosa	0.00025 (NA)	0.7854 (NA)	0.00453	0.00356 (NA)	1
Roupala brasiliensis	0.00066 (0.001)	14.52987 (7.22)	0.01939	0.2817 (0.14)	2
Sapium glandulatum	0.00119 (NA)	27.48894 (NA)	0.01107	0.30418 (NA)	1
Sapium glandulosum	0.00026 (0)	4.4127 (3.635)	0.01108	0.04888 (0.04)	19
Schefflera calva	0.0062 (NA)	37.69911 (NA)	0.01367	0.51532 (NA)	1
Siphoneugena reitzii	4e-04 (0)	9.55865 (7.345)	0.01242	0.11873 (0.091)	22
Solanum mauritianum	0.00133 (NA)	0.7854 (NA)	0.00570	0.00448 (NA)	1
Solanum pseudoquina	0.00012 (0)	8.63938 (5.554)	0.00674	0.0582 (0.037)	2
Sorocea bonplandii	0.00012 (0)	6.55986 (4.197)	0.00950	0.0623 (0.04)	22
Symplocos tetrandra	5e-04 (0)	3.82882 (2.568)	0.00840	0.03216 (0.022)	4
Tetrorchidium rubrivenium	0.00141 (0.002)	18.13779 (21.068)	0.00766	0.13899 (0.161)	8
Tibouchina sellowiana	0.00078 (0.001)	3.88772 (5.498)	0.00884	0.03437 (0.049)	2
Trichilia claussenii	0.00055 (0.001)	27.37674 (22.012)	0.00830	0.22734 (0.183)	7
Trichilia lepidota	0.00125 (0.001)	51.44358 (64.078)	0.00982	0.50527 (0.629)	4
Trichilia pallens	0.00147 (NA)	21.99115 (NA)	0.00727	0.15994 (NA)	1
Vernonanthura discolor	7e-04 (0.001)	7.98488 (10.182)	0.01412	0.11278 (0.144)	3
Virola bicuhyba	0.00211 (0.002)	13.82301 (8.192)	0.00806	0.11136 (0.066)	5
Weinmannia paulliniifolia	0.00101 (0.001)	23.09071 (32.075)	0.00792	0.18284 (0.254)	5
Xylosma pseudosalzmanii	0.00024 (NA)	7.06858 (NA)	0.01271	0.08984 (NA)	1
Zanthoxylum rhoifolium	0.00022 (NA)	4.71239 (NA)	0.00773	0.03642 (NA)	1

Table 4: Linear models with annual growth rate (AGR) and species metrics of mean crown area (ellipse and circle) and volume (cylinder and ellipsoid), considering individuals with 5 cm or

more DBH. The table shows the model's standardized coefficients, Akaike's value (AICc), ΔAIC (AICi - AICmin), and Akaike weights (*wi*), and are shown for each model. Lower AICc values are underlined, showing the model with the best goodness of fit and a higher probability of being the best model. Moreover, the table shows the models with adjusted R^2. All models have significant coefficients (p-value < 0.001).

Growth Model	Coefficient	AICc	ΔAIC	*wi*	R^2
AGR ~ Ellipse	0.7645	327.7	0	0.682	0.4156
AGR ~ Circle	0.7568	329.5	1.77	0.281	0.4071
AGR ~ Ellipsoid	0.736	334	6.35	0.029	0.3847
AGR ~ Cylinder	0.7249	336.4	8.68	0.009	0.3729

Table 5: The table shows tested models to species level (individuals with DBH equal to or greater than 5 cm) aiming to determine the best predictor for annual tree growth (AGR). These models incorporate crown area (CA-ellipse), total photosynthetic mass (Mp), and leaf mass per area (LMA). For each model, we provide standardized coefficients, Akaike's value (AICc), ΔAIC (AICi - AICmin), and Akaike weights (*wi*). Lower AICc values are highlighted, indicating the model with the best fit and higher likelihood of being superior. Significant models ($p < 0.01$) are denoted with an asterisk (*).

Growth Models	Coefficient	AICc	ΔAIC	*wi*	R^2
AGR ~ CA	0.7645	327.7	0	0.995	0.4156*
AGR ~ Mp	0.715	338.4	10.7	0.005	0.3625*
AGR ~ LMA	0.01406	394.7	67.07	0	-0.008121

Table 6: List of 100 species from a total of 565 individuals with a DBH (diameter at breast height) of 10 cm or greater. Growth represents the mean variation in basal area among

individuals of same specie ($cm^2/ha.y^{-1}$); crown area is the average ellipse area of individuals within a specie (m^2); LMA stands for average leaf mass (1/SLA) of each specie; Mp indicates the mean total photosynthetic mass per specie; Abundance is the count of individuals for each specie, with standard deviation values shown in parentheses.

Specie	Annual Growth Rate ($cm^2/ha.y^{-1}$)	Crown area (ellipse, m^2)	LMA	Mp	Number of Individuals
Actinostemon concolor	0.00023 (0)	16.68971 (11.298)	0.00989	0.165 (0.112)	4
Aegiphila integrifolia	0.00012 (NA)	2.35619 (NA)	0.01640	0.03863 (NA)	1
Alchornea triplinervia	0.00569 (0.011)	36.04978 (20.25)	0.01103	0.39906 (0.26)	5
Annona neosericea	0.00056 (NA)	28.27433 (NA)	0.00858	0.24271 (NA)	1
Araucaria angustifolia	0.00174 (0.001)	27.55313 (32.782)	0.01230	0.33891 (0.403)	52
Blepharocalyx salicifolius	0.00024 (NA)	7.85398 (NA)	0.00809	0.06352 (NA)	1
Brosimum glaziovii	0.00017 (NA)	7.06858 (NA)	0.01233	0.08718 (NA)	1
Cabralea canjerana	0.00141 (0.001)	28.79793 (16.67)	0.00638	0.18537 (0.11)	12
Calyptranthes grandifolia	7e-04 (0.001)	22.98075 (9.215)	0.01035	0.23786 (0.095)	6
Campomanesia xanthocarpa	0.001 (0.001)	20.12583 (7.915)	0.00649	0.13056 (0.051)	4
Casearia decandra	0.00034 (0)	13.03929 (10.31)	0.00578	0.07543 (0.06)	14
Casearia sylvestris	0.00056 (0)	26.87184 (7.681)	0.00705	0.18748 (0.049)	7
Cecropia glaziovii	0.00402 (NA)	37.69911 (NA)	0.00620	0.23386 (NA)	1
Cedrela fissilis	0.0013 (NA)	27.48894 (NA)	0.00510	0.14033 (NA)	1
Chrysophyllum inornatum	0.00044 (0)	24.1812 (13.568)	0.01039	0.25116 (0.141)	13
Cinnamomum amoenum	0.00049 (NA)	4.71239 (NA)	0.01202	0.05663 (NA)	1
Cinnamomum glaziovii	0.00402 (0.002)	38.28816 (30.823)	0.01419	0.50223 (0.336)	2
Clethra scabra	0.00174 (NA)	18.84956 (NA)	0.01560	0.29404 (NA)	1
Cordia trichotoma	0.00125 (0.001)	26.04904 (10.685)	0.00673	0.17532 (0.072)	3
Coussapoa microcarpa	0.00839 (0.011)	64.40265 (75.529)	0.01164	0.74995 (0.88)	2
Croton macrobothrys	0.00202 (NA)	62.83185 (NA)	0.00524	0.32948 (NA)	1
Cryptocarya aschersoniana	0.00039 (NA)	2.35619 (NA)	0.01125	0.02651 (NA)	1
Cupania vernalis	0.0012 (NA)	30.78761 (NA)	0.00778	0.23962 (NA)	1
Daphnopsis fasciculata	0.00038 (0)	9.94838 (4.988)	0.01282	0.12749 (0.064)	3
Drimys angustifolia	0.00097 (0.001)	8.92498 (6.354)	0.00923	0.08239 (0.059)	11
Drimys brasiliensis	0.00035 (NA)	11.78097 (NA)	0.01293	0.15233 (NA)	1
Endlicheria paniculata	0.00092 (0.001)	32.59402 (23.88)	0.00807	0.26314 (0.193)	2
Esenbeckia grandiflora	8e-04 (NA)	18.84956 (NA)	0.01437	0.27082 (NA)	1
Eugenia handroi	0.00073 (0.001)	20.44653 (16.391)	0.01304	0.26662 (0.214)	15
Eugenia multicostata	0.002 (0.002)	23.95464 (13.535)	0.01072	0.2567 (0.145)	4
Eugenia oeidocarpa	0.00027 (0)	14.00627 (7.072)	0.01009	0.14133 (0.071)	3
Eugenia rostrifolia	0.00595 (NA)	27.48894 (NA)	0.01183	0.32509 (NA)	1
Eugenia subterminalis	0.00045 (0)	17.57093 (5.867)	0.01105	0.19419 (0.065)	10
Eugenia uruguayensis	0.00027 (0)	22.77655 (16.236)	0.01078	0.24545 (0.175)	4
Eugenia verticillata	0.00022 (NA)	15.70796 (NA)	0.00953	0.14969 (NA)	1
Euterpe edulis	0.00018 (0)	13.33774 (5.377)	0.00769	0.10262 (0.041)	42

Faramea montevidensis	0.00053 (NA)	32.98672 (NA)	0.00820	0.27043 (NA)	1
Ficus adhatodifolia	0.00192 (0.002)	33.37942 (10.946)	0.01044	0.34846 (0.114)	3
Garcinia gardneriana	8e-04 (0.001)	27.22714 (17.303)	0.01230	0.33494 (0.213)	3
Guapira opposita	0.00026 (0)	10.34108 (11.652)	0.00660	0.06824 (0.077)	3
Hennecartia omphalandra	0.00086 (0.001)	26.37629 (14.882)	0.00647	0.17063 (0.096)	6
Hieronyma alchorneoides	0.00335 (0.003)	50.31457 (34.258)	0.01186	0.59685 (0.406)	8
Hirtella hebeclada	0.00053 (0)	35.63744 (3.749)	0.01598	0.56954 (0.06)	2
Ilex dumosa	0.00102 (NA)	4.71239 (NA)	0.03134	0.14769 (NA)	1
Ilex microdonta	0.00104 (0.001)	21.41477 (14.088)	0.01695	0.36296 (0.239)	31
Ilex paraguariensis	0.00035 (0)	18.76602 (12.644)	0.01704	0.31983 (0.215)	11
Inga marginata	0.00075 (0.001)	18.32596 (14.929)	0.00842	0.15438 (0.126)	3
Lamanonia ternata	0.00289 (0.004)	24.03879 (14.023)	0.00751	0.18061 (0.105)	7
Laplacea acutifolia	0.00159 (0.001)	25.63764 (31.372)	0.01240	0.31798 (0.389)	7
Lonchocarpus cultratus	0.00399 (NA)	37.69911 (NA)	0.00563	0.21237 (NA)	1
Machaerium stipitatum	4e-05 (NA)	1.5708 (NA)	0.00737	0.01158 (NA)	1
Matayba elaeagnoides	0.00038 (NA)	47.12389 (NA)	0.00803	0.37821 (NA)	1
Matayba intermedia	2e-04 (NA)	25.52544 (NA)	0.01698	0.4333 (NA)	1
Meliosma sellowii	0.00066 (0)	12.95907 (8.734)	0.00629	0.08154 (0.055)	4
Mimosa scabrella	0.00578 (0)	37.69911 (6.664)	0.00605	0.22805 (0.04)	2
Mollinedia schottiana	0.00147 (NA)	2.35619 (NA)	0.00423	0.00997 (NA)	1
Muellera campestris	0.00383 (NA)	23.56194 (NA)	0.00612	0.14425 (NA)	1
Myrceugenia euosma	0.00154 (0.002)	17.29943 (14.315)	0.01256	0.21733 (0.18)	19
Myrceugenia mesomischa	0.00029 (0)	13.8181 (12.803)	0.00862	0.1191 (0.11)	8
Myrceugenia miersiana	0.00036 (0)	11.91691 (4.399)	0.00989	0.11789 (0.044)	13
Myrceugenia myrcioides	0.00077 (0.001)	13.095 (8.421)	0.01035	0.1356 (0.087)	13
Myrceugenia oxysepala	0.00024 (NA)	7.06858 (NA)	0.00814	0.05753 (NA)	1
Myrcia guianensis	0.00054 (0)	16.49336 (16.653)	0.01849	0.30498 (0.308)	6
Myrcia lajeana	3e-04 (0)	17.43584 (9.382)	0.01071	0.18668 (0.1)	5
Myrcia pubipetala	0.00081 (0.001)	32.98672 (42.207)	0.01202	0.39655 (0.507)	2
Myrcia retorta	0.00123 (0.002)	21.8537 (20.916)	0.02077	0.45393 (0.434)	40
Myrcia tijucensis	0.00046 (0)	14.72622 (12.496)	0.00700	0.10305 (0.087)	2
Myrciaria floribunda	0.00046 (0.001)	32.59402 (28.765)	0.00954	0.31086 (0.274)	6
Myrsine coriacea	0.00204 (NA)	32.98672 (NA)	0.00888	0.29289 (NA)	1
Myrsine guianensis	0.00038 (NA)	2.94524 (NA)	0.01329	0.03913 (NA)	1
Myrsine lorentziana	6e-04 (0.001)	16.68971 (1.388)	0.01138	0.18993 (0.016)	2
Nectandra grandiflora	0.00036 (0)	7.26493 (3.92)	0.01786	0.12973 (0.07)	4
Nectandra oppositifolia	0.00114 (0.002)	16.49336 (16.661)	0.01667	0.27499 (0.278)	2
Nectandra puberula	0.00014 (NA)	12.56637 (NA)	0.01218	0.1531 (NA)	1
Ocotea bicolor	0.00088 (0.001)	16.07756 (17.14)	0.01499	0.24104 (0.257)	17
Ocotea elegans	0.00029 (0)	7.42856 (3.655)	0.01124	0.08348 (0.041)	6
Ocotea porosa	0.00082 (0.001)	25.06318 (14.486)	0.01119	0.28039 (0.162)	7
Ocotea pulchella	0.00016 (NA)	2.35619 (NA)	0.01185	0.02792 (NA)	1
Ocotea silvestris	0.00018 (NA)	27.48894 (NA)	0.00944	0.25958 (NA)	1
Pachystroma longifolium	0.00059 (0.001)	17.82854 (16.037)	0.01366	0.24357 (0.219)	5
Piptocarpha angustifolia	0.00431 (NA)	62.83185 (NA)	0.01101	0.69192 (NA)	1
Piptocarpha axillaris	0.00178 (0.001)	16.06139 (9.061)	0.02028	0.32564 (0.184)	8

Podocarpus lambertii	0.00062 (0.001)	14.92257 (7.775)	0.01228	0.18331 (0.096)	2
Prunus myrtifolia	0.00221 (NA)	19.63495 (NA)	0.01051	0.20634 (NA)	1
Prunus subcoriacea	0.00012 (NA)	21.20575 (NA)	0.01079	0.22876 (NA)	1
Pseudobombax grandiflorum	8e-04 (0.001)	23.56194 (13.329)	0.01071	0.25233 (0.143)	2
Roupala brasiliensis	0.00124 (NA)	19.63495 (NA)	0.01939	0.38068 (NA)	1
Sapium glandulatum	0.00119 (NA)	27.48894 (NA)	0.01107	0.30418 (NA)	1
Sapium glandulosum	0.00037 (0)	6.31889 (3.752)	0.01108	0.06999 (0.042)	11
Schefflera calva	0.0062 (NA)	37.69911 (NA)	0.01367	0.51532 (NA)	1
Siphoneugena reitzii	0.00058 (0)	12.87726 (7.089)	0.01242	0.15995 (0.088)	12
Solanum pseudoquina	0.00012 (0)	8.63938 (5.554)	0.00674	0.0582 (0.037)	2
Sorocea bonplandii	0.00025 (0)	8.63938 (5.548)	0.00950	0.08204 (0.053)	6
Tetrorchidium rubrivenium	0.00216 (0.003)	27.64602 (21.747)	0.00766	0.21185 (0.167)	5
Trichilia claussenii	0.00075 (0.001)	28.90265 (24.095)	0.00830	0.24002 (0.2)	5
Trichilia lepidota	0.00162 (0.001)	67.28244 (68.218)	0.00982	0.66084 (0.67)	3
Trichilia pallens	0.00147 (NA)	21.99115 (NA)	0.00727	0.15994 (NA)	1
Vernonanthura discolor	0.00097 (0.001)	10.21018 (13.329)	0.01412	0.14421 (0.188)	2
Virola bicuhyba	0.00333 (0.002)	15.70796 (10.883)	0.00806	0.12655 (0.088)	3
Weinmannia paulliniifolia	0.00155 (0)	37.17551 (36.242)	0.00792	0.29436 (0.287)	3

Table 7: The table shows tested models to species level (individuals with DBH equal to or greater than 10 cm) aiming to determine the best predictor for annual tree growth (AGR). These models incorporate crown area (CA-ellipse), total photosynthetic mass (Mp), and leaf mass per area (LMA). For each model, we provide standardized coefficients, Akaike's value (AICc), ΔAIC (AICi - AICmin), and Akaike weights (*wi*). Lower AICc values are highlighted, indicating the model with the best fit and higher likelihood of being superior.

Growth Models	Coefficient	AICc	ΔAIC	*wi*	R^2
AGR ~ Ellipse	0.6393	251.7	0	0.75	0.3663
AGR ~ Circle	0.6245	254.3	2.7	0.195	0.3489
AGR ~ Cylinder	0.6021	258.2	6.51	0.029	0.3237
AGR ~ Ellipsoid	0.6011	258.3	6.67	0.027	0.3226

Table 8: The table shows tested models to species level (individuals with DBH equal to or greater than 10 cm) aiming to determine the best predictor for annual tree growth (AGR). These models incorporate crown area (CA-ellipse), total photosynthetic mass (Mp), and leaf mass per area (LMA). For each model, we provide standardized coefficients, Akaike's value

(AICc), ΔAIC (AICi - AICmin), and Akaike weights (*wi*). Lower AICc values are highlighted, indicating the model with the best fit and higher likelihood of being superior. Significant models ($p < 0.01$) are denoted with an asterisk (*).

Growth Models	Coefficient	AICc	ΔAIC	*wi*	R^2
AGR ~ CA	0.6393	251.7	0	0.997	0.3663*
AGR ~ Mp	0.5688	263.3	11.67	0.003	0.2878*
AGR ~ LMA	-3086	298.2	46.54	0	-0.009327

Table 9: Community-level mean growth ($cm^2.y^{-1}$) and Crown Packing (CP) data are presented for the permanent plots spanning the 9 study sites. The table also provides information about the census interval between measurements and the corresponding measurement year.

Site	Plot	CP	Mean growth ($cm^2.y^{-1}$)	Census interval	Time 1	Time 2
ENN-01	NE1	0.112698	85.99684349	6	2014	2020
ENN-01	NE2	0.261799	83.80222442	6	2014	2020
ENN-01	NE3	0.220229	285.6733957	6	2014	2020
ENN-01	NW10	0.864183	215.3559295	6	2014	2020
ENN-01	NW11	0.245942	55.2228008	6	2014	2020
ENN-01	NW12	0.271445	93.02768055	6	2014	2020
ENN-01	SE4	0.204358	111.0757912	6	2014	2020
ENN-01	SE5	0.141834	15.71056199	6	2014	2020
ENN-01	SE6	0.549903	205.1975329	6	2014	2020
ENN-01	SW7	0.126854	22.70891505	6	2014	2020
ENN-01	SW8	0.222731	11.56560353	6	2014	2020
ENN-01	SW9	0.196588	28.34553881	6	2014	2020
ENN-02	E1	0.462649	98.10330782	5	2014	2019
ENN-02	E10	0.63788	21.45120891	5	2014	2019
ENN-02	E11	0.531322	14.87388768	5	2014	2019
ENN-02	E12	0.240365	9.101642716	5	2014	2019
ENN-02	E2	0.395855	75.4479368	5	2014	2019
ENN-02	E3	0.497645	50.03072608	5	2014	2019
ENN-02	E4	0.33319	46.5880929	5	2014	2019
ENN-02	E5	0.226379	27.89734276	5	2014	2019
ENN-02	E6	0.435023	50.02796424	5	2014	2019

ENN-02	E7	0.501771	41.81839575	5	2014	2019
ENN-02	E8	0.581718	16.45227907	5	2014	2019
ENN-02	E9	0.476641	120.8318676	5	2014	2019
MFO-01	MF1.1	0.737293	108.5350372	6	2014	2020
MFO-01	MF1.10	0.312123	20.47165551	6	2014	2020
MFO-01	MF1.11	0.905433	172.8410634	6	2014	2020
MFO-01	MF1.12	0.843076	215.4431373	6	2014	2020
MFO-01	MF1.2	0.619256	32.32359959	6	2014	2020
MFO-01	MF1.3	0.457427	49.17729322	6	2014	2020
MFO-01	MF1.4	0.294167	25.38301966	6	2014	2020
MFO-01	MF1.5	0.682106	106.7464248	6	2014	2020
MFO-01	MF1.6	0.522552	106.3925214	6	2014	2020
MFO-01	MF1.7	0.495263	22.00566116	6	2014	2020
MFO-01	MF1.8	0.599589	51.16959102	6	2014	2020
MFO-01	MF1.9	0.507202	40.67215483	6	2014	2020
PNA-01	I1NE1	0.278635	47.40704245	7	2014	2021
PNA-01	I1NE2	0.221528	43.07284448	7	2014	2021
PNA-01	I1NE3	0.338594	93.59036083	7	2014	2021
PNA-01	I1NW10	0.399167	80.42796791	7	2014	2021
PNA-01	I1NW11	0.336145	69.2406348	7	2014	2021
PNA-01	I1NW12	0.095591	52.1141048	7	2014	2021
PNA-01	I1SE4	0.141372	4.709865838	7	2014	2021
PNA-01	I1SE5	0.360921	68.72339061	7	2014	2021
PNA-01	I1SE6	0.568011	56.62211924	7	2014	2021
PNA-01	I1SW7	0.566714	77.64690427	7	2014	2021
PNA-01	I1SW8	0.219937	91.72323545	7	2014	2021
PNA-01	I1SW9	0.725668	78.88184231	7	2014	2021
PNA-02	I2NE2	0.11781	7.748730884	7	2014	2021
PNA-02	I2NE3	0.531162	75.18459311	7	2014	2021
PNA-02	I2NW10	0.115153	26.5658582	7	2014	2021
PNA-02	I2NW11	0.441191	61.39674487	7	2014	2021
PNA-02	I2NW12	0.201586	41.14308706	7	2014	2021
PNA-02	I2SE4	0.477223	67.75161448	7	2014	2021
PNA-02	I2SE5	0.469097	149.9695178	7	2014	2021
PNA-02	I2SE6	0.233571	33.39008925	7	2014	2021
PNA-02	I2SW7	0.782698	135.7635112	7	2014	2021
PNA-02	I2SW8	0.048695	8.715899937	7	2014	2021
PNA-02	I2SW9	0.731767	41.70774311	7	2014	2021
PNA-03	I3NE1	0.403917	39.55446256	7	2014	2021
PNA-03	I3NE2	0.526937	29.20817692	7	2014	2021
PNA-03	I3NE3	0.224175	31.21407514	7	2014	2021
PNA-03	I3NW10	0.268689	17.55966945	7	2014	2021
PNA-03	I3NW11	0.090592	7.584846443	7	2014	2021
PNA-03	I3NW12	0.265465	38.65594352	7	2014	2021
PNA-03	I3SE4	0.420987	18.1918568	7	2014	2021
PNA-03	I3SW7	0.110573	18.54649848	7	2014	2021

PRM-01	P1NE1	0.521897	63.73666639	6	2013	2019
PRM-01	P1NE2	0.53682	188.9183827	6	2013	2019
PRM-01	P1NE3	0.706858	92.18561337	6	2013	2019
PRM-01	P1NW10	0.517708	76.38384968	6	2013	2019
PRM-01	P1NW11	0.525137	141.7930498	6	2013	2019
PRM-01	P1NW12	0.367897	78.99294454	6	2013	2019
PRM-01	P1SE4	0.488125	152.5137167	6	2013	2019
PRM-01	P1SE5	0.564773	84.80568465	6	2013	2019
PRM-01	P1SE6	0.432296	79.7462341	6	2013	2019
PRM-01	P1SW7	0.521754	55.76074421	6	2013	2019
PRM-01	P1SW8	0.660247	60.11741312	6	2013	2019
PRM-01	P1SW9	0.973108	200.1210394	6	2013	2019
PRM-02	P2NE1	0.765202	79.44845805	8	2013	2021
PRM-02	P2NE2	0.684278	89.56611137	8	2013	2021
PRM-02	P2NE3	0.602139	35.4831799	8	2013	2021
PRM-02	P2NW10	0.226784	27.47703684	8	2013	2021
PRM-02	P2NW11	0.227352	43.08980907	8	2013	2021
PRM-02	P2NW12	0.334355	59.28093896	8	2013	2021
PRM-02	P2SE4	0.119381	18.27235209	8	2013	2021
PRM-02	P2SE5	0.956338	83.24600348	8	2013	2021
PRM-02	P2SE6	0.014835	2.622080362	8	2013	2021
PRM-02	P2SW7	0.501941	33.02119356	8	2013	2021
PRM-02	P2SW8	0.57459	48.59646629	8	2013	2021
PRM-02	P2SW9	0.147084	21.21029362	8	2013	2021
PRM-03	P3NE1	0.080157	23.64861055	7	2014	2021
PRM-03	P3NE2	0.26319	93.15890353	7	2014	2021
PRM-03	P3NE3	0.276853	113.3290365	7	2014	2021
PRM-03	P3NW10	0.105811	33.39812543	7	2014	2021
PRM-03	P3NW11	0.278424	37.6143721	7	2014	2021
PRM-03	P3NW12	0.181631	61.90593804	7	2014	2021
PRM-03	P3SE4	0.082467	24.35675036	7	2014	2021
PRM-03	P3SE5	0.188496	56.69859193	7	2014	2021
PRM-03	P3SE6	0.21029	74.77837913	7	2014	2021
PRM-03	P3SW7	0.34767	206.551643	7	2014	2021
PRM-03	P3SW8	0.116668	86.65083199	7	2014	2021
PRM-03	P3SW9	0.314159	98.72180102	7	2014	2021

Capítulo 2

Chapter 2

The effect of neighbor species' traits on tree growth in subtropical moist forests depend on relative individual height and performance

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The effect of neighbor species' traits on tree growth in subtropical moist forests depend on relative individual height and performance

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Abstract

To comprehensively understand ecological dynamics within a forest ecosystem, it is vital to explore how surrounding trees influence the growth of individual trees in a community. Biotic interactions have the potential to impact individual tree growth significantly, and their effects can be evaluated through trait and phylogenetic-based approaches. This study aimed to investigate the relative importance of biotic interactions on tree growth by examining various metrics, including hierarchical and absolute trait differences of focal trees to neighbors, neighborhood crowding index, functional community structure, and phylogenetic distance. Our results indicated that the phylogenetic distance between the focal tree and its neighbors positively impacted the growth, whereas different traits have distinct effects. Specific leaf area (SLA), leaf area (LA), and wood density (WD) showed hierarchical relevance to tree growth. Trees surrounded by neighbors with higher SLA than themselves grow more than the opposite, particularly for smaller trees. Similarly, but for taller trees only, those with smaller LA than the neighbors grew more. The absolute distance in WD was also relevant for smaller trees, positively impacting the growth, whereas such distance in height negatively impacted tree growth. Moreover, communities with higher SLA and WD positively impacted the growth of those trees that were categorized as faster-growing individuals. We conclude that the interactions between trees are mediated by their ecological differences, but the performance and responses to surrounding competitors vary along with their position within a community. The tree's relative height and its intrinsic growth rate mediate the effect of traits and phylogeny of surrounding trees on individual tree growth.

Keywords: Absolute trait difference, Focal tree, Hierarchical trait difference, Neighborhood, Growth Rate

1. Introduction

Tree growth involves changes in physical dimensions over time, which are accompanied by distinct physiological and morphological traits that enable the plant to acquire essential resources such as light, water, and nutrients (West & Ratkowsky, 2022). The availability of resources strongly depends on neighboring plants, making tree interactions crucial for individual growth (Britton et al., 2023; Coomes & Allen, 2007). Moreover, these interactions can scale up to generate emergent community-level properties (Hart et al., 2016; Uriarte et al., 2010; Webb et al., 2002). For instance, the coverage and size of neighboring plants, trait similarities and phylogenetic relatedness of interacting trees can impact resources availability (Castillo et al., 2010; Kunstler et al., 2012), consequently, a tree's ability to compete with its neighbors will determine how well it can grow. Investigating the linkage between individual tree performance and the strength of neighborhood interactions is a promising approach to understanding the organization and dynamics of forest communities in response to future climates or other anthropogenic factors.

Previous studies have demonstrated that neighborhood interactions can have both positive (Lasky et al., 2014a; Uriarte et al., 2010) or negative effects (Ding et al., 2019; Yang et al., 2021) on tree growth in tropical, subtropical, and temperate forests. The neighborhood crowding index (NCI) is a common measure that relates to neighborhood interaction and considers both neighborhood density and the distance between a tree (hereafter, focal tree) and its neighbors within a specified area (Lasky et al., 2014a; Uriarte et al., 2016). High tree density in a limited area can result in negative density dependence caused by shading and competition for light when photosynthesis is negatively affected and ultimately reduces growth rate (Yang et al., 2021). However, the effect of NCI on tree growth can differ. Overcrowding of trees can stimulate them to grow taller and escape light competition, leading to increased growth rates. Additionally, if resources such as water and nutrients are abundant, trees may be able to sustain their growth rates even in crowded conditions.

Regardless of negative density dependence, neighborhood biotic interactions can be different depending on their functional and phylogenetic structure in relation to the focal trees. By examining the dissimilarity of functional traits between focal trees and their neighbors, we can enhance our understanding of how neighborhood interactions mediate the focal tree's growth rate (Cadotte & Tucker, 2017; Kraft et al., 2014; Kunstler et al., 2016). With such approach, similar trait values between focal individuals and neighboring trees may be expected to lead to stronger competition (Macarthur & Levins, 1967), resulting in lower focal growth (hereafter, absolute trait difference). Absolute trait difference follow the limiting similarity principle (Kunstler et al., 2012), with values closer to zero indicating a greater similarity between the focal individual and its neighbors, i.e., a nondirectional trait dissimilarity. However, these trait-based density dependence effects can be asymmetric, and species can establish a trait-based competitive hierarchy where a dominant phenotype emerges (Mayfield & Levine, 2010). In this scenario, as the dissimilarity in traits increases (i.e., more dissimilar from the dominant phenotype), competition intensifies, ultimately forming trait-based competitive hierarchies (hereafter, hierarchical trait difference) (Kunstler et al., 2012). The prevalence of the hierarchical trait difference mechanism indicates directional trait dissimilarity between the focal tree and its neighbors (Carmona et al., 2019), with positive values indicating higher trait values in the focal tree compared to its neighbors and negative values indicating the opposite. It is important to note that both mechanisms of trait differentiation can coexist simultaneously for different functional traits (Carmona et al., 2019; Yin et al., 2021).

Traits and phylogenetic community metrics can also inform about the effects of biotic interactions on tree growth. Higher functional diversity and phylogenetic dissimilarity are expected to facilitate resource partitioning and experience lower susceptibility to natural enemy attacks (Uriarte et al., 2010; Yue et al., 2022), enabling species to coexist in distinct ecological niches and avoid competition (Chen et al., 2016). Moreover, phylogenetic relatedness can be a valuable surrogate for characterizing species similarity, especially in cases where functional trait data is unavailable (Lebrija-Trejos et al., 2014; Swenson et al., 2007). Focal trees in more diverse communities in terms of traits and phylogenetic relationships are expected to exhibit higher growth rates compared to those surrounded by more similar neighbors. Additionally, the mean trait value of the neighboring community can reflect the overall resource-use and acquisition strategies (HilleRisLambers et al., 2012), which can drive individual tree growth as well. For example, a community where the predominantly resource-use strategy is conservative can lead to reduced growth rates among neighboring trees, allowing focal trees greater access to resources and thus facilitating their growth (Westbrook et al., 2011).

In this study, we simultaneously investigated the influence of functional dissimilarity, neighborhood crowding index, and functional and phylogenetic community structure on individual tree growth. We utilized two approaches to explore these factors: quantifying interaction strength by measuring the influence of neighboring individuals on the growth rate of focal trees (Figure 1a) and examining the effect of community structure on individual tree growth (Figure 1b). For this purpose, we selected 120 focal trees growing in mature subtropical Atlantic forests. Additionally, we categorized focal trees based on growth rate (fast, intermediate, and slow) and position within the community canopy, once taller focal trees may respond distinctly than smaller ones in relation to their neighbors' height (West & Ratkowsky, 2022). On these groups of focal trees, we expected overcrowding of trees restricting individual tree growth and increased functional diversity and phylogenetic distance between focal trees and their neighbors, enhancing focal tree growth. Similarly, higher functional diversity should aid resource partitioning, promoting the improvement of focal tree growth. Notably, neighborhood effects on focal tree growth also depend on whether trees are winners or losers, determined by canopy position and growth class.

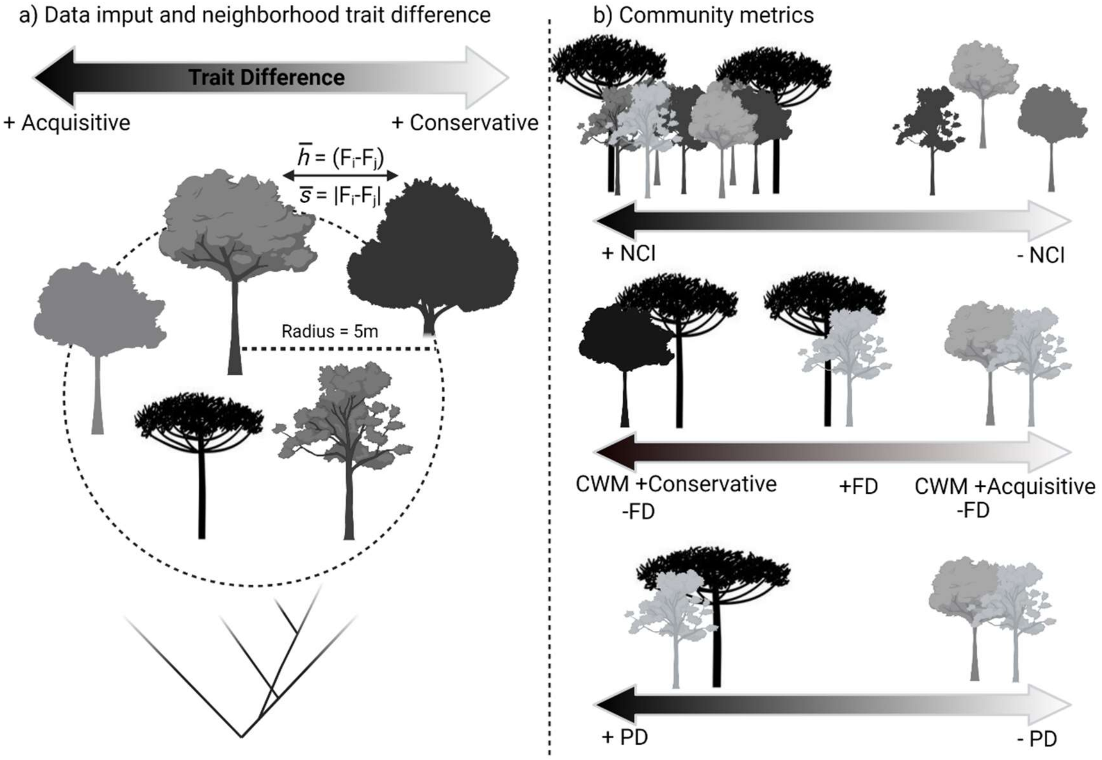

Figure 1: Schematic representation of the data collection and biotic interactions metrics potentially affecting individual tree growth in forests. In (a) differences of focal trees from their neighboring individuals are considered, including trait differences ($\overline{h}$ = neighborhood hierarchical mean trait difference and $\overline{s}$ = neighborhood absolute mean trait difference) between focal tree (F_i) and neighbor tree (F_j). In (b), overall community metrics were evaluated, including neighborhood crowding index (NCI), community weighted mean (CWM), functional diversity (FD) and phylogenetic distance (PD).

2. Methods

2.1 Study site

The study was conducted in permanent forest plots located in the Long-term Ecological Research in Subtropical Atlantic Forests (LERSAF) project in southern Brazil. Studied plots are located in Araucaria forests at elevations from 900 to 930 m a.s.l. The climate is humid subtropical, with temperate summers – according to the Cfb Köppen's climate classification (Alvares et al., 2013). The mean temperature in our study region is 18 °C, frost is frequent in the winter, and the mean annual precipitation is 1,800 mm, without dry season.

We used vegetation data of six permanent plots in old-growth forests within protected areas distributed in two sites: Pró-Mata Nature Research and Conservation Center (29º26'27"S e 50º14'W) and Aparados da Serra National Park (29º07 'to 29º15'S and 50º01' to 50º10'W). The plots were censused in 2014 and 5 years after following the RAINFOR protocols (Phillips et al., 2001). In each plot, every individual with a woody stem ≥ 5 cm in diameter at breast height (DBH measured at 1.3 m from the ground) is tagged with a unique number, identified at the species level, and measured height and steam size.

2.2 Sampling design

For this study, we randomly selected a subset of trees from the forest plots. For 826 trees, we first measured the annual growth rate (AGR), which was calculated as (basal area$_{t+1}$ - basal area$_t$)/ years interval, i.e., the interval of time between the two censuses (2014 and 2019). Secondly, the trees were divided into three growth classes using quartiles: the lower growth rate in the first quartile (25th percentile), the medium growth rate in the second quartile (50th percentile), and the higher growth rate in the third quartile (75th percentile). Thirdly, from each growth class, 40 trees were randomly selected (totaling 120 focal trees - 60 in each site) using the 'slice_sample' function in the "dplyr" package. Finally, to measure the neighborhood of each focal tree, we identified all trees ≥ 5 cm DBH within a 5 m radius (Figure 1a). We then measured the stem size, height, and distance between the focal tree and each neighboring tree (dij) while also identifying the species of each tree. This information was used to calculate neighborhood variables used in the models.

We utilized plant functional traits, which are indicators of plant functional strategies and are expected to be related to individual tree growth and performance (Chave et al., 2009; Díaz et al., 2015; Wright et al., 2004). These traits included height (H, m), leaf area (LA, cm^2), specific leaf area (SLA, cm^2.g-1), leaf dry matter content (LDMC, mg.g-1), and wood density (WD, $g.cm^3$). Focal tree leaf traits were collected at the individual level, while neighborhood tree leaf traits were obtained from the Plant Ecology Lab database, in which the data were collected from other fieldwork projects in the same study region (e.g. Klipel et al., 2023) and are available within the Try Plant Trait Database (Kattge et al., 2020), and the average value per species was considered. These species trait values are based on collected leaves from individuals of the same study region. Height data was collected at the individual level, while WD information was obtained mostly from regional measurements (Missio et al., 2017; Oliveira et al., 2019) but also from a global database (Chave et al., 2009). Measurements and procedures to obtain functional trait information from species available in our database followed standardized protocols (Pérez-Harguindeguy et al., 2013).

2.3 Neighborhood variables

To evaluate the impact of local neighborhood on focal tree growth, we measured neighborhood variables. We calculated a neighborhood crowding index (NCI) based on the size of the steam and the spatial distance of neighboring trees within a fixed radius of 5 m. The calculation is as the following equation 1:

$$NCI_j = \sum_j \frac{DBH_j^2}{d_{ij}^2} \qquad (1)$$

where *dij* is the spatial distance between a focal individual *i* and a neighbor tree *j* and DBHj is the DBH of neighbor tree *j*.

To enhance our comprehension of the relationship between tree growth and neighborhood competition, we calculated distinct indices for measuring the influence of neighborhood in the focal tree growth by using *neighborhood hierarchical mean trait difference* ($\bar{h}$) and *neighborhood absolute mean trait difference* ($\bar{s}$) (Figure 1a). These indices are associated with competitive abilities' trait-mediated ranks and niche differentiation, respectively (Carmona et al., 2019; Kunstler et al., 2012; Lasky et al., 2014b). We calculated these both indices in two distinct ways: one was just the average of the difference in traits from the focus individual to its neighbors, and the other was weighted by neighbor coverage and size (Yang et al., 2021). However, the Pearson correlation analysis between these two ways showed a strong relationship. Then, we utilized the first way following equations 2 and 3:

$$\bar{h} = \sum \frac{F_i - F_j}{n_j} \quad (2);$$

and

$$\bar{s} = \frac{\sum |F_i - F_j|}{n_j} \quad (3);$$

The values of the functional trait of interest for the focal individual (*i*) and neighbors (*j*) are represented by *Fi* and *Fj*, n_j is the number of neighbors. The individual focal trait data were obtained from the tree used to measure growth, while the average trait value at the species level was used to represent the neighbors' traits, except by tree height, which was used at an individual level. Specific traits used for equations 2 and 3 were hereafter identified by the letters '$\bar{h}$' and '$\bar{s}$', respectively, for example, H$\bar{h}$ and H$\bar{s}$ for the trait height (H).

Also, to test if the community of tree neighbors influences the focal growth tree, we calculated mean phylogenetic distance of the focal tree with all their neighborhood trees (mean PD), functional diversity (FD), and community trait composition ('community weighted mean', CWM). To calculate mean PD, we constructed an ultrametric phylogeny using the '*V.PhyloMaker*' package for all 73 species in the dataset. We used the *PhytoPhylo magaphylogeny* as a backbone and added species absent from the megaphylogeny as basal polytomies within their genera (scenario 1 (Qian & Jin, 2016). Our phylogenetic tree contains polytomies, which result in uncertainty about the correct branching order of taxa. To address this, we used the '*bifurcatr*' function in the '*PDcalc*' package (Rangel et al., 2015) to randomly resolve polytomies. We ran the algorithm 1000 times to explore the range of potential solutions and used all trees to calculate phylogenetic diversity. Then, we calculated the mean phylogenetic distance between the focal individual to all neighbor trees within the radius (Castillo et al., 2010). We calculated mean PD using 1000 phylogenetic trees extracting the average value. To compute functional diversity, we calculated Rao weighted by species relative abundance in each community, i.e., all trees within the radius ('*mpd*' function in the "picante" package) (de Bello et al., 2016; Kembel et al., 2010). We calculated FD using all traits (H, LA, SLA, LDMC, and WD). Finally, we calculated the mean trait values of each community of tree neighbors (CWM) accounting for species relative abundance in each community (function '*functcomp*' in the "FD" package) (Laliberté et al., 2015). We excluded the focal species from the CWM and FD calculations.

2.4 Statistical analyses

To assess the effects of neighborhood interactions and community structure on tree growth, we performed linear mixed-effect models with AGR as the response variable and non-correlated neighborhood variables as predictors. Before constructing the models, we analyzed Pearson's correlation between predictor variables to improve model estimation and reduce collinearity (Supplementary Material Table 1). We selected variables for our models among those with a correlation below 0.7. The variables selected included NCI, neighborhood hierarchical trait difference ($\bar{h}$), neighborhood absolute trait difference ($\bar{s}$, except for SLA), CWM, FD, and mean PD (Supplementary Material Table 2).

To better understand how neighborhood variables affect focal tree growth, we constructed three types of models based on the described categories of focal trees: (a) a model including all focal trees, (b) models separating trees by growth class (i.e., faster, intermediary, and slower growth), and (c) models separating trees by height (i.e., taller and smaller focal trees) by using the height hierarchical difference (H$\bar{h}$ eq.3). We are considering these last model type because the competitive effects of tree may be proportional to its size (West & Ratkowsky, 2022). The H$\bar{h}$ equation postulates that positive values indicate that the focal tree has higher trait values than neighboring trees (or taller focal trees), while negative values indicate that the focal tree has lower trait values than neighboring trees (or smaller focal trees).

In the specific models considered, we fitted global linear-mixed effect models (i.e., AGR ~NCI + neighborhood hierarchical trait difference ($\bar{h}$) + neighborhood absolute trait difference ($\bar{s}$) + mean PD + FD + CWM, random = ~ focal species identity) to predict the AGR of focal trees. Separate models were considered for each type of model. To identify the most parsimonious set of neighborhood variables influencing focal tree growth, we used step-wise backward regression analysis based on AIC (McCullagh & Nelder, 1989). The '*stepAIC*' function in the MASS package was used for this purpose (Venables & Ripley, 2002). Species were included as a random variable, which allow us to show the conditional and marginal coefficients of determination (R^2c and R^2m, respectively). To enable better comparison between predictors at different measurement units, we standardized these variables to zero mean and unit variance (Schielzeth, 2010). We used the '*lme*' function in the "nlme" R package (Pinheiro et al., 2023). All statistical analyses were performed in R version 3.6.3 (R Core Team, 2020).

3. Results

When considering all focal tree individuals together, the best predictors included specific leaf area hierarchical trait difference (SLA$\bar{h}$) and mean phylogenetic distance of the focal tree and their neighborhood (mean PD; Table 1 and Figure 2). Lower SLA$\bar{h}$ values and higher mean PD values were linked to higher growth (Figure 2a), which means that trees with lower SLA values than their neighbor species (i.e., negative SLA$\bar{h}$ values, SM Table 2) and surrounded by more distantly related species (i.e., higher mean PD) are growing more. These effects were maintained only partially when separating the focal trees by growth class and size. SLA$\bar{h}$ was more strongly affecting smaller individuals and PD taller ones. PD also affected faster-growing individuals, whereas SLA$\bar{h}$ was not significant in models splitting the trees into growth class categories. Moreover, when splitting focal individuals by growing classes and size, we found some different predictors. We specifically found that trees with faster AGR were negatively associated with height absolute trait difference (H$\bar{s}$) (Figure 2b) and positively associated with mean PD, CWM SLA, and CWM WD (Figure 2c). While the increase in CWM SLA could be conceptually linked to SLA$\bar{h}$ (i.e. neighbors having higher SLA values than focal trees), the two values were considerably related to growth. So, trees that are in the faster AGR category grow more when they are more similar in height but distantly related to the neighborhood, and these neighbors reveal higher SLA and WD mean community values. Trees in the intermediary growth class were only associated with wood density hierarchical trait difference (WD$\bar{h}$) (Figure 2a), growing more when they had higher WD than the neighbors. The growth of trees of the slower-growth class was not associated with any variable. Finally, the growth of taller focal trees was negatively associated with LA$\bar{h}$ (i.e., those with smaller leaves than their neighbors grow more, Figure 2a), while smaller trees were negatively associated with SLA$\bar{h}$ (as for all trees) and positively with WD$\bar{s}$ (i.e., more dissimilar trees grow more, Figure 2b) (Table 1). NCI and FD were not relevant in predicting the growth rates of studied trees. Also, see Supplementary Material Figure 1.

Table 1: Results of linear mixed-effect models used to assess the impact of neighborhood trait differences, both hierarchical ($\bar{h}$) and absolute ($\bar{s}$), as well as community structure (mean phylogenetic distance - PD, and community-weighted mean of traits - CWM), on the absolute growth rate (AGR) of focal trees. The models were analyzed separately for all focal trees and for focal trees categorized by growth classes (slower, intermediary, and faster) and height

(smaller and taller). The functional traits include specific leaf area (SLA), individual height (H), leaf area (LA), and wood density (WD). Information on R^2 values, standardized coefficients, and p-values for significant variables in the models are included.

				Neighborhood trait difference										Community Structure					
				SLA$\bar{h}$		H$\bar{s}$		LA$\bar{h}$		WD$\bar{h}$		WD$\bar{s}$		Mean PD		CWM SLA		CWM WD	
Models		R^2m	R^2c	Coef.	p	Coef.	p	Coef.	p	Coef.	p	Coef.	p	Coef.	p	Coef.	p	Coef.	p
All focal		0.15	0.17	-0.27	0.04									0.41	0.01				
AGR class	Faster AGR	0.41	0.47			-0.17	0.03							0.30	0.001	0.26	0.002	0.3	0.0009
	Intermediary AGR	0.36	0.36							0.10	0.04								
	Slower AGR	0.20	0.20																
Height class	Taller	0.27	0.39					-0.40	0.03					0.69	0.004				
	Smaller	0.25	0.31	-0.64	0.02							0.53	0.02						

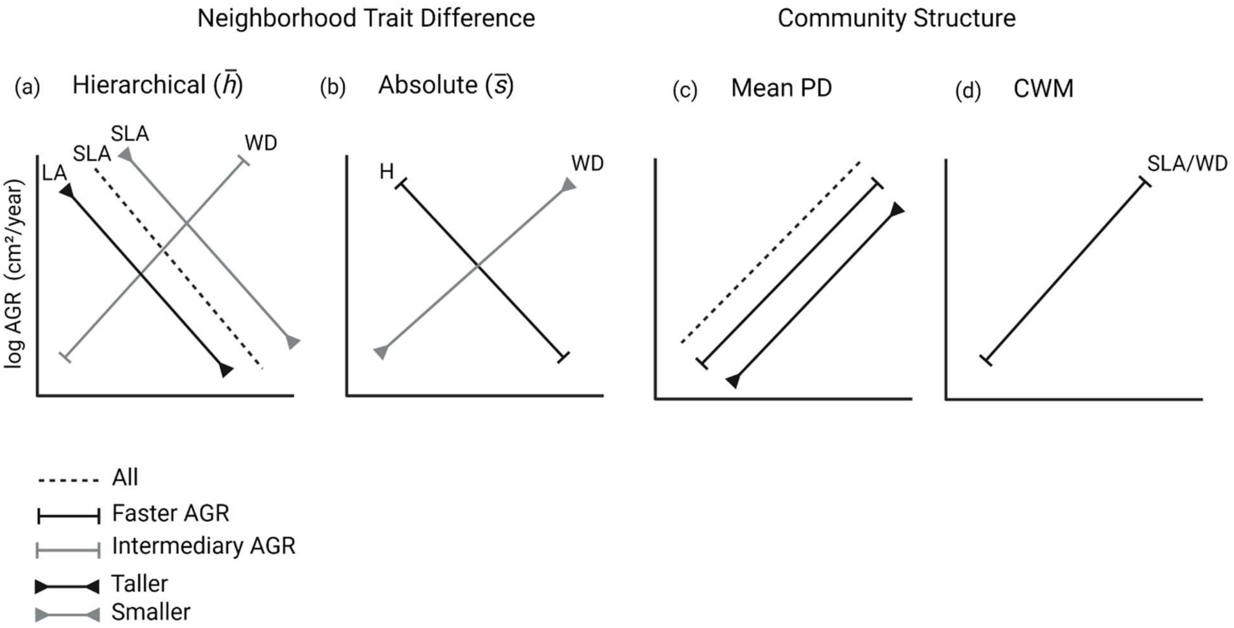

Figure 2: Schematic representation showing the effect of neighborhood hierarchical and absolute trait difference (a, b) and community structure, considering mean phylogenetic distance (c) and community-weighted mean (d), on the focal tree growth. The functional traits considered were specific leaf area (SLA), leaf area (LA), wood density (WD), and individual height (H). Schemes reflect significant results for all focal trees or different categories according to growth rate (faster and intermediary) or relative height (taller and smaller).

4. Discussion

In our study, we aimed to investigate the influences of neighboring trees on the growth of focal trees in different ways. Our findings revealed that both functional and phylogenetic distances influence the growth of focal trees but that their effects are modulated depending on the light-capture ability of the focal trees. Specifically, the patterns observed varied depending partially on the traits examined and the categories of focal trees analyzed, demonstrating the complexity of trait interactions in determining tree growth. We found that the surrounding neighborhood composed by distant clades (higher phylogenetic distance) caused focal trees to grow more, particularly for all focus trees, taller and faster-growing ones, indicating limiting similarity. Additionally, we observed that the absolute height and wood density differences between a focal tree and its neighbors did impact the growth rate of faster-growing trees and smaller trees, respectively. Among other consistent effects, communities composed of species with acquisitive leaves (higher CWM SLA) but denser steam structures (higher WD) positively affected faster-growing trees. In general, greater SLA than focal species (SLA$\bar{h}$) decreased the growth of focal trees, which was also observed for smaller trees. For taller trees, greater LA than focal individuals (LA$\bar{h}$) decreased the growth of trees, whereas lower WD than focal individuals (WD$\bar{h}$) increased, but only for intermediary-growing trees. Thus, different specific predictors depend on focal AGR and size. Overall, our models revealed that differences in trait hierarchies, specifically related to construction cost and hydraulic conductance, significantly influenced the growth of trees in South Atlantic forests. By examining the relationships between neighboring trees and focal tree growth, our study provides valuable insights into the complex dynamics of tree interactions and their implications for overall forest ecosystem dynamics.

4.1 Overall strategies that improve tree performance

The annual growth rate considering all focal trees and the most successful ones, which had faster growth and reached the highest heights, were positively correlated with the mean phylogenetic distance between the focal tree and its neighboring trees. Our results indicate that the evolutionary relationships among co-occurring species in our study area significantly predict individual performance. Specifically, the greater the phylogenetic distance between the focal tree and its neighbors, the greater the individual performance. This finding emphasizes that functional and ecological similarities are influenced by common ancestry patterns (Webb et al., 2008), wherein distantly related species contribute to coexistence patterns and individual performance. Consequently, more distantly related species may exhibit greater ecological differentiation due to limiting of similarity (i.e., lower niche overlap) (Webb, 2000), reducing competition and enhancing growth. Additionally, phylogenetic relatedness can impact individual performance indirectly since phylogenetically distant species can promote reduced competition by avoiding host-specific pathogens and pests (Gilbert et al., 2015).

Trait hierarchy differences were a significant growth driver, considering all focal and taller trees, as well as the intermediary-growing trees. However, it is important to highlight that the relationships between traits and specific types of focal trees exhibited variation. Notably, traits related to nutrient conservation (SLA) showed a negative association with growth for all focal trees and smaller ones. In addition, traits associated with light capture (LA) exhibited a similar negative association with growth, but specifically for taller trees. These patterns follow a hierarchical structure. For instance, trees with relatively lower SLA and LA values than their neighbors demonstrated improved individual performance. Consequently, the observation that focal trees with better performance and greater competitive ability possessed tougher and smaller leaves compared to their neighbors suggests that local conditions, including low nutrient availability and temperatures, favor conservative leaf strategies associated with lower SLA and LA values to optimize resource uptake (Bennett et al., 2016; Klipel et al., 2023; Kraft et al., 2014). Additionally, it is important to note that taller trees are likely to receive an adequate amount of light for photosynthesis, but they are also exposed to varying temperatures, ranging from low to high temperatures on the forest canopy. Therefore, having smaller leaves becomes a successful strategy for thriving in the community in such subtropical Atlantic forests.

We observed that the absolute height difference ($\mathrm{H}\bar{s}$) between a focal tree and its neighbors did affect the growth rate of faster-growing trees. Tree height is a good predictor of crown exposure and light competition. It is widely observed that taller trees tend to have a competitive advantage over smaller ones, leading to variations in tree heights (Kraft et al., 2014). However, contrary to findings in other studies (Carmona et al., 2019; Goldberg et al., 2017; Yue et al., 2022), our study revealed that individuals surrounded by neighbors of more similar heights exhibited greater growth. The mechanisms explaining this effect still need to be fully understood but could result from complementary crown architectures, where species coexist and compete relatively equally, partitioning resources (Hubbell, 2006; Sapijanskas et al., 2014).

Furthermore, the local neighborhood trait composition was significantly associated with the performance of faster-growing trees. For instance, trees that exhibit faster growth tend to be surrounded by a trait environment characterized by high WD and SLA values. WD represents the plant's investment in biomass per unit of wood volume, indicating that tree communities with denser wood are often associated with slow-growing species (Chave et al., 2009). Typically, low wood density species prioritize height growth for better light conditions in the canopy, while high wood density species focus on expanding their crowns horizontally for enhanced light interception in the shaded forest understory (Iida et al., 2012). Then, the similar heights between faster-growing trees and their neighbors, especially in a community dominated by trees with high wood densities that prioritize canopy expansion, once again suggests the presence of complementary crown architecture interactions.

Additionally, tree communities with soft leaves, represented by high SLA values, generally exhibit high nitrogen concentrations, photosynthetic assimilation, respiration rates, and shorter leaf lifespan (Wright et al., 2004). High SLA enables rapid resource acquisition (acquisitive strategy) and generally predominates in communities under less stressful conditions, whereas species with more conservative leaf strategies predominate under more stressful conditions (e.g., lower temperature and soil fertility). Concerning the local environmental conditions in subtropical Atlantic forests, in a community where neighboring trees generally possess softer leaves and denser wood, focal individuals may experience facilitation rather than competition from their neighbors. The co-existence of trees differing in architecture and light capture strategy can result in faster growth for the focal trees.

4.1 Additional strategies for performance enhancement - the case of smaller trees with moderate growth

Focal trees in the intermediary growth class, which have higher wood density than their neighbors, exhibited a higher growth rate. While high WD is typically associated with slow-growing species, the mechanical properties of wood density play a significant role in shaping the expansion of tree stems and crowns, allowing them to utilize favorable light conditions while maintaining mechanical stability effectively (Iida et al., 2012). Consequently, wood with high density facilitates efficient horizontal branch expansion and promotes enhanced persistence in the shaded forest understory. This may be a strategy particularly important for focal trees in the sub-canopy, as they interact with other trees.

Smaller trees improved performance when they possess lower specific leaf area values than their neighbors (SLA$\bar{h}$). This finding aligns with the pattern identified in the overall focal trees model. The local conditions (i.e., low nutrient availability and temperatures) favor conservative leaf strategies associated with lower SLA to optimize resource uptake. Furthermore, these smaller trees exhibit increased growth when surrounded by trees that exhibit high dissimilarity in wood density (WD$\bar{s}$). WD is associated with the hydraulic properties of the xylem and the acquisition of soil nutrients (Chave et al., 2009), with higher dissimilarity in WD indicating a greater level of niche differentiation among individual trees, facilitating resource partitioning. These differences in WD$\bar{s}$ and SLA$\bar{h}$ contribute to smaller trees' growth dynamics within their specific environmental context, such as the understory and shade conditions.

5. Conclusion

Overall, our results indicated that multiple factors influence the relative growth and competitive outcome among subtropical trees. These factors include differences in leaf construction cost, hydraulic conductance, tree size, as well as the phylogenetic distance between the focal tree and its neighboring trees. In general, trees with more conservative leaves relative to their neighborhood performed better than the opposite, which seems to be a better strategy considering the local environmental conditions of studied forests (cold, moist, low fertility). Similar heights but more distinct wood density relative to the neighbors also affected the growth rate of focal trees, revealing the influence of whole-plant structure on tree growth patterns inside mature forests. Finally, being phylogenetically distant from species present in the neighborhood positively impacts the individual performance of studied tree species.

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Supplementary Material

Table1: Correlations of variables including neighborhood crowding index (NCI), absolute (s) and hierarchical (h) trait differences, community weighted mean (CWM), functional diversity (FD), and mean phylogenetic diversity (mean PD) are examined. The considered traits are height (H, m), leaf area (LA, cm²), specific leaf area (SLA, cm².g-1), leaf dry matter content (LDMC, mg.g-1), and wood density (WD, g.cm³).

	NCI	NCIH-LA	NCIH-SLA	NCIH-LDMC	NCIH-H	NCIS-LA	NCIS-SLA	NCIS-LDMC	NCIS-H	Lah	SLAh	LDMCh	Hh	Las	SLAs	LDMCs	Hs	CWM LA	CWM SLA	CWM LDMC	CWM WD	CWM H	FD	WDh	WDs	Mean PD
NCI	1																									
NCIH-LA	**0.98**	1																								
NCIH-SLA	**1**	**0.98**	1																							
NCIH-LDMC	**-0.99**	**-1**	**-0.99**	1																						
NCIH-H	**-0.81**	**-0.85**	**-0.81**	**0.82**	1																					
NCIS-LA	**0.99**	**0.99**	**0.98**	**-0.99**	**-0.83**	1																				
NCIS-SLA	**1**	**0.98**	**1**	**-0.99**	**-0.81**	**0.98**	1																			
NCIS-LDMC	**1**	**0.99**	**0.99**	**-1**	**-0.82**	**1**	**0.99**	1																		
NCIS-H	**0.83**	**0.83**	**0.81**	**-0.81**	**-0.94**	**0.86**	**0.81**	**0.83**	1																	
Lah	-0.06	-0.08	-0.05	0.07	0.23	-0.07	-0.05	-0.06	-0.21	1																
SLAh	0.11	0.1	0.11	-0.1	-0.1	0.1	0.11	0.1	0.08	0.26	1															
LDMCh	-0.06	-0.06	-0.07	0.06	0.04	-0.05	-0.07	-0.06	-0.02	-0.44	-0.55	1														
Hh	-0.03	-0.01	-0.02	0.01	0.01	-0.04	-0.02	-0.02	-0.04	-0.31	-0.48	0.15	1													
Las	0.01	0.06	-0.01	-0.02	-0.26	0.05	-0.01	0.02	0.25	-0.16	0.02	-0.02	0.01	1												
SLAs	0.1	0.09	0.1	-0.09	-0.1	0.09	0.1	0.09	0.08	0.04	**0.74**	-0.5	-0.15	0.05	1											
LDMCs	0	0.02	0	-0.01	0	0	0	0	-0.03	0.09	0.35	-0.18	-0.11	0.36	0.33	1										
Hs	-0.08	-0.09	-0.09	0.09	0.14	-0.08	-0.08	-0.08	-0.12	-0.23	-0.38	0.13	0.52	-0.01	0.01	-0.04	1									
CWM LA	0	0	0	-0.01	0.05	0	0	0	-0.05	0.12	0.11	0.02	-0.27	-0.06	0.03	0.08	-0.06	1								
CWM SLA	-0.14	-0.16	-0.14	0.15	0.18	-0.16	-0.14	-0.15	-0.16	0.06	-0.06	0.04	0.07	-0.2	-0.06	-0.19	0.15	0.16	1							
CWM LDMC	0.16	0.18	0.16	-0.17	-0.16	0.17	0.16	0.17	0.17	-0.19	-0.12	-0.03	0.19	0.09	-0.05	-0.04	0.03	-0.43	-0.37	1						
CWM WD	0.11	0.14	0.11	-0.13	-0.06	0.12	0.11	0.12	0.04	-0.04	-0.11	0.09	0.23	0.02	-0.13	-0.15	-0.2	-0.26	-0.16	0.44	1					
CWM H	0.01	-0.03	0	0.03	-0.18	-0.01	0	-0.02	0.19	-0.07	0.08	0.01	-0.11	0.14	0.11	-0.01	0	-0.27	-0.05	-0.04	-0.35	1				
FD	-0.05	-0.04	-0.05	0.04	-0.01	-0.05	-0.04	-0.05	-0.02	0.11	0.04	-0.06	-0.08	-0.07	0.03	0.01	-0.07	0.02	-0.14	0.02	0.11	-0.02	1			

WDh	-0.07	-0.1	-0.08	0.09	0.01	-0.07	-0.08	-0.08	0.01	0.09	0.12	-0.09	-0.21	-0.13	0.04	-0.15	-0.13	0.18	0.15	-0.15	-0.12	-0.01	0.1	1		
WDs	0.02	0	0.02	-0.01	0.07	0.01	0.02	0.02	-0.01	0.08	0.08	0.13	0	-0.08	0.01	0.02	-0.04	0.18	-0.18	0.04	0.09	-0.06	0.23	0	1	
Mean PD	-0.02	-0.04	-0.02	0.04	0.01	-0.04	-0.02	-0.03	0	0.05	-0.02	-0.16	0.05	-0.04	0.13	0.03	0.26	-0.25	-0.04	0.11	-0.31	0.22	0.52	0.02	0.18	1

Table 2: List of focal trees selected for this study, including their growth class and annual growth rate data. The table also displays community data surrounding the focal tree, such as the neighborhood crowding index (NCI), absolute (s), and hierarchical (h) trait differences, community weighted mean (CWM), functional diversity (FD), and mean phylogenetic diversity (mean PD). The considered traits are height (H, m), leaf area (LA, cm²), specific leaf area (SLA, cm².g-1), leaf dry matter content (LDMC, mg.g-1), and wood density (WD, g.cm³).

site	species	class	AGR	H	LA	SLA	LDMC	WD	NCI	LAh	SLAh	LDMCh	Hh	WDh	LAs	LDMCs	Hs	WDh	CWM LA	CWM SLA	CWM LDMC	CWM WD	CWM H	FD	PD
PM	My re	higher	0.000734	11	7.22	61.81	453.96	0.81	206399.53	9.92	21.56	0.64	-3.46	2.771	11.28	29.04	3.46	2.771	12.65	48.14	479.13	0.81	16.00	0.17	0.48
PM	Oc el	higher	0.000736	14	5.15	76.26	491.52	0.62	78062.70	-0.92	83.64	-74.97	-2.14	1.393	4.77	74.97	2.67	1.393	40.14	78.03	307.29	0.46	11.00	0.13	0.37
PM	Sa gl	higher	0.000774	8	31.23	238.44	177.72	0.38	64230.17	-7.52	48.41	-54.95	-3.40	-1.360	8.05	71.57	4.00	-1.360	15.09	90.28	290.08	0.50	16.00	0.17	0.55
PARNA	Ar au	higher	0.000918	19	1.34	60.99	382.12	0.50	52701.22	-7.00	-52.78	41.34	10.38	-1.613	7.51	51.57	10.38	-1.613	3.93	81.30	415.48	0.60	11.00	0.16	0.57
PARNA	My me	higher	0.000941	9.5	4.64	73.85	386.39	0.73	379357.51	-8.39	-6.34	64.50	-3.50	1.400	8.39	64.50	4.39	1.400	3.67	81.30	374.25	0.50	220.00	0.16	0.48
PM	Il pa	higher	0.000996	12	15.43	89.87	368.46	0.53	42972.53	-3.39	-7.62	22.45	3.00	-0.631	4.14	66.47	3.00	-0.631	12.65	48.14	479.13	0.81	16.00	0.10	0.11
PARNA	My me	higher	0.001001	8	5.04	184.61	315.60	0.73	333993.37	-0.97	43.92	-32.73	-3.50	2.343	4.56	49.63	4.50	2.343	3.67	116.02	374.25	0.50	11.00	0.18	0.55
PARNA	Ar au	higher	0.001011	17	1.54	55.35	362.34	0.50	128691.98	-7.19	16.07	24.65	1.07	-1.777	8.35	43.85	2.53	-1.777	3.67	81.30	374.25	0.50	220.00	0.17	0.52
PM	My lo	higher	0.001024	14	20.04	122.52	314.16	0.46	112792.89	1.93	77.35	-72.32	1.40	-2.932	4.89	72.32	2.20	-2.932	12.65	48.14	479.13	0.81	16.00	0.20	0.46
PARNA	Il mi	higher	0.00103	10	12.24	87.98	439.24	0.57	42246.07	-8.48	-37.87	-0.45	7.28	-1.126	8.77	55.79	7.28	-1.126	7.21	99.10	392.41	0.75	12.00	0.11	0.52
PM	My eu	higher	0.001039	6.5	1.58	114.25	367.57	0.65	121080.83	-7.56	74.64	-97.71	6.00	0.492	7.56	99.09	6.00	0.492	1.24	79.60	412.62	0.65	11.00	0.16	0.49
PARNA	La te	higher	0.001057	13	9.85	152.81	330.24	0.50	427987.85	0.01	2.59	-5.92	1.00	-1.490	6.78	30.36	3.00	-1.490	6.32	90.48	397.86	0.73	13.00	0.16	0.44
PARNA	Ar au	higher	0.001083	20	0.79	62.58	364.24	0.50	154273.73	0.44	29.50	-6.94	3.45	-1.005	8.87	71.79	3.45	-1.005	3.67	81.30	374.25	0.50	220.00	0.16	0.48
PM	Sy te	higher	0.001085	10	8.52	156.82	272.49	0.49	146126.10	1.25	68.59	-104.51	2.46	-1.008	6.30	104.51	3.46	-1.008	3.67	81.30	412.62	0.50	22.00	0.17	0.62
PM	My co	higher	0.001102	7	10.11	137.40	337.12	0.59	102047.39	-3.83	24.44	-68.44	3.21	0.343	5.68	68.44	3.40	0.343	7.96	81.30	374.25	0.50	13.00	0.17	0.63
PARNA	Il mi	higher	0.001108	11.5	10.65	56.59	330.70	0.57	63645.49	29.07	21.25	-120.63	-4.75	-0.197	29.21	120.63	5.25	-0.197	7.70	59.00	374.25	0.57	17.00	0.19	0.53
PM	Il mi	higher	0.001175	14	6.17	93.36	366.49	0.57	27112.56	2.17	22.43	-15.70	-0.20	-1.082	8.27	26.33	2.60	-1.082	12.65	48.14	311.15	0.71	13.00	0.23	0.43
PM	Eu han	higher	0.001185	13	6.25	173.29	338.30	0.71	102302.52	-0.56	44.74	-99.87	-2.88	1.884	2.92	100.40	2.93	1.884	20.63	90.28	290.08	0.38	16.00	0.15	0.45
PARNA	Ar au	higher	0.001224	11	0.99	64.06	387.77	0.50	119763.07	-5.58	-49.41	18.94	7.29	-1.521	5.58	18.94	7.29	-1.521	0.97	80.51	465.11	0.75	13.00	0.15	0.57

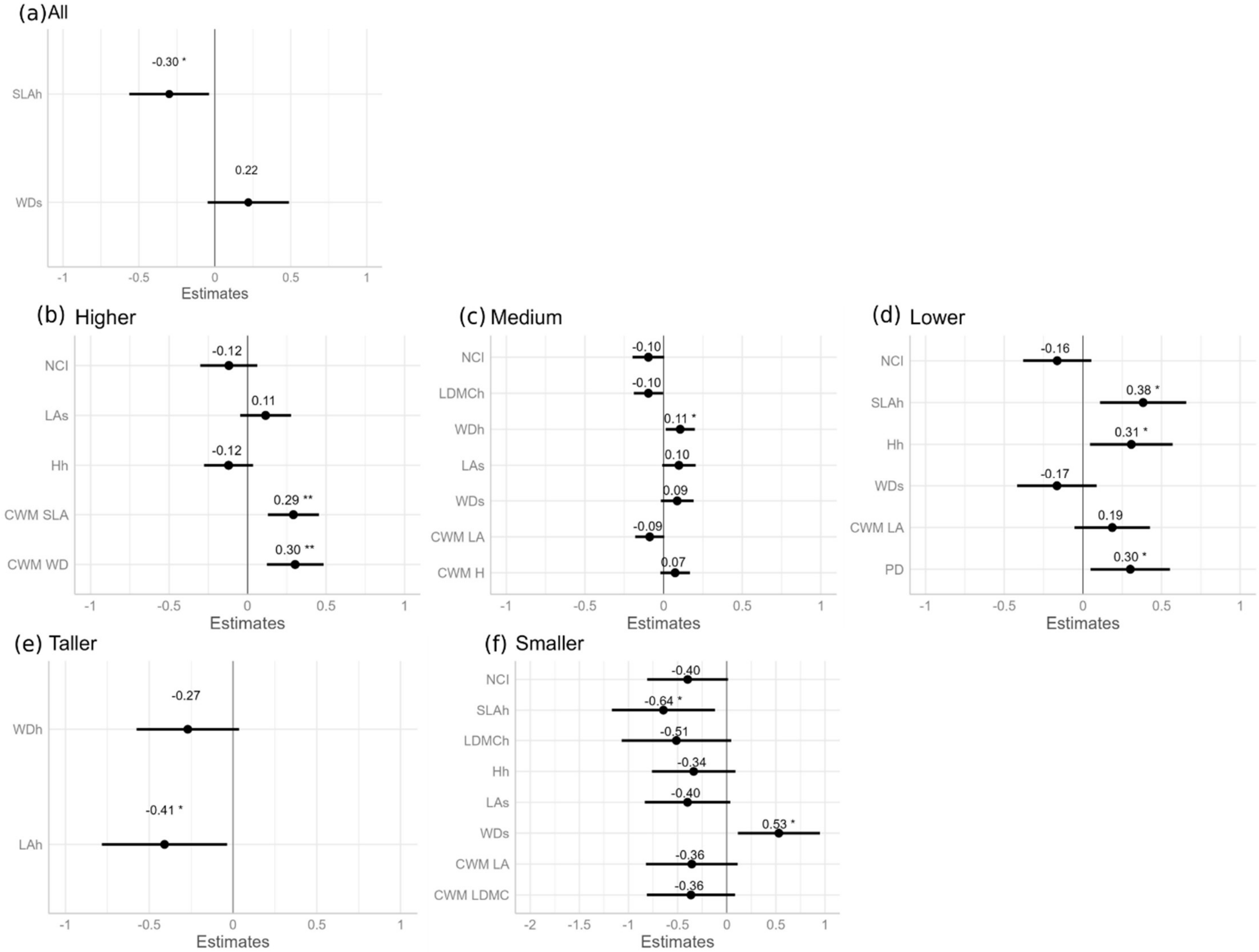
PM	My my	higher	0.001266	13	19.94	125.93	284.50	0.71	121736.11	-1.76	37.22	44.23	-3.25	2.523	1.76	50.17	3.69	2.523	16.81	96.57	311.15	0.71	13.00	0.13	0.34
PARNA	We pa	higher	0.001334	15	1.37	170.19	299.03	0.60	183707.24	-7.66	-35.57	24.51	0.54	-0.555	7.66	52.49	2.96	-0.555	6.32	90.48	397.86	0.73	15.00	0.18	0.38
PM	Ce fis	higher	0.00136	13	19.07	89.51	413.52	0.45	64514.43	-7.05	0.43	35.56	4.53	-2.533	8.14	48.29	4.63	-2.533	12.65	48.14	479.13	0.81	16.00	0.16	0.24
PARNA	My me	higher	0.001426	10	4.49	153.48	364.51	0.73	3795361.10	-25.17	45.89	-12.85	0.75	1.608	25.17	54.91	1.65	1.608	3.67	81.30	374.25	0.50	220.00	0.17	0.53
PARNA	Ar au	higher	0.001437	16	1.70	56.22	398.73	0.50	134277.95	-7.29	-10.26	22.65	-2.50	-1.411	7.29	29.86	2.50	-1.411	26.64	77.34	333.33	0.40	11.00	0.14	0.32
PARNA	Ar au	higher	0.001452	13	1.30	73.30	333.71	0.50	72717.59	-8.45	12.93	40.46	-6.41	-1.477	8.70	40.46	6.41	-1.477	3.67	81.30	374.25	0.50	220.00	0.17	0.52
PM	My re	higher	0.001518	15	7.09	47.89	511.39	0.81	68397.61	0.55	30.72	-39.78	4.52	3.292	5.14	39.78	4.52	3.292	6.32	90.48	397.86	0.73	15.00	0.14	0.41
PARNA	My fl	higher	0.001733	15	3.28	86.07	508.69	0.71	110575.30	-1.73	-23.68	-3.70	-1.82	0.493	2.62	14.73	2.73	0.493	13.23	87.87	392.41	0.73	15.00	0.11	0.37
PM	My re	higher	0.001791	13	10.10	61.07	444.53	0.81	71567.19	-19.76	-18.99	103.48	4.22	0.636	19.76	109.57	4.67	0.636	16.81	96.57	311.15	0.81	13.00	0.15	0.30
PARNA	Ar au	higher	0.001799	19	1.87	40.40	454.86	0.50	151016.30	-12.02	-12.38	-72.58	6.50	-1.680	12.02	87.83	6.61	-1.680	0.97	80.51	465.11	0.66	15.00	0.17	0.64
PARNA	Ar au	higher	0.002005	16	0.94	67.92	344.97	0.50	65672.51	3.68	-4.19	-5.12	0.54	-2.934	4.89	24.26	3.13	-2.934	3.61	76.69	357.88	0.71	16.00	0.15	0.39
PM	Ar au	higher	0.002386	14	2.14	44.11	396.50	0.50	60148.80	-9.02	1.06	86.74	1.63	-1.322	9.22	86.74	3.25	-1.322	7.70	59.00	415.48	0.57	17.00	0.20	0.59
PM	My eu	higher	0.002477	9	2.46	121.83	367.60	0.65	112821.01	-1.31	-10.53	44.79	0.25	-0.180	4.89	44.79	1.75	-0.180	16.81	96.57	311.15	0.71	13.00	0.10	0.26
PARNA	Ar au	higher	0.003037	20	1.34	60.99	382.12	0.50	59707.05	-2.22	0.63	40.00	-1.15	-2.800	9.01	54.79	1.75	-2.800	13.97	101.08	388.75	0.60	12.00	0.12	0.41
PM	Ar au	higher	0.003082	14	1.16	54.87	352.05	0.50	64541.26	-20.89	-14.93	157.48	5.38	-3.470	20.89	157.48	5.38	-3.470	12.65	48.14	479.13	0.81	16.00	0.17	0.40
PARNA	Oc po	higher	0.003108	12.5	9.33	136.07	387.43	0.57	94614.24	8.01	0.54	20.83	1.64	-2.057	8.01	39.57	2.09	-2.057	2.27	83.41	396.29	0.81	16.00	0.16	0.39
PARNA	Ar au	higher	0.00356	20	1.34	60.99	382.12	0.50	74673.48	-6.22	-33.11	-29.68	8.61	-2.089	6.33	35.08	8.83	-2.089	13.97	101.08	388.75	0.60	11.00	0.15	0.51
PM	Oc bi	higher	0.00405	14	4.66	73.13	475.19	0.59	48093.04	-6.15	-3.77	-50.30	1.63	-0.938	6.87	54.24	3.50	-0.938	12.65	48.14	479.13	0.81	16.00	0.15	0.48
PM	Ar au	higher	0.00412	15	1.87	49.69	370.77	0.50	91144.79	-7.33	-4.66	45.91	4.96	-1.966	8.11	49.33	4.96	-1.966	16.81	96.57	311.15	0.71	13.00	0.10	0.22
PM	My re	higher	0.00526	14	7.48	70.93	393.61	0.81	29384.99	2.85	32.72	-28.29	-3.00	2.588	2.85	41.82	3.07	2.588	24.55	172.87	483.89	0.60	17.00	0.17	0.50
PARNA	Ar au	higher	0.007264	18	0.77	49.65	410.73	0.50	105273.90	-0.64	-21.02	-8.76	-2.35	-1.340	5.38	33.67	2.81	-1.340	5.97	81.30	410.54	0.73	11.00	0.16	0.47
PARNA	My cu	lower	1.57E-05	4.5	8.50	167.15	281.71	0.74	41980.34	-4.95	9.53	8.19	-0.57	0.370	5.29	29.32	4.50	0.370	24.55	138.77	341.37	0.67	10.50	0.14	0.31
PM	My mi	lower	1.63E-05	11	13.78	138.79	371.64	0.60	71186610.53	-4.12	63.39	-62.24	0.00	-1.580	5.21	62.24	2.44	-1.580	12.65	48.14	479.13	0.81	16.00	0.14	0.40
PM	My ox	lower	1.73E-05	4	8.56	147.38	311.19	0.71	51148.43	9.05	41.08	-9.73	-2.00	1.889	9.05	25.05	3.00	1.889	16.81	96.57	311.15	0.71	13.00	0.19	0.44
PM	My my	lower	1.79E-05	6	18.17	104.58	307.39	0.71	111870.93	-0.73	-18.95	65.86	-1.20	0.487	4.49	68.63	2.02	0.487	12.65	48.14	479.13	0.81	16.00	0.19	0.36
PM	My re	lower	1.80E-05	6	11.18	105.27	347.69	0.81	227117.16	-3.21	37.29	-29.84	-1.23	2.125	4.94	38.32	1.77	2.125	12.65	48.14	479.13	0.81	16.00	0.13	0.30
PARNA	Eu sub	lower	1.85E-05	6	2.61	107.96	423.59	0.73	200343.05	-2.63	90.69	-87.97	-3.32	1.148	3.75	90.66	3.42	1.148	13.23	58.68	404.05	0.53	15.00	0.13	0.40
PARNA	My me	lower	1.85E-05	5	4.06	163.87	332.17	0.73	132418.09	13.16	22.14	-76.14	-1.43	0.844	13.16	77.72	2.39	0.844	13.97	101.08	388.75	0.60	12.00	0.14	0.44
PARNA	My eu	lower	2.15E-05	11.5	1.37	101.24	384.57	0.65	83780.80	-6.94	-32.75	-25.64	7.75	-0.297	6.94	25.64	8.35	-0.297	1.24	79.60	412.62	0.65	11.00	0.11	0.24
PM	My my	lower	2.43E-05	7.5	13.33	128.54	314.60	0.71	83000.38	-6.11	-15.07	31.98	2.08	0.556	7.70	49.87	2.63	0.556	16.81	96.57	311.15	0.71	13.00	0.14	0.26
PM	Il mi	lower	2.58E-05	9	8.55	85.89	416.92	0.57	101603.93	-24.77	38.60	-65.89	-1.40	-3.128	35.81	90.94	2.60	-3.128	12.65	48.14	479.13	0.81	16.00	0.11	0.34

PARNA	Xy pse	lower	2.59E-05	8.5	7.53	78.96	435.84	0.65	2765.11	3.63	1.75	40.32	1.57	-0.068	8.19	46.04	2.43	-0.068	13.97	101.08	388.75	0.60	12.00	0.10	0.25
PARNA	Eu uru	lower	2.88E-05	11	12.26	111.08	360.23	0.75	1196493.66	22.30	39.59	-117.78	-3.14	1.484	22.61	117.78	3.93	1.484	3.67	81.30	374.25	0.50	220.00	0.12	0.49
PM	In le	lower	2.88E-05	8	3.06	165.22	438.11	0.56	1061481.08	-6.52	-20.01	28.26	-2.71	-0.125	6.88	29.40	3.29	-0.125	29.93	108.32	313.23	0.46	14.00	0.19	0.49
PM	Eu han	lower	3.12E-05	5	7.26	189.97	355.41	0.71	196908.92	-5.15	66.90	-55.38	-8.00	1.917	5.40	55.38	8.00	1.917	13.23	58.68	404.05	0.53	15.00	0.25	0.58
PARNA	My ol	lower	3.15E-05	4.5	2.34	81.20	475.12	0.81	42874.98	-5.25	29.29	-15.70	-1.25	2.059	5.59	33.81	1.75	2.059	7.95	104.85	479.02	0.71	12.00	0.16	0.47
PARNA	Si re	lower	3.29E-05	5	0.93	108.13	497.41	0.66	29583.21	-5.47	-25.71	-65.22	1.79	0.315	5.47	65.22	4.07	0.315	1.24	81.30	374.25	0.65	11.00	0.17	0.49
PARNA	Eu uru	lower	3.49E-05	10.5	10.85	107.17	385.48	0.75	110820.76	-0.81	-30.17	-38.46	0.25	1.314	8.11	49.19	5.50	1.314	24.55	172.87	357.88	0.62	16.00	0.17	0.44
PARNA	My fl	lower	3.49E-05	8.5	3.54	131.45	443.07	0.71	2740507.01	-4.26	35.64	-35.85	2.27	1.565	6.08	35.85	3.00	1.565	3.67	81.30	374.25	0.50	220.00	0.17	0.52
PARNA	Po la	lower	3.80E-05	7.5	1.53	87.45	401.66	0.46	119961.63	-2.31	62.23	-23.51	-1.35	-1.907	2.94	31.72	2.50	-1.907	6.32	90.48	397.86	0.73	13.00	0.17	0.50
PM	Ne gr	lower	4.99E-05	5	17.33	77.13	490.17	0.61	66433.69	-7.23	9.77	105.61	-4.29	-0.159	7.23	105.61	4.29	-0.159	3.67	81.30	374.25	0.50	15.00	0.17	0.63
PM	Oc el	lower	5.40E-05	10	5.47	82.34	450.76	0.62	45280.05	12.31	40.55	-30.20	-0.75	-0.292	12.31	30.20	1.50	-0.292	16.81	96.57	311.15	0.71	13.00	0.14	0.42
PM	Sa gl	lower	5.43E-05	11	28.33	124.56	258.25	0.38	53487.89	3.68	46.15	-97.53	4.60	-2.400	7.76	101.27	4.60	-2.400	16.81	96.57	311.15	0.71	13.00	0.20	0.46
PARNA	Il mi	lower	5.99E-05	12	9.61	93.48	384.60	0.57	109157.75	-12.42	80.52	3.15	3.20	-1.075	12.94	42.43	3.70	-1.075	5.97	116.02	410.54	0.73	11.00	0.17	0.45
PM	Pr my	lower	6.03E-05	7	11.55	121.18	386.54	0.68	132983.30	4.65	27.46	-51.98	4.25	0.561	9.39	51.98	4.25	0.561	1.24	79.60	412.62	0.65	11.00	0.12	0.39
PARNA	Il mi	lower	6.18E-05	9	12.81	88.94	360.83	0.57	550198.35	5.07	27.32	-24.05	-4.36	-1.084	6.05	24.05	5.36	-1.084	24.55	172.87	365.67	0.67	16.00	0.17	0.46
PM	Sa gl	lower	6.75E-05	13	24.11	118.59	276.43	0.38	73371.92	-3.80	37.96	78.99	-5.14	-2.035	3.80	78.99	5.14	-2.035	20.63	90.28	290.08	0.38	16.00	0.13	0.43
PM	My mi	lower	7.04E-05	9	15.66	117.25	360.23	0.60	336216.55	9.14	13.24	-57.74	2.05	-0.831	9.14	59.67	2.58	-0.831	12.65	48.14	479.13	0.81	16.00	0.29	0.44
PARNA	Ca co	lower	7.10E-05	6	10.26	84.34	435.15	0.74	31757.09	-14.15	-55.09	51.09	9.29	1.582	14.15	54.53	9.29	1.582	26.64	77.34	333.33	0.40	8.00	0.15	0.47
PM	La ac	lower	7.35E-05	8	7.60	100.90	343.67	0.64	73384.70	0.35	41.59	0.18	3.09	2.347	6.36	25.89	3.68	2.347	16.81	96.57	311.15	0.71	13.00	0.33	0.57
PARNA	My de	lower	8.13E-05	5	2.07	122.76	454.03	0.82	57845.79	2.34	24.08	-80.55	0.67	1.216	2.34	80.55	0.67	1.216	2.27	83.41	396.29	0.81	9.00	0.20	0.48
PARNA	Eu sub	lower	8.24E-05	10	5.44	146.20	350.41	0.73	55046.21	-2.49	65.15	-85.34	1.36	0.305	12.80	85.68	1.91	0.305	5.97	116.02	410.54	0.73	16.00	0.13	0.25
PARNA	Da fa	lower	8.29E-05	6	39.34	106.65	272.78	0.46	247461.94	20.90	42.58	-120.49	-1.77	-1.349	21.47	120.49	1.92	-1.349	7.70	59.00	374.25	0.57	11.00	0.17	0.54
PARNA	Ar au	lower	8.50E-05	7.5	2.03	74.03	368.85	0.50	304302.24	-9.71	95.66	-38.58	-5.33	0.115	10.31	56.79	5.67	0.115	3.67	81.30	374.25	0.50	220.00	0.09	0.40
PM	Da fa	lower	8.54E-05	7	43.89	109.77	252.57	0.46	34676.81	-2.61	26.04	-94.57	-3.21	-0.714	10.07	94.57	3.71	-0.714	40.14	78.03	307.29	0.46	11.00	0.13	0.28
PARNA	My mi	lower	8.89E-05	6	16.41	107.49	417.43	0.60	53575.98	-7.15	-24.11	-21.40	2.23	-0.313	7.16	33.75	3.50	-0.313	0.97	80.51	465.11	0.66	15.00	0.15	0.68
PM	Ca de	lower	9.02E-05	9	9.81	232.19	307.73	0.67	130011.76	0.64	42.28	-60.20	-3.13	0.240	7.49	60.20	3.25	0.240	12.65	89.39	365.67	0.81	16.00	0.18	0.40
PM	So pse	lower	9.12E-05	12	8.37	116.26	298.08	0.51	84252.20	16.09	155.38	-177.04	-1.75	-2.562	16.09	177.04	2.35	-2.562	16.81	96.57	311.15	0.71	13.00	0.13	0.42
PARNA	Pl pse	lower	9.53E-05	8	11.79	128.38	360.01	0.95	41434.55	1.14	60.41	-72.91	3.94	2.223	5.16	72.91	4.61	2.223	24.55	83.41	397.86	0.73	16.00	0.13	0.26
PM	My my	lower	9.90E-05	5	17.73	134.42	304.99	0.71	298499.67	-9.06	25.37	5.72	4.38	0.585	9.29	51.99	4.88	0.585	16.81	96.57	311.15	0.71	13.00	0.14	0.30
PM	My my	lower	0.000106	7	17.81	176.29	260.09	0.71	72072.07	-1.12	45.75	4.63	0.88	2.479	2.01	15.48	2.13	2.479	16.81	96.57	311.15	0.71	16.00	0.15	0.38
PM	My my	medium	0.00016	5.5	13.63	133.10	293.69	0.71	106824.34	-5.64	-27.84	49.94	2.73	0.952	6.65	49.94	3.09	0.952	16.81	96.57	311.15	0.71	13.00	0.14	0.32

PM	Da fa	medium	0.000177	8	38.28	114.34	277.88	0.46	62398.27	-4.70	-16.81	64.79	-3.36	-2.695	5.19	66.92	3.73	-2.695	12.65	48.14	479.13	0.81	16.00	0.18	0.33
PARNA	My mi	medium	0.00019	11	17.40	96.65	408.58	0.60	142527.09	-9.85	-32.29	-46.15	6.64	-0.506	9.85	46.15	6.64	-0.506	13.97	92.79	414.43	0.75	8.50	0.18	0.44
PM	Sa gl	medium	0.000194	14	17.04	88.29	300.89	0.38	175212.48	8.19	-0.14	95.48	-5.25	-1.015	9.60	95.48	5.25	-1.015	29.93	108.32	313.23	0.46	14.00	0.13	0.35
PM	Da fa	medium	0.000208	7	39.60	120.89	253.13	0.46	39826.30	-4.10	44.36	-42.84	-5.03	-0.903	6.80	52.96	5.03	-0.903	40.14	78.03	307.29	0.46	17.00	0.16	0.41
PARNA	Il mi	medium	0.000211	8	9.68	102.27	384.17	0.57	1789910.07	-1.30	26.91	12.04	0.29	-2.241	8.88	41.44	4.21	-2.241	2.27	76.69	396.29	0.81	9.00	0.13	0.35
PARNA	My ol	medium	0.000224	8	3.52	92.95	408.53	0.81	245864.09	-7.12	-19.26	64.74	3.56	0.730	8.77	86.68	4.56	0.730	5.97	116.02	410.54	0.73	16.00	0.12	0.29
PM	My mi	medium	0.000234	6	13.93	133.75	305.26	0.60	276470.91	-8.67	-3.77	84.20	-2.73	1.106	12.38	86.73	3.81	1.106	20.63	90.28	290.08	0.38	16.00	0.16	0.39
PM	Za rh	medium	0.000238	11	2.16	127.47	367.18	0.51	19442.34	9.47	21.32	-74.70	2.17	-0.707	10.11	74.70	3.10	-0.707	16.81	96.57	311.15	0.71	13.00	0.21	0.36
PM	My my	medium	0.00024	7.5	28.73	123.35	287.02	0.71	167305.82	2.96	47.65	-38.05	-1.83	2.004	7.37	57.86	2.17	2.004	16.81	96.57	311.15	0.71	13.00	0.13	0.32
PARNA	Eu sub	medium	0.000241	8	3.51	97.51	449.32	0.73	126385.63	-11.16	-6.36	-9.81	2.83	0.829	11.22	22.75	2.83	0.829	6.32	90.48	397.86	0.73	13.00	0.14	0.34
PM	Dr ang	medium	0.000244	9	7.50	121.53	283.02	0.46	47072.29	-6.62	2.37	113.60	5.33	-3.735	6.62	113.60	5.33	-3.735	16.81	96.57	311.15	0.71	13.00	0.13	0.30
PARNA	Si re	medium	0.000247	10	1.60	101.96	476.86	0.66	685991.71	-4.71	136.51	-104.80	-2.64	0.229	6.19	104.80	3.91	0.229	13.97	101.08	388.75	0.60	12.00	0.14	0.48
PARNA	Eu sub	medium	0.00026	7	5.07	131.09	357.67	0.73	50071.20	0.37	-18.76	-30.64	-1.31	0.601	6.68	31.09	2.54	0.601	2.27	83.41	396.29	0.81	9.00	0.22	0.51
PARNA	Eu uru	medium	0.000286	10	10.67	83.59	470.58	0.75	38606.54	-13.95	-37.26	26.65	9.29	0.645	14.10	40.24	9.29	0.645	0.97	80.51	465.11	0.66	15.00	0.13	0.61
PARNA	Ca co	medium	0.000288	4	12.87	83.30	440.24	0.74	140100.85	-9.05	-36.59	-18.94	12.09	1.330	9.16	42.04	12.09	1.330	13.97	101.08	388.75	0.65	11.00	0.15	0.60
PM	Eu sub	medium	0.000307	11	3.61	139.43	387.55	0.73	52418.27	10.73	26.42	-41.84	-1.36	0.532	11.06	41.84	2.32	0.532	24.55	96.61	359.24	0.81	16.00	0.21	0.37
PARNA	My la	medium	0.000324	12	3.67	102.05	436.17	0.81	2619242.65	4.92	-6.98	27.13	-5.09	2.937	7.88	36.99	5.09	2.937	13.97	101.08	388.75	0.60	12.00	0.12	0.41
PM	My re	medium	0.000337	7.5	10.39	54.53	475.26	0.81	74008.56	-7.41	-12.80	87.13	1.53	4.263	8.01	94.83	1.93	4.263	12.65	48.14	479.13	0.81	16.00	0.19	0.54
PM	Il pa	medium	0.000343	10	18.92	145.33	309.19	0.53	107828.37	-2.18	48.44	-91.19	-1.31	-1.518	4.30	91.19	1.81	-1.518	12.65	48.14	479.13	0.81	11.00	0.19	0.39
PM	My re	medium	0.000345	11	6.30	65.24	476.28	0.81	379074.72	-5.26	61.38	-75.19	-3.46	1.660	6.12	75.22	3.75	1.660	12.65	48.14	479.13	0.81	16.00	0.27	0.47
PM	My my	medium	0.00035	11	20.86	109.71	312.80	0.71	105117.67	-7.30	3.73	14.89	-1.42	2.325	7.55	28.62	3.17	2.325	16.81	96.57	311.15	0.71	13.00	0.17	0.51
PM	Eu uru	medium	0.000352	12	7.28	74.69	429.77	0.75	48253.51	-6.53	-33.51	109.64	5.26	1.330	6.98	109.64	5.26	1.330	16.81	96.57	311.15	0.71	13.00	0.25	0.48
PARNA	Eu sub	medium	0.000356	10	4.78	125.12	411.03	0.73	29714.49	-5.01	11.67	-9.80	3.56	0.366	5.03	48.06	3.56	0.366	2.27	172.87	396.29	0.81	16.00	0.17	0.33
PARNA	Il mi	medium	0.00036	11	14.16	111.20	379.92	0.57	66565.14	-7.94	33.07	-69.08	0.11	0.305	8.35	69.08	2.11	0.305	3.67	81.30	374.25	0.50	12.00	0.18	0.55
PM	Il mi	medium	0.00036	12	7.75	68.15	427.70	0.57	121080.08	4.57	-7.90	15.09	2.00	-1.871	9.00	21.88	3.27	-1.871	12.65	48.14	479.13	0.81	16.00	0.14	0.32
PM	My my	medium	0.000361	6	18.66	120.98	315.53	0.71	41535.67	-6.46	-18.22	-18.61	5.00	-0.389	7.39	46.49	5.00	-0.389	16.81	96.57	311.15	0.71	13.00	0.12	0.14
PARNA	My gu	medium	0.000373	12	4.53	87.24	342.67	0.83	243319.77	-2.83	24.62	-40.40	-0.94	3.086	4.48	48.43	2.28	3.086	13.23	58.68	404.05	0.53	15.00	0.16	0.50
PM	Ne gr	medium	0.000376	8	13.06	80.19	451.65	0.61	80702.85	4.72	51.73	-102.88	-3.64	0.703	10.39	107.19	4.07	0.703	16.26	49.32	377.95	0.43	14.00	0.16	0.44
PM	My my	medium	0.00038	6	20.30	119.76	316.78	0.71	7813527.78	-34.52	-12.46	53.52	0.60	0.016	36.13	56.76	2.40	0.016	12.65	48.14	479.13	0.81	16.00	0.17	0.29
PARNA	My ol	medium	0.00038	6	5.11	148.37	312.20	0.81	32969.60	-5.18	26.59	-92.13	-3.88	0.487	5.80	92.13	4.38	0.487	2.27	83.41	396.29	0.81	13.00	0.11	0.22
PARNA	My fl	medium	0.000393	7.5	3.46	137.90	389.85	0.71	51494.01	-10.95	27.66	30.67	0.38	-0.423	11.41	48.39	2.13	-0.423	2.27	90.48	396.29	0.73	9.00	0.10	0.15

PARNA	Dr bras	medium	0.000395	7	7.45	65.85	413.54	0.40	201015.40	-6.01	-29.72	-20.60	10.38	-2.971	6.09	35.06	10.38	-2.971	0.97	80.51	465.11	0.66	15.00	0.14	0.65
PARNA	My ol	medium	0.000397	7	3.03	145.94	331.63	0.81	254523.96	4.31	19.25	-14.65	-0.97	1.771	5.29	32.33	3.03	1.771	2.27	90.28	290.08	0.81	16.00	0.22	0.47
PARNA	Ar au	medium	0.000406	11	1.56	66.45	395.05	0.50	519009.53	-3.68	-36.82	-37.58	4.39	-2.574	3.68	37.58	5.50	-2.574	3.67	81.30	374.25	0.50	220.00	0.18	0.67
PM	Pr my	medium	0.000411	6.5	13.47	127.29	385.11	0.68	25621.22	-0.29	-12.97	-33.76	3.17	0.390	9.49	37.37	3.50	0.390	1.24	79.60	412.62	0.65	11.00	0.03	0.07
PARNA	Xy pse	medium	0.000417	13	7.53	78.96	435.84	0.65	35885.58	-6.42	1.93	-13.09	6.88	-0.065	6.54	62.08	6.88	-0.065	13.23	172.87	404.05	0.53	13.00	0.13	0.32
PARNA	My me	medium	0.000419	8	4.80	167.20	323.78	0.73	21193.37	-12.16	79.64	35.67	-2.19	0.256	12.16	62.73	3.31	0.256	3.61	76.69	388.75	0.73	16.00	0.11	0.22
PARNA	My eu	medium	0.000466	10	2.42	99.61	411.48	0.65	85590.94	-3.68	-16.86	-23.53	1.53	0.576	3.97	49.43	3.90	0.576	13.97	101.08	388.75	0.60	12.00	0.15	0.48
PM	My re	medium	0.000611	12	7.12	62.52	454.10	0.81	47309.92	6.45	47.83	-59.42	-3.25	5.029	8.49	59.42	3.25	5.029	40.14	78.03	307.29	0.46	11.00	0.15	0.36

Supplementary Material Figure 1: Standardized regression coefficients of the best-fitted model for modelling focal tree growth, considering the three types of models: (a) model including all focal trees, (b), (c), and (d) model separating trees by growth class (e.g., higher, medium, and lower growth), (e) and (f) model separating trees by height (e.g., taller and smaller focal trees) by using the height hierarchical difference. Each point is a standardized regression coefficient, and each line segment is a 95% percentile interval respectively. CIs that do not cross the zero baseline indicate statistically significant effects (**, P < 0.005; *, P < 0.05).



Capítulo 3

Chapter 3

Variability in leaf traits reveals contrasting strategies between forest and grassland woody communities across southern Brazil

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Variability in leaf traits reveals contrasting strategies between forest and grassland woody communities across southern Brazil

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Abstract

Forests and grasslands often form mosaics in subtropical regions such as in southern Brazil. Currently, we observe the processes of woody species encroachment and forest expansion over grasslands due to changes in climate conditions and disturbance regimes. Woody plants occurring across such mosaics can be specialists from one habitat type (forest or grassland) or a generalist species (those occurring in both of these contrasting habitats). Here, we explore if their occurrence in distinct habitats is coordinated by functional traits, considering both intra- and interspecific variability and phylogenetic relatedness between species, thereby assessing changes between habitats from the individual to the community scale. We surveyed forest and grassland vegetation forming mosaics in nine sites in southern Brazil. We found that grassland-forest communities do not differ in phylogenetic diversity, irrespective of considering or not the gymnosperms of the communities. Furthermore, forests presented lower diversity in leaf area than grasslands, with a predominance of large leaves but higher diversity of specific leaf area and leaf dry matter content, with leaves predominantly with an acquisitive resource strategy. When considering species with different habitat preferences, forest-specialist species showed traits related to resource acquisition, while grassland-specialist species showed trait values associated with resource conservation. Generalist species have trait values according to habitat occurrence, showing high intraspecific variability and trait plasticity to establish on both forest and grassland habitats. Assessing the trait variability from woody individuals is important to understanding the contrasting strategies used by different species in grassland-forest mosaics and can be essential to predict the dynamics of these ecosystems, given the changes in climate and disturbances regimes.

Keywords: Ecotones, Functional traits, Habitat preferences, Intraspecific variability, Interspecific variability, Woody plant communities

1. Introduction

In southern America, subtropical forests often form mosaics with natural grasslands (Rambo, 1956). Forest-grassland mosaics typically represent contrasting habitats for woody plants, therefore, the density and composition of woody species in forests and the adjacent grasslands may vary, as many woody species have adaptive strategies to occur in either one or both habitats. Such adaptive strategies are associated with species' evolutionary history (Cadotte et al., 2010) and functional traits (Cornwell and Ackerly, 2009; Díaz and Cabido, 2001), which may also vary between species and at the individual scale (McGill et al., 2006; Siefert et al., 2015). Consequently, integrating functional information at different ecological scales can provide valuable insights into the adaptation of woody species in contrasting habitats (Cornwell and Ackerly, 2009). This is particularly important for understanding woody encroachment processes that have been occurring due to climate change favoring tree growth instead of grasses in many open ecosystems worldwide (Bond 2008), especially in understudied regions, such as southern Brazil (Overbeck et al 2007).

Leaf traits are strongly influenced by the abiotic and biotic environment (Freschet et al., 2011). In grasslands, abiotic filters (e.g., light incidence, fire, frost, water, and nutrient availability) may result in a predominance of conservative resource-use strategies, such as low specific leaf area, thick leaves, and small leaf area (Carlucci et al., 2012; Cornwell and Ackerly, 2009; HilleRisLambers et al., 2012). Open ecosystems, such as grasslands, are evolutionarily younger habitats that may have experienced recent diversification in woody lineages. These lineages have adapted to the new open and sunny environments, leading to the presence of closely related species (phylogenetic clustering) that are well-suited to these specific environmental conditions (Gerhold et al., 2015; Pennington et al., 2006). In contrast, woody plants growing in forests face strong competition, which can result in local divergence of traits, but an overall predominance of acquisitive strategies if compared with woody species occurring in nearby open ecosystems (Macarthur and Levins, 1967; Mayfield and Levine, 2010). Concerning the phylogenetic relatedness in forests, we can expect a co-occurrence of basal (e.g. Magnoliids, restricted to shady habitats) and younger clades (e.g. Eurosids) (Cássia-Silva et al., 2020; Wiens and Donoghue, 2004), resulting in a phylogenetic overdispersion once Neotropical forests have been considered a much older habitat (Davis et al., 2005; Debastiani et al., 2015; Pennington et al., 2006). However, as forest-grassland ecotones share many generalist taxa of woody plants (Duarte, 2011), the phylogenetic diversity can be similar between the habitats.

Grasslands were the predominant vegetation type in south Brazil, from the last glacial maximum (LGM) until the early to mid-Holocene (Behling, 2002). Since the mid-Holocene, the climate has become hot and wetter, resulting in woody encroachment and forest expansion over these grasslands (Oliveira and Pillar, 2004; Schinestsck et al., 2019). This expansion process is slowed or prevented by the presence of fire, frost, and cattle (Frangipani et al., 2021; Pillar et al., 2010). However, the establishment of woody species in grasslands, mainly those considered woody grassland specialist that predominantly have conservative traits (Carlucci et al., 2012; Flake et al., 2021; Frangipani et al., 2021; Rossatto et al., 2009), is still observed under varied disturbance regimes, resulting in distinct patterns of density and distribution (Müller et al., 2012). These species are mostly shrubs, promoting woody encroachment, which may later facilitate the expansion of shade-tolerant forest specialists and generalists in the absence or under changes in disturbance regimes (Carlucci et al., 2012; Charles-Dominique et al., 2018). Forest specialists will be rare in the initial forest expansion phase. Such species usually have an acquisitive resource strategy related to competition for light and soil nutrients, allowing them to be faster-growing shade-tolerant species (Passos et al., 2018).

Generalist tree species can occur in both forests and grasslands, and they seem to be important to the dynamics of forest expansion (Charles-Dominique et al., 2018; Flake et al., 2021; Maracahipes et al., 2018), because they can colonize and grow in open sites after disturbance is suppressed, near the forest boundary or in safe sites (*e.g.*, near rock outcrops) (Carlucci et al., 2012). However, generalist strategies are still poorly characterized across distinct grassland ecosystems and forest-grassland mosaics. On the one hand, these species might have intermediate trait values in the conservative-acquisitive spectrum between the habitats. On the other hand, their traits and strategy may vary according to the habitat where they are established, allowing them to resist contrasting habitats. The latter situation would reflect the intraspecific responses of generalist species to different biotic and abiotic factors (Derroire et al., 2018), and their intraspecific variability probably underlies the ability of species to persist in these contrasting habitats (Maracahipes et al., 2018).

Considering different ecological scales (community and individual scale, with variation between and within species) and the context of forest expansion in South Brazilian grasslands, we aim to explore the role of leaf functional traits and phylogeny influencing woody species distribution in forest-grasslands mosaics. Specifically, we aim to: (i) compare shifts in the functional diversity (FD), phylogenetic diversity (standardized effect size phylogenetic diversity- SES PD), and functional composition (community weighted-mean- CWM) of woody species among forests and grasslands; (ii) evaluate if forest-specialist, grassland-specialist, and generalist woody species have distinct ecological strategies in terms of their leaf traits; (iii) evaluate shifts in leaf traits of woody species with populations occurring in both habitats (i.e., generalist species). We expect that, although forest and grassland habitats may share generalist species from distinct genus and families (i.e., similar SES PD patterns between habitats), communities differ in their FD, which could be lower in grasslands where the environmental conditions and competition with grasses can be more restrictive. Concerning the functional composition, we expect means of leaf traits related to acquisitive strategies in forests, contrasting with conservative ones in grasslands, because of the predominance of distinct sets of woody species within these habitats (i.e., forest-specialist *vs.* grassland-specialist) and of intraspecific trait variability of generalist species. Finally, we expect that generalist species will have higher intraspecific trait variability, which should match the habitat in which they are established (forest or grassland).

2. Materials and Methods

2.1 Study region

We selected nine sites (2 x 2 km) of forest-grassland mosaics in the South Brazilian grassland region. These sites were selected to reflect the different physiographic regions forming mosaics of forest-grasslands transition in Southern Brazil: three sites located at Serra do Sudeste region, with mosaics of grasslands and seasonal forests (altitude between 93 and 382); three sites located in the highland plateau, with mosaics of highland grasslands (*Campos de Cima da Serra*) and Araucaria Forest (altitude between 835 and 979); and three sites located in the Pampa region where grasslands dominate (altitude between 113 and 279 m a.s.l.), and some riverine forests and enclaves of forests occur with elements of the seasonal forest (Müller et al., 2012).

The climate is humid subtropical (Cfa) in most sites and subtropical highland (Cfb) in the Araucaria Forest sites, following the Köppen classification (Alvares et al., 2013). The mean annual precipitation ranges from 1259 to 1959 mm, and the mean annual temperature is from 15 to 20 ºC. The sites located in the Pampa region experience a short dry season during summer, which is an important factor influencing the species composition and vegetation adaptations at forest-grassland mosaics (Oliveira-Filho et al., 2013). The soil has different origins in the study sites: basaltic and granitic, differing in aluminum and organic matter content (Streck et al., 2008).

2.2 Sampling design

In 2012, in each of the nine sites (2 x 2 km), two transects of rectangular areas with 140 x 70 m along the forest-grassland ecotone were surveyed. Each transect consisted of two adjacent plots of 70 x 70 m, one located within the forest and the other in the grassland, resulting in 18 forest plots and 18 grassland plots in a paired design. We considered that the grassland plot started when the continuous canopy from the forest ended, and the grass layer could be identified as the predominant vegetation. In each plot, 15 subplots of 100 m² were randomly distributed, and all woody individuals were sampled inside them. In the forest, we sampled individuals with a diameter at breast height greater or equal to 5 cm, whereas, in grasslands, this criterion was at soil height.

2.3 Leaf traits sampling

In each site, leaf samples were collected from 3 individuals for each species per plot per habitat (forest and grassland) for leaf trait measurements. We measured the following functional traits: fresh leaf area (LA, cm²), specific leaf area (SLA, cm²/g), and leaf dry matter content (LDMC, mg/g). The measurements of leaf traits followed the methodology proposed by Pérez-Harguindeguy *et al.* (2013), consisting of the collection of mature fresh leaf samples of each individual to be weighted and scanned. The material was dried at a temperature of 60 °C for three days. Leaf area (LA) was obtained through the scanned leaf images using the ImageJ 1.44 Software. LDMC and SLA were calculated from the (dry and fresh) weight values and the fresh leaf area. With the measurement of the leaves of each individual, we obtained average values for each trait by species specific to each habitat (forest and grassland). These habitat-specific species trait means were used in the subsequent analyses.

2.4 Parameters and statistical analyses

To address the first aim of this study, we calculated phylogenetic and functional diversity and community-weighted mean (e.g., LA, SLA, and LDMC) for each woody plant community for all 36 plots. Phylogenetic diversity reveals how evolutionary variability accumulates in a community, and functional diversity reveals trait variation associated with species coexistence processes in a local community. To calculate phylogenetic diversity, we first constructed an ultrametric phylogeny generated by function *phylo.maker* in 'V.PhyloMaker' package for all species (171 species) in the dataset, using the PhytoPhylo magaphylogeny as a backbone and taking the scenario 1 (add genera or species absent from megaphylogeny as basal polytomies within their families or genera) (Qian and Jin, 2016). Our phylogenetic tree contains polytomies (nodes with more than two descendent branches), resulting in uncertainty about the correct branching order of taxa. Therefore, we used an algorithm to randomly resolve polytomies in a phylogenetic tree with the function '*bifurcatr'* in package 'PDcalc' (Rangel et al., 2015). Because trees are resolved randomly, we run the algorithm 1000 times to explore the range of potential solutions, and we used all trees to run the subsequent analyses.

To compute functional diversity (hereafter FD), we extracted functional dissimilarities (de Bello et al., 2017) to calculate mean pairwise dissimilarity (MPD) (Webb et al., 2002), which reflects the average dissimilarity between species coexisting in a community weighted by species density (function 'mpd' in the "picante" package) (Kembel et al., 2010). The FD was calculated for each trait separately. To calculate phylogenetic diversity (PD), we used 1000 phylogenetic trees by incorporating and excluding gymnosperms since they may strongly influence PD results (Supplementary Material Figure 1). Then, we calculated the standardized effect size of MPD for phylogenetic diversity (SES PD), where negative values indicate lower diversity than expected by the null model (independent swap, Kembel et al., 2010).

We also calculated the mean trait values of each community ('community-weighted mean'- CWM) (function 'functcomp' in the "FD" package) (Laliberté et al., 2015), accounting for species relative abundance in each community (Supplementary Material Table 1). FD and CWM were calculated using average trait values sampled from forest and grassland habitats separately. After calculating SES PD, FD, and CWM, we performed linear mixed-effect models to test for differences in SES PD, FD, and CWM among forest and grassland habitats. We included transects as a random factor because the forest and grassland plots are organized in a paired design, which allow us to show the conditional and marginal coefficients of determination (e.g., R^2c and R^2m, respectively). We used the “lme” function in the “nlme” R package (Pinheiro *et al.* 2016).

To address the second aim, we classified the species according to their habitat preference following the method proposed by Chazdon et al. (2011). The method allows classifications from a multinomial analysis of species relative abundance in specialists, generalists, and too rare to classify with confidence. Species classified as too rare were also excluded from the analyses. Then, to test differences in functional traits among species groups (forest-specialist species, grassland-specialist species, generalist species), we then ran ANOVAs combined with Tukey’s *post hoc* comparisons.

To address the third aim, we used only the set of 35 generalist species and performed t-tests to evaluate if the leaf traits of these species vary according to forest and grassland habitats (Supplementary Material Table 3). Functional traits distributions were log-transformed to meet model assumptions. The p-values were adjusted using the false discovery rate procedure to control for possible type I error using the function “p.adjust” and Benjamini-Hochberg method. All statistical analyses were performed in R version 3.6.3 (R Core Team, 2020).

3. Results

3.1 Grassland and forest communities differ in diversity and functional composition

The phylogenetic diversity did not differ significantly among forest and grassland communities when considering all species, with gymnosperms and angiosperms (Table 1, Figure 1a), and when considering only angiosperms (Table 1, Figure 1b). However, functional diversity calculated from LA, SLA, and LDMC differed significantly between forest and grassland habitats. Forest communities showed lower FD LA, higher FD SLA, and higher FD LDMC than grassland communities (Table 1, Figure 1b, 1c, and 1d, respectively). Considering the CWM of traits, we found that LA, SLA, and LDMC differed significantly between the contrasting habitats (Table 1, Figure 1e, 1f, and 1g), showing that the forests are composed, on average, of individuals/species with higher LA and SLA values and lower LDMC values (Figure 1).

Table 1: Results for linear mixed-effects models for standardized effect size phylogenetic diversity (SES PD) with all species and only with angiosperms (ang), functional diversity (FD), and community-weighted mean (CWM) of woody species communities in forest-grassland ecotones in southern Brazil in response to forest and grassland habitats. The functional traits used were leaf area, LA; specific leaf area, SLA; leaf dry matter content, LDMC. The table shows the models with marginal R^2 (R^2m, related to fixed effect, i.e. habitat type), conditional (R^2c, random effects, i.e. transects), standardized coefficients, and *p* values.

Response variable	R^2m	R^2c	Coefficient	p-value
SES PD	0.0001	0.40	-0.17	0.62
SES PD (ang)	0.007	0.009	-0.15	0.67
FD LA	0.81	0.92	1.85	< 0.01
FD SLA	0.16	0.44	-0.44	< 0.01
FD LDMC	0.47	0.48	-0.83	< 0.01
CWM LA	0.29	0.50	-0.66	< 0.01
CWM SLA	0.17	0.78	-0.21	< 0.01
CWM LDMC	0.25	0.25	0.05	< 0.01

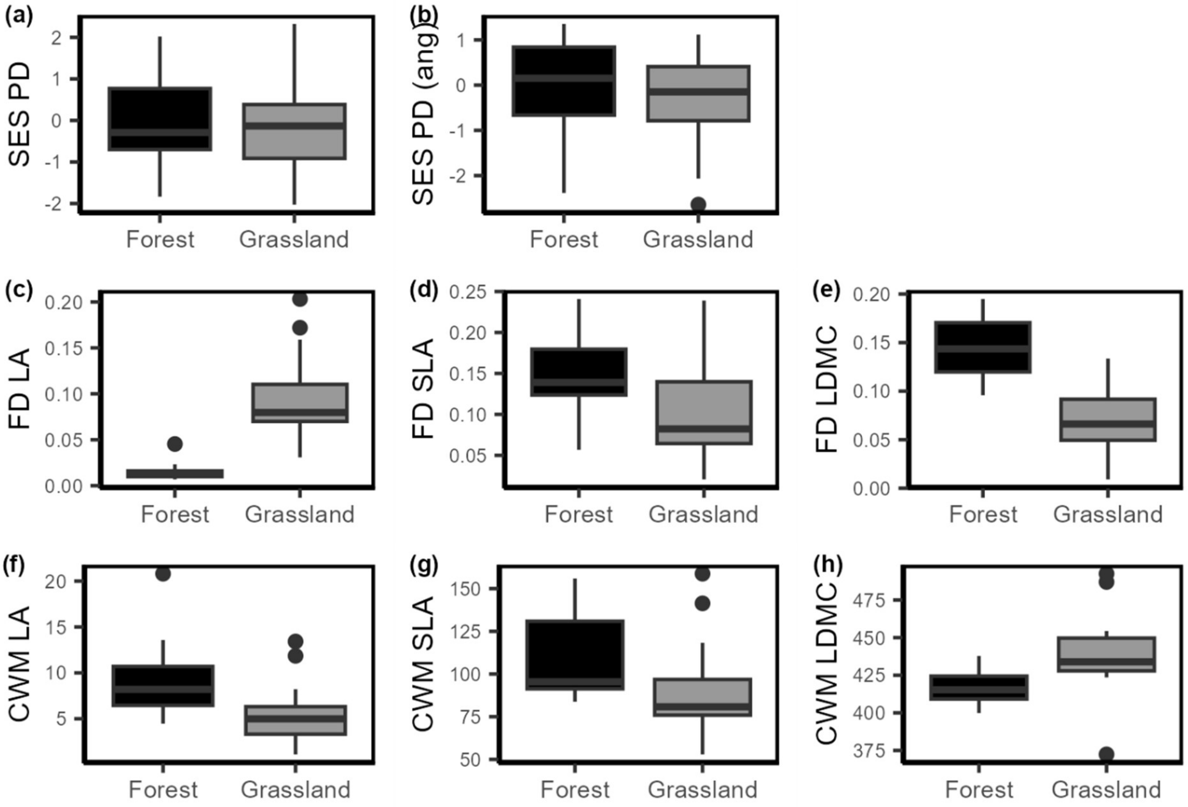

Figura 1:Boxplots showing the standardized effect size phylogenetic diversity (a), standardized effect size phylogenetic diversity with only angiosperm (b) functional diversity (FD – (c), (d), (e)), and CWM differences among forest and grassland sites (f), (g), (h). Boxplots represent median and 1st and 3rd quantile. The functional traits used were leaf area, LA; specific leaf area, SLA; leaf dry matter content, LDMC. The functional traits plotted on the y-axis are with original values. FD and CWM from the leaf traits differ significantly among forest and grassland.

3.2 Specialist species differ in functional traits from generalist species

Overall, 31 species were forest-specialist, 12 grassland-specialist species, and 40 species considered generalist species (Chazdon et al. 2011) (Supplementary Material Table 2). We have excluded generalist species without functional traits collected in forest and in grassland habitats, resulting in 35 generalist species. Our results showed that forest-specialist had higher leaf area (DF = 3, F = 3.47, P < 0.01) than grassland-specialist (Figure 2a). Forest-specialist species and generalist species sampled in forests had higher SLA than generalist species sampled in grasslands (DF = 3, F = 9.38, P < 0.01) (Figure 2b). Leaf dry matter content was higher in grassland-generalist species than in forest-generalist species (DF = 3, F = 2.96, P = 0.02) (Figure 2c).

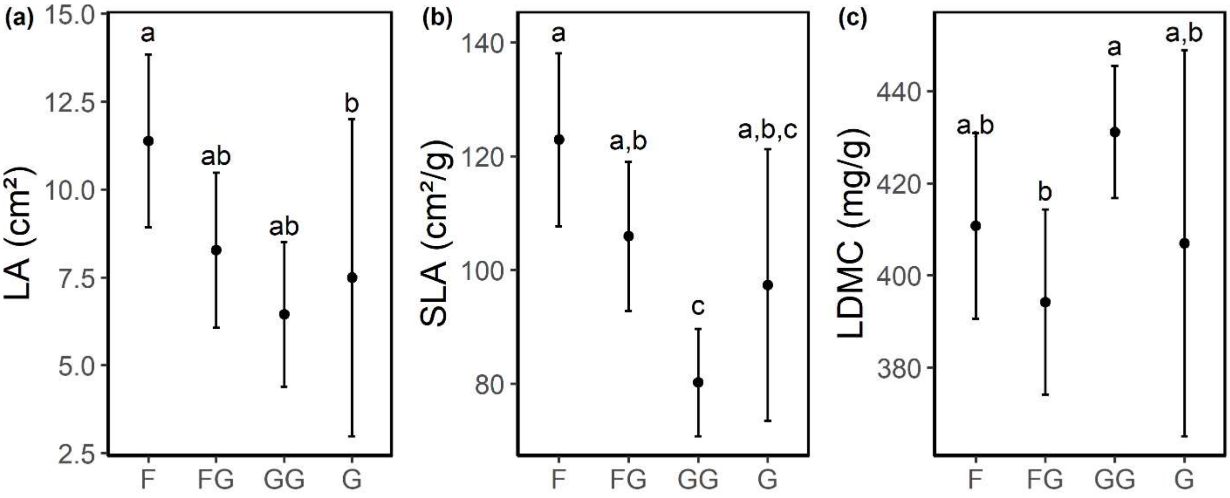

Figure 2: Mean trait values (with 95% confidence intervals) of species with distinct habitat preferences sampled in forest-grassland mosaics (leaf area, LA; specific leaf area, SLA; leaf dry matter content, LDMC; - (a), (b), (c), respectively). Forest-specialist species (F), generalist species sampled in forests (FG), and grasslands (GG) and grassland-specialist species (G). Different letters indicate significant differences among habitat preferences according to Tukey t-test ($p < 0.05$).

3.3 Intraspecific responses of leaf traits to habitats

The paired t-test showed significant differences (i.e., intraspecific leaf traits variation) for generalist species with individuals sampled in both forest and grassland habitats, for the LA (DF = 34, T = 4.90, P < 0.01), SLA (DF = 34, T = 5.14, P < 0.01), and LDMC (DF = 34, T = -4.73, P < 0.01). In general, individuals occurring in forests exhibited higher values of LA and SLA and lower values of LDMC than those from grasslands, considering the same species (Figure 3).

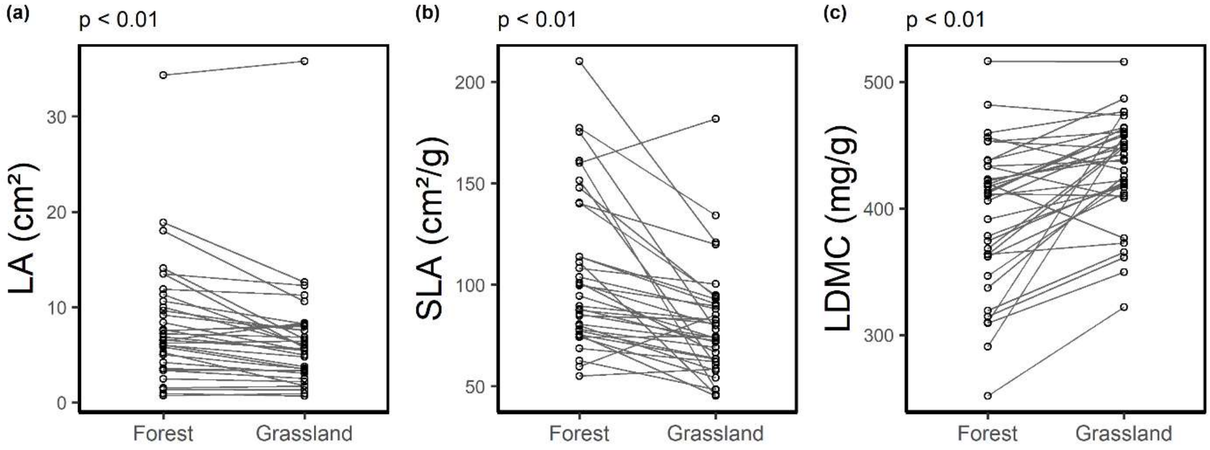

Figure 3: Intraspecific trait variability for 35 species collected in both forest and grassland habitats. P-values of paired t-tests were calculated after controlling for the False Discovery Rate ($\alpha = 5\%$). The functional traits used were leaf area, LA; specific leaf area, SLA; leaf dry matter content, LDMC and values presented are calculated means per species per habitat.

4. Discussion

We showed that woody plant communities are phylogenetically similar between the grassland-forest habitats. In contrast, by considering shifts in FD and functional composition across the forest-grassland transition, our results showed that forest contrasts with grassland in terms of woody plant community assembly: in forests, communities had lower diversity in leaf area with a predominance of large leaves but higher diversity in structural leaf traits and leaves predominantly with an acquisitive resource strategy (i.e., higher SLA and lower LDMC values). This pattern was also corroborated by the results of the comparisons between species with different habitat preferences, with forest-specialist species having traits more related to resource acquisition, while grassland-specialist species had trait values more associated with resource conservation. Nevertheless, generalist species displayed trait values that aligned with the habitat in which they were sampled, with enough intraspecific variability to adapt to either forest or grassland habitats. The strong and consistent intra and interspecific leaf trait changes among forest-grassland transitions without changes in phylogenetic diversity (no lineage turnover) reinforce the role of phenotypic plasticity in structuring woody plant communities and populations.

4.1 Functional and phylogenetic patterns of woody plant communities in response to habitat type

Across grassland-forest transitions, woody communities did not differ in phylogenetic diversity when gymnosperms were considered in the analysis. This result indicated that both forest and grassland habitats share generalist gymnosperm species (Duarte, 2011), specifically *Araucaria angustifolia* and *Podocarpus lambertii*, as well as generalists angiosperms such as some species from Myrtaceae and Asteraceae. Generalist species seems be able to adapt and colonize grassland habitats without any evidence of a phylogenetic filter in grassland habitats. As a result, the phylogenetic diversity of the two habitats becomes similar, as they share many species (e.g., generalist) with leaf trait adaptations to each habitat.

Community assembly throughout the grassland-forest transition is marked by changes in dispersion and community-weighted mean of the leaf traits that are consistent with a shift from stress tolerance to competitiveness. We found lower FD LA, higher FD SLA, and LDMC in the forest than in grassland communities. Thus, the open environment of grassland communities has more variability of leaf area, but functional clustering in traits related to structural leaf production cost and defense, essential strategies in an environment with stressors such as fire and frost (Flake et al., 2021; Frangipani et al., 2021; Rossatto et al., 2009). In addition, forest communities are predominantly characterized by trees with acquisitive resource strategy (higher LA and SLA and lower LDMC), which could confer a competitive advantage in light-limited habitat, whereas in grassland communities, conservative strategies predominate (Westoby et al., 2002).

Woody plant communities in grasslands face harsher environmental conditions than forests, such as higher light intensity, herbivory, fire, and frost events (Flake et al., 2021;

Rossatto et al., 2009). Additionally, these communities are characterized by competition for resources of wood species with grasses, which can result in a competitively dominant phenotype selecting similar traits of woody species which would allow them to establish and grow in grassland habitats. These abiotic and biotic conditions in grassland habitats can drive the assembly of woody species through a selection of a certain set of functional traits (Freschet et al., 2011; Pellegrini et al., 2023), resulting in a convergence pattern in SLA and LDMC with a predominance of lower SLA and higher LDMC values. LA was also lower in terms of community mean, but it showed a divergence pattern (higher FD LA). Forest communities, however, had a clustering pattern in LA and a wider range of SLA and LDMC values, indicating that the overall light availability limitation drives community structure in terms of leaf area, selecting individuals with large leaves to tolerate shade conditions. On the other hand, such communities varied more in terms of SLA and LDMC (higher FD SLA and LDMC compared to grasslands), indicating these traits seem to respond to local heterogeneity in forest habitats, e.g., among canopy and understory conditions.

4.2 Individual resource acquisition and conservation strategies shift among habitat types

We found a strong relationship between habitat specialization and leaf traits, as observed by recent studies carried out in savanna and forest ecotones (e.g., Carrijo et al., 2021; Flake et al., 2021; Maracahipes et al., 2018). The intraspecific shifts in ecological strategies among grassland and forest habitats related to conservative to acquisitive resource use could be essential to their adaptive adjustment in communities under distinct environmental conditions.

Forest-specialist species tend to have functional traits related to fast-growing strategies, with larger LA and SLA that allow for better capture and use of light, maximizing photosynthesis without investing much in structure. Those traits are thus related to acquisitive resource strategies and allow species to be successful under dense shade conditions or on more fertile soils and without hydric stress (Milla and Reich, 2007; Pilon et al., 2021). On the other hand, grassland-specialist species showed higher amplitude in their trait values, and only for LA, the mean was significantly smaller in comparison to forest-specialist species. Lower values of LA could thus be indicative of a successful strategy in open environments with high solar incidence and frost events (Flake et al., 2021; Rossatto et al., 2009). Small leaves offer a decrease in water loss through transpiration and maintain higher thermal stability (less overheating and freezing). The observed amplitude in leaf traits of our category of grassland-specialist species is associated with distinct strategies of woody species often sampled in grasslands, varying among shrub species (e.g., *Baccharis uncinella*, *Eupatorium buniifolium, Vachellia caven*), trees (e.g., *Schinus* spp, *Xylosma tweediana*) and species often restricted to edge conditions (e.g., *Miconia hiemalis*, *Celtis brasiliensis*).

Generalist tree species that occur in the forest did not differ in terms of leaf area but showed thinner leaves and higher specific leaf area than generalist species that occur in grasslands. Thinner leaves with high SLA values usually represent an adaptation to optimize growth in shady conditions, as found in forests (Rossatto et al., 2009; Wigley et al., 2016), while denser leaves and lower SLA seem to be important to plants occurring in grassland habitats (Hoffmann et al., 2005; Solofondranohatra et al., 2018). Adopting different ecological strategies by generalist species matches the requirements to persist in the habitat where they occur.

Plant species that are able to establish populations in both forests and grasslands habitats evidence greater intraspecific trait variability in the leaf traits, which seem to be a key determinant driving the dynamics of forest expansion. While forest specialist species are unable to occur in grasslands, generalist species can adapt by shifting their leaf traits according to the environmental conditions (i.e., from an acquisitive to a conservative strategy) and establish populations in grassland habitats (Maracahipes et al., 2018). The increase in generalist populations results in lower light incidence, excluding the shade-intolerant species and contributing to shade-tolerant species expansion (Charles-Dominique et al., 2018). Then, this set of generalist species can work as nurse plants and lead to forest expansion as nurse plants since they can have the traits values essential to tolerate the open environment and create microclimatic conditions for the establishment of forest species (Carlucci et al., 2011; Duarte et al., 2006).

5. Conclusion

Our study showed that forest and grasslands habitats share similar phylogenetic diversity. Moreover, habitat specialist species are clearly associated with distinct ecological strategies, while generalists can have both strategies, with individuals shifting according to the habitat of occurrence. Leaf trait values related to acquisitive resource strategies were associated with forests at both the community and individual scales, whereas in grasslands, we found that the trait values of woody plants were mostly related to conservative strategies. These contrasting strategies reflect the adjustment in community assembly under distinct competitive interactions and environmental conditions, from competitive traits to stress-tolerant ones. Generalist species can vary their trait values according to habitat occurrence, which can be associated with high intraspecific trait variability in LA, SLA, and LDMC. Our study has therefore shown that generalist woody species can have a key role in forest expansion over grasslands. Moreover, we have here shown how functional traits from woody plant species can be used as a tool for understanding and predicting how grassland-forest plant community dynamics will unfold in the future given the predicted changes in climate and disturbance regimes.

Data accessibility statement

The diversity metrics of the communities and the functional traits used to calculate intraspecific analysis are available in Supplementary Information, and all functional trait data have been deposited on the TRY database (Kattge et al., 2020). The statistical analysis scripts will be available after the acceptance of the manuscript on.

Authors' contributions

J.K., R.S.B., M.G., L.D., M.B.C., and S.C.M. conceived of the research idea; R.S.B., M.G.S. and M.B.C. collected data; J.K. performed statistical analyses; J.K. wrote the paper with support from R.S.B and S.C.M.; all authors discussed the results and reviewed the manuscript.

Declaration of Competing Interest

None.

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Supplementary Information

Table 1: List of communities and their respective information concerning, community-weighted mean (CWM) of traits, functional diversity (FD), phylogenetic diversity (PD) with its standard deviation (SD), and the standardized effect size of this index (ses PD). Plant functional traits used were leaf area (LA- cm²), specific leaf area (SLA- cm² g^{-1}), and leaf dry-matter content (LDMC- mg g^{-1}). To run the analysis, we calculated using 1000 phylogenetic trees considering gymnosperms (PD) and excluding them (ang), and we extracted the mean value of diversity metrics measured in each community, and the standard deviation (SD), which represents the phylogenetic uncertainty.

Habitat	Transects	CWM LA	CWM SLA	CWM LDMC	PD	SD PD	PD (ang)	SD PD (ang)	SES PD	SES PD (ang)	FD LA	FD SLA	FD LDMC
Forest	EN1	13.33	122.94	408.6	0.422	0.017	0.728	0.035	-0.43	0.62	0.02	0.22	0.17
Forest	EN2	13.58	118.99	425.33	0.381	0.017	0.616	0.035	-0.75	-0.69	0.02	0.15	0.17
Forest	HE1	7.74	96	418.09	0.363	0.017	0.634	0.035	-1	-0.41	0.01	0.18	0.13
Forest	HE2	7.2	86.52	429.56	0.353	0.019	0.618	0.038	-1.15	-0.59	0.01	0.11	0.12
Forest	PA1	8.66	94.93	403.32	0.462	0.009	0.735	0.019	0.35	0.88	0.01	0.13	0.16
Forest	PA2	4.47	94.03	421.66	0.312	0.011	0.486	0.024	-1.63	-2.27	0.01	0.08	0.14
Forest	PM1	12.72	91.25	403.94	0.522	0.008	0.766	0.016	1.35	1.31	0.02	0.13	0.19
Forest	PM2	9.8	83.78	416.64	0.493	0.008	0.743	0.015	0.85	1.09	0.01	0.14	0.19
Forest	SF1	20.81	134.15	414.01	0.426	0.014	0.758	0.029	-0.39	1.08	0.05	0.2	0.17
Forest	SF2	10.87	155.16	411.05	0.454	0.011	0.731	0.021	0.44	0.99	0.02	0.2	0.15
Forest	SL1	7.3	92.29	437.8	0.387	0.013	0.694	0.025	-0.32	0.67	0.01	0.06	0.14
Forest	SL2	6.13	90.79	429.21	0.368	0.016	0.652	0.031	-0.36	0.46	0.01	0.06	0.12
Forest	ST1	9.73	149.16	405.51	0.288	0.009	0.511	0.019	-1.84	-1.88	0.01	0.13	0.1
Forest	ST2	10.19	155.94	399.89	0.393	0.012	0.700	0.026	-0.42	0.59	0.02	0.14	0.12
Forest	SV1	6.27	119.4	412.76	0.536	0.01	0.641	0.034	1.24	-0.16	0.01	0.24	0.18
Forest	SV2	6.4	133.54	425.52	0.412	0.012	0.583	0.029	-0.16	-0.61	0.01	0.18	0.1
Forest	TA1	6.02	91.26	412.72	0.583	0.01	0.624	0.038	2.03	-0.82	0.01	0.14	0.15
Forest	TA2	6.64	91.48	416.72	0.541	0.008	0.545	0.030	1.32	-1.62	0.01	0.12	0.12
Grassland	EN1	6.52	75.67	423.56	0.394	0.028	0.458	0.064	-0.35	0.29	0.08	0.07	0.09
Grassland	EN2	4.17	74.17	428.54	0.584	0.015	0.447	0.063	1.65	0.08	0.07	0.14	0.08
Grassland	HE1	5.32	76.63	427.72	0.4	0.024	0.486	0.064	-0.59	0.34	0.1	0.1	0.11
Grassland	HE2	5.49	70.93	439.76	0.369	0.025	0.437	0.065	-0.94	-0.29	0.07	0.07	0.09
Grassland	PA1	1.4	89.95	432.79	0.116	0.003	0.148	0.020	-1.73	-2.01	0.05	0.02	0.01
Grassland	PA2	2.87	83.4	432.54	0.472	0.008	0.444	0.047	0.4	-0.31	0.09	0.08	0.05
Grassland	PM1	8.22	77.26	449.77	0.431	0.012	0.410	0.047	0.43	0.34	0.16	0.06	0.04
Grassland	PM2	13.42	79.24	438.87	0.336	0.009	0.424	0.039	-0.86	-0.59	0.2	0.06	0.06
Grassland	SF1	11.85	118.26	372.39	0.419	0.011	0.518	0.029	-0.02	1.16	0.17	0.13	0.12
Grassland	SF2	7.32	96.53	424	0.405	0.013	0.304	0.044	0.29	-0.66	0.13	0.08	0.09

Grassland	SL1	5.7	79.75	454.41	0.416	0.02	0.491	0.063	-0.09	1.03	0.08	0.08	0.07
Grassland	SL2	3.51	81.85	449.44	0.207	0.023	0.247	0.048	-2.05	-2.5	0.03	0.05	0.03
Grassland	ST1	1.92	141.36	487	0.276	0.014	0.312	0.041	-1.13	-0.94	0.07	0.24	0.05
Grassland	ST2	1.12	158.74	492.5	0.192	0.008	0.212	0.027	-1.09	-1.07	0.05	0.15	0.05
Grassland	SV1	5	109.9	425.51	0.382	0.02	0.447	0.052	-0.11	0.66	0.1	0.22	0.13
Grassland	SV2	4.97	96.89	450.71	0.5	0.009	0.391	0.041	0.78	0.01	0.07	0.16	0.09
Grassland	TA1	4.48	65.8	429.55	0.655	0.005	0.448	0.043	2.28	1.14	0.11	0.08	0.07
Grassland	TA2	3.25	52.93	435.09	0.552	0.005	0.162	0.027	1.92	-0.77	0.08	0.04	0.05

Table 2: List of species with the number of individuals sampled in forest and grassland communities, and their habitat preference.

Species	Forest	Grassland	Habitat Preference
Acca sellowiana	9	4	Generalist
Achatocarpus praecox	19	0	Forest Specialist
Actinostemon concolor	34	0	Forest Specialist
Allophylus edulis	49	13	Generalist
Allophylus guaraniticus	2	0	Too Rare
Aloysia gratissima	0	24	Grassland Specialist
Annona neosalicifolia	63	0	Forest Specialist
Apuleia leiocarpa	5	0	Too Rare
Araucaria angustifolia	137	55	Generalist
Aspidosperma australe	4	0	Too Rare
Baccharis dentata	1	0	Too Rare
Baccharis dracunculifolia	0	2	Too Rare
Baccharis uncinella	0	151	Grassland Specialist
Banara tomentosa	38	0	Forest Specialist
Berberis laurina	0	5	Too Rare
Blepharocalyx salicifolius	126	78	Generalist
Brunfelsia australis	4	0	Too Rare
Brunfelsia uniflora	3	0	Too Rare
Cabralea canjerana	5	0	Too Rare
Calliandra tweediei	2	0	Too Rare
Calyptranthes concinna	7	0	Too Rare
Calyptranthes grandifolia	5	0	Too Rare
Campomanesia guazumifolia	3	0	Too Rare
Campomanesia xanthocarpa	23	0	Forest Specialist
Casearia decandra	45	1	Forest Specialist
Casearia sylvestris	37	2	Forest Specialist
Celtis brasiliensis	1	7	Grassland Specialist
Celtis ehrenbergiana	1	0	Too Rare
Celtis iguanaea	6	2	Too Rare
Chrysophyllum gonocarpum	4	0	Too Rare
Chrysophyllum marginatum	19	2	Generalist

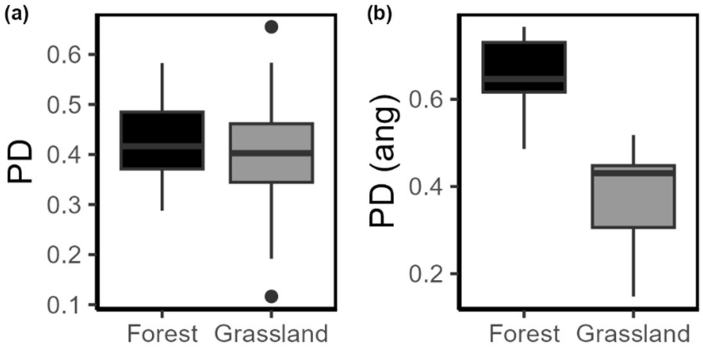
Cinnamomum amoenum	2	0	Too Rare
Cinnamomum glaziovii	1	0	Too Rare
Citharexylum montevidense	8	4	Generalist
Citronella gongonha	3	0	Too Rare
Citronella paniculata	4	0	Too Rare
Clethra scabra	4	1	Too Rare
Clethra uleana	3	0	Too Rare
Coccoloba cordata	32	3	Generalist
Condalia buxifolia	3	1	Too Rare
Cordia americana	80	8	Forest Specialist
Cordia ecalyculata	1	0	Too Rare
Cryptocaria aschersoniana	2	0	Too Rare
Cupania vernalis	5	1	Too Rare
Daphnopsis fasciculata	11	2	Too Rare
Daphnopsis racemosa	0	37	Grassland Specialist
Dasyphyllum spinescens	16	1	Too Rare
Dasyphyllum tomentosum	3	0	Too Rare
Dicksonia sellowiana	1	0	Too Rare
Diospyros inconstans	13	0	Forest Specialist
Drimys angustifolia	69	7	Forest Specialist
Drimys brasiliensis	12	1	Too Rare
Enterolobium contortisiliquum	8	3	Too Rare
Erythroxylum cuneifolium	1	0	Too Rare
Erythroxylum deciduum	8	7	Generalist
Esenbeckia grandiflora	2	0	Too Rare
Eugenia involucrata	7	0	Too Rare
Eugenia subterminalis	1	0	Too Rare
Eugenia uniflora	266	70	Generalist
Eugenia uruguayensis	42	10	Generalist
Eupatorium buniifolium	0	15	Grassland Specialist
Ficus luschnathiana	7	0	Too Rare
Gleditsia amorphoides	5	0	Too Rare
Gochnatia polymorpha	8	5	Generalist
Handroanthus heptaphyllus	7	0	Too Rare
Holocalyx balansae	1	0	Too Rare
Ilex dumosa	0	2	Too Rare
Ilex microdonta	103	3	Forest Specialist
Ilex paraguarienses	7	0	Too Rare
Ilex theezans	1	0	Too Rare
Inga vera	5	0	Too Rare
Lamanonia ternata	14	0	Forest Specialist
Laplacea acutifolia	23	1	Forest Specialist
Ligustrum sp.	0	4	Too Rare
Lithraea brasiliensis	114	64	Generalist
Lithraea molleoides	75	84	Generalist
Luehea divaricata	10	0	Too Rare

Machaerium paraguariensis	1	0	Too Rare
Machaonia brasiliensis	0	4	Too Rare
Malmeanthus subintegerrimus	1	0	Too Rare
Matayba elaeagnoides	10	0	Too Rare
Maytenus muelleri	3	1	Too Rare
Miconia cinerascens	1	3	Too Rare
Miconia hyemalis	1	67	Grassland Specialist
Miconia ramboi	3	2	Too Rare
Mimosa scabrella	1	1	Too Rare
Myracrodruon balansae	5	0	Too Rare
Myrceugenia alpigena	27	5	Generalist
Myrceugenia cucullata	1	0	Too Rare
Myrceugenia euosma	103	68	Generalist
Myrceugenia glaucescens	50	7	Generalist
Myrceugenia mesomischa	84	0	Forest Specialist
Myrceugenia miersiana	46	0	Forest Specialist
Myrceugenia myrcioides	7	0	Too Rare
Myrceugenia oxysepala	2	0	Too Rare
Myrcia guianensis	76	0	Forest Specialist
Myrcia lajeana	1	0	Too Rare
Myrcia oligantha	2	0	Too Rare
Myrcia palustris	56	2	Forest Specialist
Myrcia retorta	74	1	Forest Specialist
Myrcia selloi	15	9	Generalist
Myrcianthes cisplatensis	25	27	Generalist
Myrcianthes gigantea	8	0	Too Rare
Myrcianthes pungens	19	0	Forest Specialist
Myrciaria delicatula	23	0	Forest Specialist
Myrciaria tenella	18	1	Forest Specialist
Myrocarpus frondosus	1	0	Too Rare
Myrrhinium atropurpureum	15	8	Generalist
Myrsine coriacea	46	22	Generalist
Myrsine laetevirens	5	6	Generalist
Myrsine lorentziana	48	34	Generalist
Nectandra megapotamica	7	0	Too Rare
Ocotea acutifolia	1	0	Too Rare
Ocotea corymbosa	54	0	Forest Specialist
Ocotea elegans	2	0	Too Rare
Ocotea puberula	6	0	Too Rare
Ocotea pulchella	56	3	Forest Specialist
Parapiptadenia rigida	17	1	Forest Specialist
Phytolacca dioica	1	0	Too Rare
Piptocarpha axillaris	9	2	Too Rare
Piptocarpha notata	2	0	Too Rare
Plinia rivularis	4	0	Too Rare
Podocarpus lambertii	125	31	Generalist

Poecilanthe parviflora	2	0	Too Rare
Pouteria salicifolia	2	0	Too Rare
Prunus subcoriacea	8	0	Too Rare
Psidium cattleianum	2	1	Too Rare
Quillaja brasiliensis	16	8	Generalist
Randia ferox	2	0	Too Rare
Rhamnus sphaerosperma	2	0	Too Rare
Roupala rhombifolia	43	0	Forest Specialist
Ruprechtia laxiflora	14	3	Generalist
Sapium glandulosum	6	2	Too Rare
Sapium haematospermum	0	2	Too Rare
Schinus engleri	0	1	Too Rare
Schinus lentiscifolius	16	13	Generalist
Schinus longifolius	3	13	Grassland Specialist
Schinus polygamus	1	15	Grassland Specialist
Scutia buxifolia	41	22	Generalist
Sebastiania brasiliensis	14	0	Forest Specialist
Sebastiania commersoniana	72	24	Generalist
Sideroxylon obtusifolium	2	0	Too Rare
Siphoneugena reitzii	187	6	Forest Specialist
Solanum mauritianum	0	1	Too Rare
Solanum pseudoquina	1	1	Too Rare
Sorocea bonplandii	11	0	Forest Specialist
Strychnos brasiliensis	5	5	Generalist
Styrax leprosus	159	35	Generalist
Syagrus romanzoffiana	6	0	Too Rare
Symplocos tetandra	1	0	Too Rare
Symplocos uniflora	18	4	Generalist
Tabernaemontana catharinensis	5	35	Grassland Specialist
Tibouchina sellowiana	21	3	Generalist
Trichilia claussenii	76	0	Forest Specialist
Trichilia elegans	7	0	Too Rare
Urera baccifera	1	0	Too Rare
Vachellia caven	0	71	Grassland Specialist
Vernonanthura discolor	10	6	Generalist
Vitex megapotamica	38	0	Forest Specialist
Weinmannia paulliniifolia	9	0	Too Rare
Xylosma prockia	0	1	Too Rare
Xylosma schroederi	10	13	Generalist
Xylosma tweediana	24	29	Grassland Specialist
Zanthoxylum astrigerum	30	1	Forest Specialist
Zanthoxylum fagara	20	3	Generalist

Table 3: List of generalist species with their respective LA (leaf area, cm²), SLA (specific leaf area, cm².g^{-1}), and LDMC (leaf dry matter content, mg.g^{-1}) collected in forest and grassland habitats.

Species	LA (forest)	LA (grassland)	SLA (forest)	SLA (grassland)	LDMC (forest)	LDMC (grassland)
Acca sellowiana	18.85	10.59	101.18	66.60	406.01	452.23
Allophylus edulis	5.82	3.50	140.04	119.91	411.53	409.87
Araucaria angustifolia	1.36	1.29	62.70	48.42	374.25	420.40
Blepharocalyx salicifolius	3.53	3.30	99.73	89.54	438.15	464.05
Chrysophyllum marginatum	6.01	4.81	113.82	90.53	391.35	416.54
Citharexylum montevidense	18.89	12.60	68.63	62.20	419.03	457.58
Coccoloba cordata	14.07	6.63	177.35	134.27	319.41	365.47
Erythroxylum deciduum	13.47	5.73	161.12	48.46	290.73	458.06
Eugenia uniflora	6.54	5.64	140.46	94.93	413.78	459.22
Eugenia uruguayensis	9.15	7.53	79.86	57.72	410.17	422.28
Gochnatia polymorpha	9.63	7.55	94.51	73.75	412.25	463.36
Lithraea brasiliensis	6.23	6.45	77.31	63.62	433.51	437.64
Lithraea molleoides	4.22	3.06	87.51	80.90	417.55	448.71
Myrceugenia alpigena	8.37	5.41	151.39	60.63	309.87	476.27
Myrceugenia euosma	5.22	1.76	59.79	85.29	453.08	447.35
Myrceugenia glaucescens	6.03	3.76	111.04	46.02	421.85	442.93
Myrcia selloi	3.35	2.51	210.22	120.97	314.66	361.40
Myrcianthes cisplatensis	3.38	3.35	55.11	58.56	459.89	476.64
Myrrhinium atropurpureum	5.00	3.52	88.23	71.79	437.52	486.84
Myrsine coriacea	7.50	8.12	103.89	88.25	361.83	411.99
Myrsine laetevirens	7.55	7.99	89.53	82.64	251.77	322.17
Myrsine lorentziana	13.49	12.28	80.56	72.74	368.13	450.40
Podocarpus lambertii	0.70	0.93	74.22	74.51	433.19	408.20
Quillaja brasiliensis	6.48	8.34	74.44	54.19	378.30	418.83
Ruprechtia laxiflora	10.00	6.08	160.04	181.73	419.65	376.58
Schinus lentiscifolius	0.93	0.67	75.21	45.22	481.99	473.39
Scutia buxifolia	2.47	2.17	84.78	82.77	516.40	515.79
Sebastiania commersoniana	7.64	4.97	113.82	92.95	422.94	439.15
Strychnos brasiliensis	6.90	5.44	175.51	77.95	363.50	448.30
Styrax leprosus	10.62	8.26	85.52	73.88	452.73	460.70
Symplocos uniflora	11.89	11.26	75.47	63.33	363.75	372.71
Tibouchina sellowiana	11.33	6.01	147.89	94.12	337.23	425.68
Vernonanthura discolor	34.33	35.80	100.52	80.13	346.67	419.81
Xylosma schroederi	7.23	6.83	77.99	69.23	456.27	430.30
Zanthoxylum fagara	1.53	1.71	108.19	100.41	309.22	349.66



Supplementary Material Figure 1: Boxplots showing the phylogenetic diversity (a), phylogenetic diversity with only angiosperm (b). Boxplots represent median and 1st and 3rd quantile.

By using phylogenetic diversity without the standardized effect size, we found that grassland forest communities do not differ in phylogenetic diversity when conifers are considered. However, when considering only angiosperms, we found higher phylogenetic diversity in forests ($R^2 = 0.25$, $p < 0.01$; Material Supplementary Figure 1), which indicates the higher representativeness of the ancient Magnoliids clade in forest communities, which are early-diversified from shady and humid older biogeographic domains (Oliveira-Filho and Ratter, 1995).

Oliveira-filho, A., Ratter, J.A., 1995. A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. Edinburgh J. Bot. https://doi.org/10.1017/S0960428600000949

Capítulo 4

Chapter 4

How do distinct facets of tree diversity and community assembly respond to environmental variables in the subtropical Atlantic Forest?

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How do distinct facets of tree diversity and community assembly respond to environmental variables in the subtropical Atlantic Forest?

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Abstract

This study assessed the impact of altitude, precipitation, and soil conditions on species richness (SR), phylogenetic diversity (PD), and functional diversity (FD) standardized effect sizes in subtropical Brazilian Atlantic Forest tree communities. We considered specific trait information (FDs) for FD, reflecting recent adaptive evolution, contrasting with deeper phylogenetic constraints in FD. Three functional traits (leaf area-LA, wood density-WD, and seed mass-SM) were examined for their response to these gradients. Generalized least squares models with environmental variables as predictors and diversity metrics as response variables were used, and a fourth-corner correlation test explored trait-environmental relationships. SR decreased with altitude, while PD increased, indicating niche convergence at higher altitudes. Leaf area and seed mass diversity also decreased with altitude. For LA, both FD and FDs were significant, reflecting filtering processes influenced by phylogenetic inheritance and recent trait evolution. For SM, only the specific trait structure responded to altitude. LA and SM showed significant trait-environmental relationships, with smaller-leaved and lighter-seeded species dominant at higher altitudes. Soil gradients affect diversity. Fertile soils have a wider range of LA, indicating coexistence of species with different nutrient acquisition strategies. WD variation is lower for FDs. SM diversity has different relationships with soil fertility for FDs and FD, suggesting phylogeny influences trait variation. Soil pH influences WD and LA under acidic soils, with deeper phylogenetic constraints (FD). Environmental factors impact tree communities, with evidence of trait variation constraints driven by conditions and resources. Subtropical Atlantic forests' tree assemblies are mainly influenced by altitude, pH, and soil fertility, selecting fewer species and narrower trait spectra under specific conditions (e.g., higher altitudes, pH). Functional diversity patterns reflect both phylogenetic and recent evolution constraints, with varying strength across traits and conditions. These findings highlight the intricate processes shaping long-lived species assembly across diverse environments in the Southern Brazilian Atlantic Forest.

Keywords: Biodiversity, community trait composition, functional traits, precipitation, soil variables, species richness, altitude.

Introduction

Biodiversity encompasses various components, including taxonomic (species diversity), functional (differences in species traits), and phylogenetic diversity (diversity of species lineages) (Pavoine & Bonsall, 2011). Functional and phylogenetic diversity provide different yet complementary information about ecological and evolutionary differences among species, due to trait evolution (Webb et al., 2002). While several studies have examined multiple facets of biodiversity along environmental gradients (e.g., de Bello et al., 2006; Dainese et al., 2015; Luo et al., 2019), few have distinguished between the shared information among functional traits and phylogeny (de Bello et al. 2017). The shared information can be considerable, particularly when using phylogenetically conservative traits (Diniz-Filho et al., 2011; de Bello et al. 2017), which makes understanding community assembly challenging across different regions and conditions. Frameworks that integrate species, functional, and phylogenetic diversity, while considering the overlapping and unique information from each component, may reveal new insights about species composition, ecological strategies, and adaptations across the evolutionary history of lineages in communities along environmental gradients. Such frameworks can help uncover the mechanisms driving biodiversity assembly.

Notably, functional traits provide information about species ecological differences (diversity) and habitat requirements (trait state) (HilleRisLambers et al., 2012), while phylogenetic diversity can allows us to understand the deeper evolutionary and biogeographical constraints on regional species distribution (Gerhold et al., 2015; de Bello et al., 2017). The ecological theory suggests that in addition to stochastic processes (Hubbell, 2001), deterministic processes, related to abiotic and biotic conditions, shapes local communities by selecting species from the regional pool that can survive and persist in local conditions (Vellend, 2010; Rapacciuolo & Blois, 2019). Limiting similarity and environmental filtering are mechanisms that can act simultaneously along various environmental axes in a community during deterministic assembly (Weiher et al., 1998; Cornwell & Ackerly, 2010; Gerhold et al., 2015). In general, whereas limiting similarity is expected to exclude similar species in a community, environmental filtering is expected to select species with similar habitat requirements (Kraft et al., 2007; HilleRisLambers et al., 2012; Kraft et al., 2015). However, convergence and divergence patterns in the functional and phylogenetic structures can arise from distinct processes, and these patterns can only be partially or not at all inter-related. Therefore, by separating the phylogenetic structure from the functional structure, it is potentially possible differentiate the patterns and likely drivers of both the evolutionary and ecological components, including more recent adaptive evolution, within species assemblages (Diniz-Filho et al., 2011; de Bello et al. 2017).

Altitudinal gradients provide insights into how environmental conditions drive community assembly and influence tree species, functional, and phylogenetic diversity (Pescador et al., 2015; Xu et al., 2017; Ding et al., 2019), as many variables change with altitude, such as temperature, cloudiness, atmospheric pressure, wind exposure, and area isolation. Precipitation is also a relevant factor influencing functional and phylogenetic diversity, where drier sites often limit diversity (Muscarella et al., 2016). Additionally, soil conditions like fertility, pH, and texture, along with climatic drivers, shape plant communities in terms of functional, phylogenetic, and taxonomic diversity (Ordoñez et al., 2009; Bernard-Verdier et al., 2013; Condit et al., 2013). For instance, soil fertility in terms of cation exchange capacity can act as an environmental filter for nutrient-poor tolerant species (Lambers et al., 2011; Quesada et al., 2012). Soil pH, on the other hand, can have a negative or positive effect on diversity in different floristic regions, depending on the prevailing pH conditions and the species pool that evolved to them (Pärtel, 2002). Soil texture (e.g., clay content and bulk density) is also relevant and often related to water retention, which is greater in clay-rich soils, but it can further reduce nitrogen mineralization rates and affect plant-available nutrients (Lambers et al., 2011; Quesada et al., 2012).

Overall, tree communities at higher altitudes experience harsh environmental conditions for plant establishment and growth that limit the number of coexisting species and clades (Bergamin et al., 2020). Species that are closely related and possess physiological and morphological traits allowing them to survive in these conditions are expected to exhibit phylogenetic clustering, with a reduction in trait dispersion and shifts in mean trait values along the altitudinal gradient (de Bello et al., 2013; Denelle et al., 2019). Convergence patterns in vegetative and regenerative traits of tree species (underdispersed traits), with resource conservation strategies such as smaller seeds (Qi et al., 2014; Wang et al., 2021), and lower leaf area and higher wood density (Kichenin et al., 2013; Ding et al., 2019), may arise due to environmental filtering or competitive hierarchy of specific trait values. In contrast, at lower altitudes with more favorable conditions, tree species may exhibit functional divergence (i.e., with overdispersed traits) and a prevalence of acquisitive resource strategies such as higher leaf area, lower wood density, and larger seeds (Díaz et al., 2015).

However, different climatic variables can affect each diversity component differently. Previous studies in mountain forests observed opposite trends for taxonomic and phylogenetic diversity with altitude: decreased species richness and increased phylogenetic diversity in higher altitudes (Culmsee & Leuschner, 2013). Evidence shows that phylogenetic diversity may increase with increasing altitude in tropical and subtropical altitudinal gradients (González-Caro et al., 2014; Qian, 2017; Rezende et al., 2017), as some clades expanded their distributions to cooler regions where they have diversified slowly, resulting in species more distantly related to each other with similarities in adaptations to cold environments, following the niche convergence hypothesis (Qian & Ricklefs, 2016). Therefore, at high altitudes, increasing phylogenetic diversity of tree communities can be observed. In the same way, different traits may have contrasting patterns of trait dispersion along the gradient due to different assembly mechanisms and processes (e.g. selection or dispersal ability or possible lack of independence between the functional and phylogenetic structures) act simultaneously and may operate on different aspects of the organism's phenotype (Swenson, 2013). This means that one trait may be overdispersed while another is underdispersed. For example, along the same environmental gradient, seed mass can show patterns of divergence while leaf area convergence (Grime, 2006; Kraft et al., 2008) and this pattern can be phylogenetic dependent. Then, accounting for both overlapping, which includes the deeper phylogenetic constrains in trait variation, and unique information that reflects recent adaptive evolution independent of phylogenetic constraints (Diniz-Filho et al., 2011; Gerhold et al., 2015) can be essential to unhide the multiple assembly processes that operate on the communities, as different traits may be affected by different mechanisms and processes (Diniz-Filho et al., 2011; de Bello et al. 2017).

This study aims to assess shifts in biodiversity of tree communities across environmental gradients Southern Brazil's subtropical forests. The study considers species richness (SR), functional (ses.FD), and phylogenetic (ses.PD) diversity, as well as community trait composition. By analyzing three functional traits, phylogenetic relatedness, and community species abundance, the study aims to answer the questions: (i) to what extent are the four biodiversity measures similarly influenced by altitude, climate, and soil conditions? We hypothesized that restrictive conditions and resources lead to lower values of all diversity metrics due to filtering processes. However, different environmental variables may affect each diversity facet and trait differently. In this sense, SR and ses.FD of leaf area and wood density should be lower in higher altitudes, whereas ses.FD of seed mass and ses.PD should be higher. Under harsh conditions, communities are expected to have predominance of trees with conservative strategies, such as small leaves, high wood density, and small seeds. (ii) Do the unique and overlapping information of traits and phylogeny on diversity measures respond similarly across distinct environmental gradients? The expectation is that analyzing FD from overlapping and unique information can uncover biodiversity assembly mechanisms and reveal whether species adaptations across environmental gradients follow a structured pattern in the evolutionary history of the lineages, regardless of the phylogeny.

Methods

Community dataset

Our dataset consists of tree communities in the subtropical region of the Atlantic Forest biome in Brazil. The Atlantic Forest is a phytogeographical domain that encompasses various forest types and ecosystems, resulting in a heterogeneity of environments (Oliveira-Filho & Fontes, 2000). The subtropical region is characterized by a mosaic of Araucaria Forest, natural grasslands (*Campos Sulinos*), moist coastal forests, and western semi-deciduous forests, separated by plateaus (Oliveira-Filho & Fontes 2000). The climate is humid subtropical, with temperate summers and annual precipitation ranging between 1750 and 2500 mm (Alvares et al., 2013) without a dry season. The region experiences frost frequently during the winter (Backes 2009).

We analyzed data from 50 tree community inventories in Southern Brazil, covering different altitudes from 40 m to 1750 m (Figure 1). Plots situated at higher altitudes are predominantly covered by acid volcanic rocks, while plots at lower altitudes are characterized by predominantly basalt lithology in undulating to mountainous terrain (Streck et al. 2008). These inventories were conducted by one of the authors of this study and included forests with varying sampling efforts (ranging from 1200 m² to 10,000 m²) but were all established in old-growth forests (see Supplementary Material Table 1 for details). We have standardized the tree inclusion threshold at stem diameter at breast height (DBH) > 10 cm to ensure consistency across all inventories, including both angiosperms and gymnosperms, in each community. Even by using this threshold, our sample include small tree species from the families Myrtaceae, Melastomataceae, and Rubiaceae (e.g., *Calyptranthes conccina, Miconia cinerascens, and Psychotria suterella*), which contain characteristic elements of these subtropical forests.

Moreover, the inventories encompassed representative environmental gradients in terms of altitude, precipitation, and soil types in the subtropical Atlantic Forest biome.

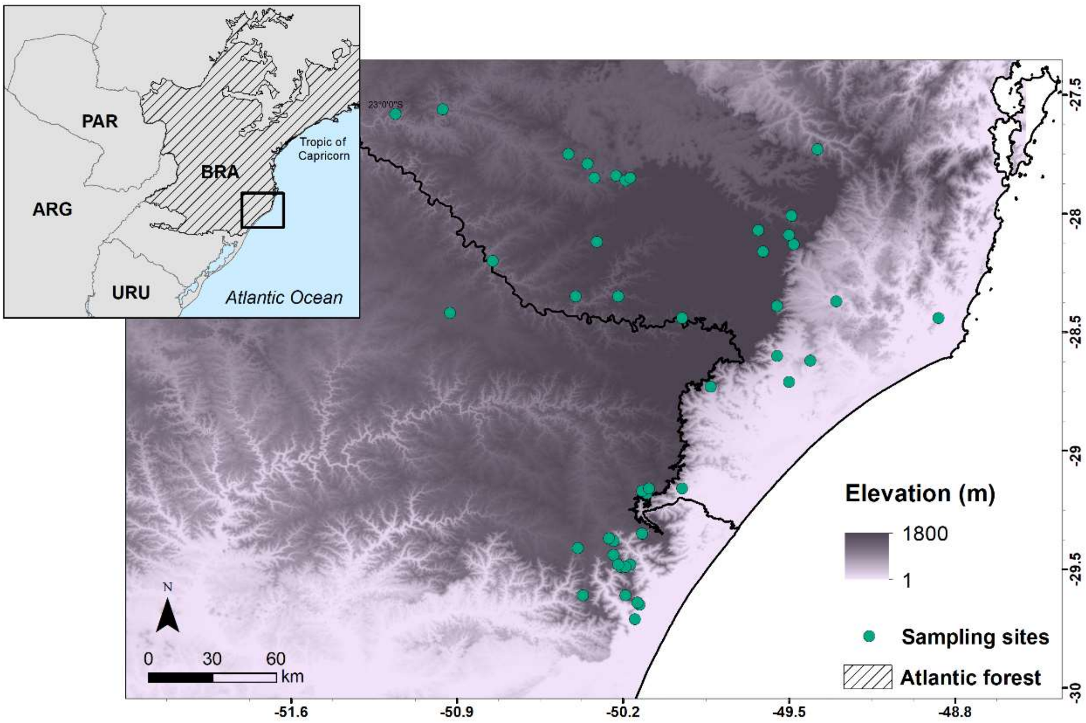

Figure 1: Location of the 50 tree community inventories along the subtropical Brazilian Atlantic Forest showing the distribution patterns of altitude (elevation, m) in the background.

Environmental data

To investigate the effect of altitude and environmental gradients on diversity components and community trait composition, we obtained data on altitude value (m), climate, and soil variables. The climatic data included annual mean temperature (°C), temperature seasonality, minimum temperature of the coldest month (°C), mean annual precipitation (MAP, mm), and precipitation seasonality. These variables were extracted at 1 km of resolution from WorldClim (Fick & Hijmans, 2017). Altitude values were obtained from community locations. The soil variables (at 15 cm depth) were cation exchange capacity (CEC, cmolc/kg), as a fertility variable, clay content (g/kg), and bulk density (cg/cm3), characterizing soil texture and water retention capacity, soil pH, and soil nitrogen (cg/kg), related to the availability of nutrients. We obtained soil variables from SoilGrids (grids cells of 1 km of resolution) (Hengl et al. 2017).

Functional traits data

Plant functional traits used were leaf area (LA, cm^2), wood density (WD, $g.cm^3$), and dry seed mass (SM, g), which represent different plant strategy axes, including vegetative (LA), structural (WD), and reproductive (SM) features. These traits are based on the current understanding of the leaf economic spectrum (Wright et al., 2004), resource acquisition, dispersal and establishment rate (Kidson & Westoby 2000), niche differentiation and persistence across different environmental conditions (Westoby et al., 2002; Reich, 2014; Moles, 2018). We were able to obtain LA and WD values to species level for up to 95% of the total species pool. For species values that were unavailable, we used genus mean values. We measured seed mass by collecting fruits from tree individuals in the study region and using bibliographic sources (e.g., Lorenzi, 2000; Sobral et al., 2006; Seger et al., 2013). We obtained SM values for 65% of the species and used the missForest algorithm (Penone et al. 2014; Debastiani et al. 2021) to estimate missing values, as seed mass is highly dependent on phylogenetic information (Moles et al. 2005). We also replaced missing data with average trait values from documented species and conducted further analysis to test if the associations between SM and environmental variables remained consistent using both methods of filling missing data (see Supplementary Material Table 4). As the analysis revealed the same patterns using SM values from both methods of filling missing data, we used SM values obtained from the missForest algorithm. We gathered leaf area information from our Plant Ecology Lab database, available in the Try Plant Trait Database (Kattge et al. 2020). WD information was obtained from both regional (Missio et al., 2017; Oliveira et al., 2019) and global databases (Chave et al., 2009). Measurements and procedures to obtain LA and SM from species available in our database followed standardized protocols

(Pérez-Harguindeguy et al. 2013). There was no correlation among these functional traits (Supplementary Material Table 2).

Phylogenetic tree

We used the *'S.PhyloMaker'* package to construct an ultrametric phylogeny for all 395 species in the community dataset, using the *PhytoPhylo megaphylogeny* as a backbone and adding genera or species absent from the megaphylogeny as basal polytomies within their families or genera (Qian & Jin 2016). The PhytoPhylo megaphylogeny is a correction in the phylogeny for plant species from Zanne et al. (2014), which includes genetic data from GenBank and is the largest resolved phylogeny for plant species worldwide. An updated and expanded version of the phylogeny (i.e., PhytoPhylo) is time-calibrated for all branches, includes all families of extant seed plants in the world. Our phylogenetic tree contains polytomies, or nodes with more than two descendent branches, which results in uncertainty about the correct branching order of taxa. To resolve polytomies, we used the function '*bifurcatr'* in package 'PDcalc' (Rangel et al. 2015), which randomly resolves polytomies in a phylogenetic tree. We ran the algorithm 1000 times to explore the range of potential solutions and used all trees in the subsequent analyses.

Data analyses

We used the '*decouple'* approach (de Bello et al. 2017) to analyze the functional trait diversity of the species in our dataset and infer the unique and overlapping information of traits and phylogeny. This approach allows us to decouple phylogenetic diversity from functional diversity (the specific component of functional diversity; FDs) and calculate functional diversity accounting for evolutionary legacy (the phylogenetic component of functional diversity; FD) using multivariate analysis. To apply the *'decouple'* framework, we needed a Euclidean distance matrix for functional traits and the phylogenetic tree, both indicating the differences between species. The distance matrix for functional traits was obtained considering all traits separately (i.e., LA, WD, and SM). The functional traits were log-transformed for normality purposes. To obtain trait information decoupled from phylogeny, the 'decouple' function used phylogeny in the form of eigenvectors from a principal coordinate analysis as an explanatory variable and traits as response variables (Diniz-Filho et al., 2011). The residuals of the model represent the variation in species' traits decoupled from phylogeny, which is computed as a distance matrix reflecting species trait distances independent of phylogeny.

We calculated functional (FD) and phylogenetic diversity (PD) using abundance-weighted standardized effect sizes for mean pairwise dissimilarity (ses.MPD) (Weiher et al., 1998; Webb, 2000; Pavoine et al., 2011). For both ses.FD and ses.PD, negative values indicate lower diversity than expected by null model (independent swap, Kembel et al. 2010). Using 1000 phylogenetic trees, we computed functional diversity with overlapping information with phylogeny (ses.FD), specific functional diversity (ses.FDs), and phylogenetic diversity (ses.PD) for each community and each trait. We then calculated MPD for FD and PD 1000 times for each community and extracted the mean value of MPD for each community using the 'mpd' function. Finally, we calculated rarefied species richness (using the 'vegan' package and function 'rarefy') for species diversity, considering 465 individuals (See Supplementary Material Table 1 for more details) (Oksanen et al. 2017).

To improve model estimation and reduce collinearity, we analyzed the correlation between predictor variables using Pearson's correlation. We observed a strong negative correlation between altitude and temperature variables (Supplementary Material Table 3). As a result, we utilized altitude as a substitute for temperature variables, such as annual mean temperature, temperature seasonality, and minimum temperature of the coldest month. In addition, we found that temperature seasonality, minimum temperature of the coldest month, mean annual precipitation, and precipitation seasonality were highly correlated. Therefore, we only used mean annual precipitation. Among the non-correlated soil variables, clay content, CEC, and soil pH were identified. However, we further used only CEC and pH because they best predicted diversity metrics (Supplementary Material Figure 1).

To evaluate shifts in species richness, phylogenetic diversity, and functional diversity (ses.FD and ses.FDs) along altitudinal, precipitation (MAP), and soil (CEC and pH) gradients, we employed generalized least squares models. We included a covariate to account for differences in sampling effort and addressed spatial autocorrelation in the data. To determine the best autocorrelation structure, we compared models with various structures, such as Gaussian, spherical, exponential, and without autocorrelation structure, in a preliminary analysis. According to AICc, a Gaussian autocorrelation structure best fits the data. We used this structure for generating all models. To enable comparison of predictor variables within models, we standardized and centered all predictor variables to have zero mean and unit variance. The analyses were conducted in R version 3.6.3 Statistical Environment, using the ‘picante’ (Kembel et al., 2010), ‘car’ (Fox et al., 2014), and ‘nlme’ (Pinheiro et al., 2016) packages.

Finally, the fourth-corner approach was conducted to investigate the links between community trait composition and the environmental variables. This approach is considered robust for evaluating true correlations between community traits and environmental variables (Peres-Neto et al., 2017; Zelený, 2018). The analysis involves a weighted correlation between community-weighted trait means and weighted standardized environment, where the weights are total community abundances (Peres-Neto et al., 2017). The fourth-corner correlation analysis is conducted using max-tests, which result in two independent permutations tests - rows or communities and columns or species. A conclusion is drawn that species sharing greater trait similarity exhibit more similar habitat affinities when row-column permutation tests are significant (ter Braak et al., 2012). The R code provided in Peres-Neto et al. (2017) was used for conducting the weighted correlation analyses.

Results

In our study, we found that species richness (SR) was negatively associated with altitude (Figure 2a1), while phylogenetic diversity (ses.PD) was positively associated with altitude (Figure 2b1) (Table 1). Leaf area functional diversity, both with overlapping information of phylogeny (ses.FD-LA) and with the specific component (ses.FDs-LA), was negatively associated with altitude (Figure 2c1 and 2d1) (Table 1) and positively associated with CEC (Figure 2c3 and 2d3). Additionally, ses.FD-LA was negatively associated with soil pH (Figure 2c4). The functional diversity of wood density (ses.FD-WD) was negatively associated with soil pH (Figure 2e4). Similarly, FDs-WD (i.e., the specific trait component) showed a negative relationship with CEC and soil pH (Figure 2f3 and 2f4, respectively, Table 1). Seed mass diversity (ses.FD-SM) was negatively associated with CEC (Figure 2g3), whereas ses.FDs-SM was positively associated with CEC (Figure 2h3) and negatively associated with altitude and soil pH (Figure 2h1 and 2h4). We also found that only species richness was positively correlated with sampling effort (Table 1), while precipitation did not appear to be relevant in the context of the region and community sets studied.

Table 1: Results for all generalized least square models tested to evaluate the influence of altitude, mean annual precipitation (MAP), cation exchange capacity (CEC), soil pH, and sampling effort (SE) on species richness, phylogenetic (ses.PD) and functional diversity (ses.FD) (LA = leaf area, WD = wood density, and SM= seed mass) in tree communities of subtropical Atlantic Forests in southern Brazil. The table shows the models with R², standardized coefficients, and *p* values for significant variables. SR = rarefied species richness, ses.FD = non-decoupled functional diversity, ses.FDs = decoupled functional diversity, ses.PD = phylogenetic diversity.

		Altitude		MAP		CEC		pH		SE	
Response	R²	Coeficient	p	Coeficient	p	Coeficient	p	Coeficient	p	Coeficient	p
SR	0.70	-0.59	<0.001	-	-	-	-	-	-	0.40	<0.001
ses.PD	0.16	0.49	0.02	-	-	-	-	-	-	-	-
ses.FD LA	0.69	-1.03	<0.001	-	-	0.52	<0.001	-0.27	0.02	-	-
ses.FDs LA	0.61	-0.91	<0.001	-	-	0.44	<0.001	-	-	-	-
ses.FD WD	0.21	-	-	-	-	-	-	-0.35	<0.001	-	-
ses.FDs WD	0.49	-	-	-	-	-0.23	0.03	-0.34	<0.001	-	-
ses.FD SM	0.44	-	-	-	-	-0.27	0.04	-	-	-	-
ses.FDs SM	0.75	-1.08	<0.001	-	-	0.32	0.006	-0.26	0.02	-	-

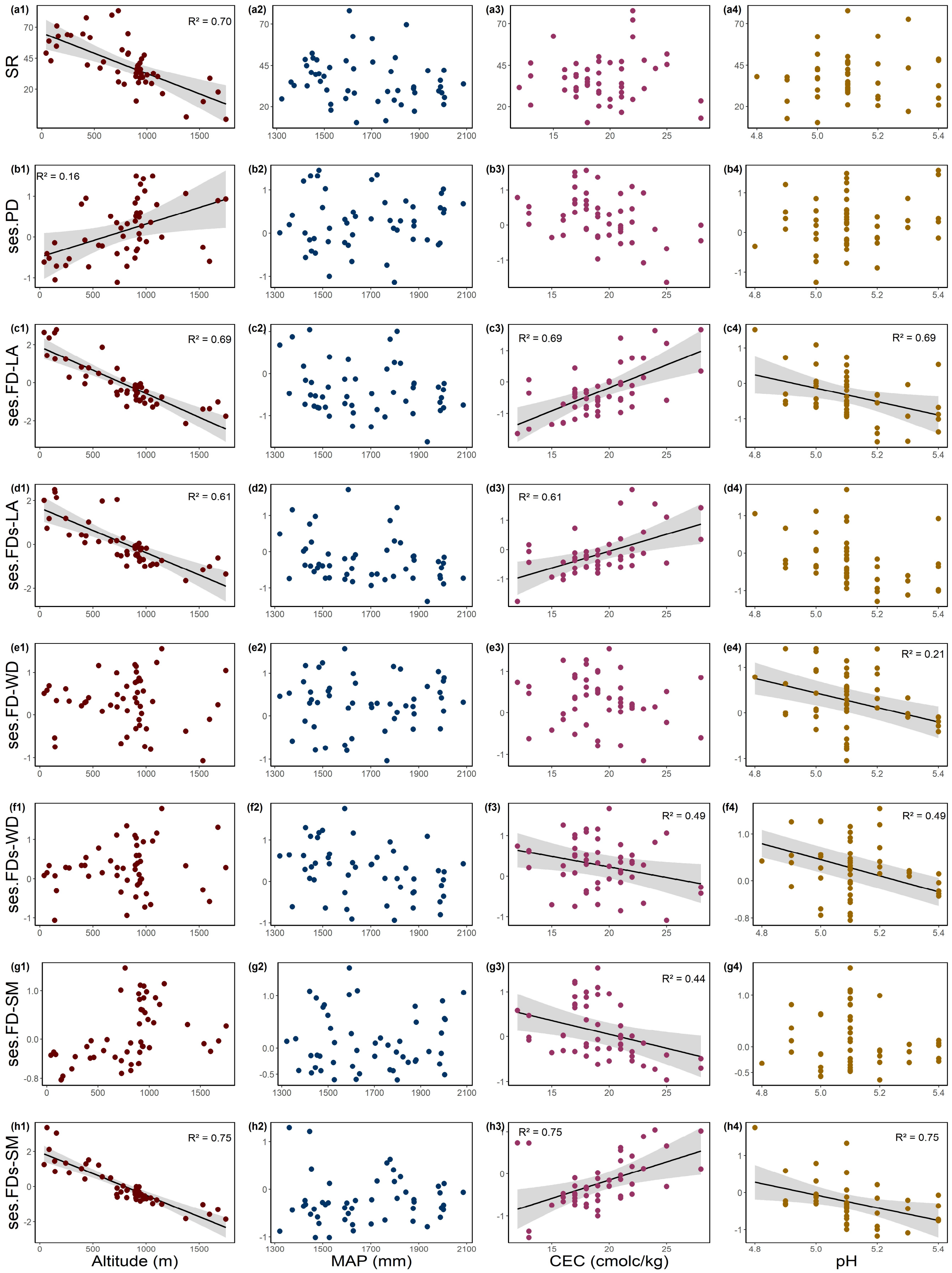

Figure 2: Relationships between species richness (SR), functional (ses.FDp and ses.FDs) and phylogenetic diversity (ses.PD) metrics, and elevation (red points), mean annual precipitation (blue points), cation exchange capacity (pink points) and clay content (yellow points) across 50

tree communities in subtropical Atlantic Forests in Southern Brazil. Significant relationships ($p < 0.05$) have regression line fit.

Our analysis using fourth-corner correlations revealed significant (max-test, $p = 0.01$) composite trait-environmental relationships, specifically between leaf area (LA) and seed mass (SM) with the altitudinal gradient (Table 2). Also, LA was positively correlated with soil pH. We observed a shift in dominance along the altitudinal gradient, with larger-leaved and heavier-seeded species being replaced by those with smaller leaf area and lighter seeds. We observed a shift in leaf size dominance along a soil pH gradient, with larger leaves being dominant in more basic soils and smaller leaves in more acidic soils.

Table 2: Results for trait-environmental relationships using fourth-corner correlation. Environmental variables are altitude, mean annual precipitation (MAP), cation exchange capacity (CEC), and soil pH. The functional traits are leaf area (LA), wood density (WD), and seed mass (SM). Max-test considers the highest p-value across species- and community-level tests. In bold are the significant p-values.

	Altitude		MAP		CEC		pH	
	Correlation	p-max	Correlation	p-max	Correlation	p-max	Correlation	p-max
LA	-0.45	**0.01**	-0.14	0.17	-0.03	0.76	0.30	**0.01**
WD	0.008	0.91	-0.04	0.53	-0.10	0.22	-0.03	0.76
SM	-0.22	**0.04**	-0.01	0.88	-0.07	0.39	0.17	0.07

Discussion

Studies investigating community assemblages across environmental gradients often use species richness, phylogenetic, and functional analyses, but they rarely evaluate these diversity facets together and often do not consider the possible overlap between functional and phylogenetic information. In this study, we demonstrated a variety of patterns of different diversity facets (species richness, phylogenetic and functional diversity), suggesting mixed processes drive tree assemblage patterns along the altitudinal gradient. Leaf area exhibited an underdispersion pattern with increasing altitude, with and without phylogenetic information, suggesting that the altitudinal gradient is a strong filter on recent diversification processes determining clustering patterns of leaf area size in tree species assemblages. Conversely, seed mass exhibited an underdispersion pattern with increasing altitude only when considering the specific functional diversity information. The specific functional diversity information evidence that tree community assembly is driven by environmental conditions in higher altitude areas (e.g., filtering process due to local harsher conditions) and/or by species interactions on the level of trait variability among species (e.g., effect of competitive hierarchy – presence and/or higher abundance of species with narrower trait values irrespective of species relatedness). In these areas, there is lower variability of leaf area and seed mass with a clear predominance of trees with small leaves and lighter seeds. Leaf area, wood density, and seed mass diversity were related to soil gradients, and the influence of phylogenetic information on these relationships varied.

Diversity patterns

Altitude strongly influences tree species richness and phylogenetic diversity, but they exhibit different tendencies. Species richness decreases with altitude due to environmental factors such as lower temperature, lower temperature seasonality, higher cloudiness, frost events, differences in land area and isolation effects at higher altitudes, which constrain the distribution of tree species to higher altitudes. However, contrary to the findings of other studies in the Atlantic Forest (Giehl & Jarenkow, 2012; Bergamin et al., 2020; Mariano et al., 2020), we observed an increase in phylogenetic diversity with altitude, suggesting that niche convergence, rather than niche conservatism, plays a primary role in driving community assembly in the subtropical forests across the altitudinal gradient (Qian & Ricklefs, 2016). Despite most species originating in tropical environments under warmer and wetter conditions, a few species from some clades evolved ecological traits to persist in colder environments at higher altitudes, although adaptations to colder conditions may be difficult (Wiens & Donoghue, 2004; Hawkins et al., 2011). Then, we found a pattern of higher phylogenetic diversity under higher altitudes in the subtropical Atlantic Forest, which is consistent with the hypothesis that a few distantly related clades might have evolved the same ecological traits through niche convergence (Qian, 2017). This pattern emerged when controlling for species richness and comparing observed communities with randomly assembled composition (i.e., ses.PD), and considering the Gymnosperms, which are early diverging lineages known to thrive at higher altitudes. Moreover, the measurement of evolutionary diversity in communities involves different metrics and species pools that can yield different results. In our study, we employed the MPD approach, which calculates the distances across the phylogenetic tree by averaging pairwise distances of all species to quantify evolutionary diversity, and thus the presence of Gymnosperms surely influenced the results. In Bergamin et al. (2020) and Mariano et al. (2020), phylogenetic diversity was based on Angiosperms species only, and an opposite pattern with altitude was observed (i.e., a negative relation). By considering all tree species present in the communities of subtropical Atlantic forests along the altitudinal gradient, we had a broader understanding of evolutionary and biogeographic constraints of local assemblies.

A decrease in functional diversity along the altitudinal gradient was observed for leaf area with and without the phylogenetic information on the traits (FD and FDs) and seed mass, but only when we removed the evolutionary legacy on the trait (FDs). Our findings highlight that shift to lower diversity of leaf area towards higher elevations reflects an adaptation to climatic (i.e., lower temperatures and frost) and non-climatic effects (i.e., land area and isolation effects) structured in both the phylogenetically inherited and recent components. Indeed, it is noteworthy that when the phylogenetic structure is removed from the trait (FDs), the resulting diversity patterns show little overlap of information. This suggests that the specific component, independent of phylogenetic constraints (i.e., deep evolutionary history), plays a crucial role in determining diversity values of leaf area along the altitudinal gradient. It indeed implies that the variation in this trait may be strongly influenced by more recent diversification processes. On the other hand, seed mass diversity across elevation gradients is independent of phylogeny, indicating that species have undergone recent trait differentiation to cope with colder environments (Webb et al., 2002). The clustered patterns observed in the diversity based on phylogeny, leaf area, and seed mass evidence that higher altitude conditions might be limiting and shaping tree community assemblies across altitudinal gradients in the Atlantic Forest, selecting similar species with a narrower range of ecological strategies in highland forests.

In fact, we observed species with similar functional traits adapted to harsh environmental conditions at higher altitude communities (Keddy, 1992), whereas at lower altitudes, in mild environmental conditions, we observed the co-occurrence of phylogenetically close related species with a wider range of ecological strategies. This was characterized by higher functional diversity in terms of leaf area and seed mass. In this context, biotic pressures might impose limiting similarity processes with higher resource partitioning among coexisting species, resulting in higher functional diversity (Chesson, 2000). Additionally, past ecological conditions can help to elucidate the current diversity patterns in the subtropical Atlantic Forest (Carnaval et al., 2014; Duarte et al., 2014; Costa et al., 2018). Lower altitude regions are characterized by long-term climate stability, resulting in higher species accumulation (i.e., higher richness) and functional diversity (Gerhold et al., 2018). In contrast, climatic fluctuations at higher altitudes probably drive lower species accumulation with species distantly related and lower functional diversity due to the neoendemisms and co-occurrence of basal and younger clades (Gerhold et al., 2018; Massante et al., 2019; Bergamin et al., 2020). Thus, species that dispersed to higher altitudes after the last glacial period were those with similar leaf area, which was smaller compared to lowland forests. However, regarding the seed mass trait, it appears to have recently diversified, as the FD pattern was evident only without the influence of deep branches in phylogeny (Diniz-Filho et al., 2011). These results emphasize that community assembly processes may diverge based on distinct functional traits.

Our study revealed significant and opposing relationships between functional diversity and soil variables, and the influence of phylogenetic information on these relationships varied. Specifically, we observed that in nutrient-rich soil with a high CEC, tend to favor tree species with a wider range of leaf area for both historical and recent components. Fertile soil facilitates rapid nutrient acquisition, conserving resources in leaf tissues (Ordoñez et al. 2009; Hodgson et al. 2011; Jager et al. 2015) and promoting different coexistence strategies, ultimately resulting in higher leaf diversity. Contrary to our expectations, greater resource availability in our forest communities favors functional convergence in woody density, and recent adaptative component (FDs) contribute the most to the overall wood diversity pattern. To our knowledge, this result has not been previously reported. Further studies are necessary to better understand the relationships between soil conditions and woody diversity patterns in high-diverse forests in tropical and subtropical regions.

Additionally, the diversity of wood density (FD and FDs) and leaf area (FD) were negatively associated to soil pH. Specifically, under more acidic soils ($pH < 5$), we observed a wider range of wood density and leaf area values, indicating functional divergence. This pattern aligns with the theory that local-scale plant diversity and soil pH are linked to evolutionary history (Pärtel, 2002). In the Brazilian subtropical region, characterized by predominantly shallow and acidic soils, we observed more species adapted to those conditions in terms of leaf and structural traits, leading to higher diversity. This suggests that the unique soil properties in this region have contributed to the evolution of distinct leaf and wood density attributes. Notably, our results also indicated little overlap of information between wood density and phylogeny. This finding further supports the notion that the variation in wood density is influenced not only by deep evolutionary history but also by more recent diversification processes.

Interestingly, seed mass diversity exhibited opposite relationships with soil fertility depending on the component considered, either phylogenetic or specific. In nutrient-poor soil, seed mass diversity tends to be higher due to the inherent phylogenetic component on the trait variation. In sites with limited resources, a broader range of reproductive strategies can coexist, and this relationship is dependent on older lineages that retain ancestral trait states (Diniz-Filho et al., 2011). However, when considering seed mass diversity without phylogenetic information, we observed a wider range of reproductive strategies in nutrient-rich soil, and the same was true for more acidic soils (pH < 5). Unexpectedly, pH was associated with the specific component. This suggests that specific trait variation allows co-occurrence of species with different seed mass, and it is driven by recent diversification. Additionally, reproductive traits may exhibit different trends than foliar and structural traits with soil variables (Jager et al. 2015), and these relationships need to be further explored.

Trait composition patterns

We found significant shifts in leaf area and seed mass (LA, SM) along the altitudinal gradient in community trait composition, and LA was positive correlated with soil pH, which reflect different ecological strategies according to distinct environmental conditions (Poorter et al., 2008; Díaz et al., 2015). LA is associated with a light-capture surface and is essential for photosynthesis and plant thermodynamics (Zhang et al., 2017; Moles, 2018) and often is associated with soil conditions (Ordoñez et al. 2009). Larger leaves can capture more light for photosynthesis but maintain lower thermal stability (more overheating and freezing) (Swenson et al., 2011). Under less stressful conditions, such as the lowland Atlantic forests, where species compete for light without having to maintain thermal stability, species with higher LA predominate in communities. Similarly, more alkaline soils have a predominance of larger leaves, which may be associated with increased nutrient availability (White, 2012). In contrast, species with more conservative strategies (lower LA) predominate under more stressful conditions, such as those observed at higher altitudes. The prevalence of lower LA values in tree communities at higher altitudes in subtropical Atlantic Forest reflects abiotic filters mediating the selection for smaller leaves to maintain thermal stability, since such communities experience lower temperatures and frost events, especially during the winter.

Moreover, we found that in tree communities at higher altitudes, there was a predominance of small seeds compared to those at lower altitudes. Seed mass is considered a trait highly phylogenetically dependent (Moles et al., 2005) since it reflects fundamental aspects of reproductive strategy (Moles et al., 2004). However, our study revealed a recent pattern of adaptation toward lighter seed mass in highland forests, independent of phylogenetic information (Fig. 2e), indicating convergence in SM values toward higher altitude conditions. Past evolution and phylogenetic history determine seed mass (Wang et al., 2021), which affects the ability of lineages to colonize sites or persist under different environmental conditions. Since higher altitudes impose more stressful environments, such as lower temperatures, frost events, and lower resource availability to plants (e.g., lower radiation due to cloudiness), the conditions in highland forests may have selected species with lighter seed mass that produce more seeds in the same reproductive event, promoting higher dispersal opportunities (Cornelissen et al., 2003).

Conclusions

Our study highlights the importance of considering various diversity facets and traits to understand the impact of environmental gradients on community assembly. We found that different facets of tree diversity respond differently to environmental gradients, and the phylogenetic and specific trait component reveal different mechanisms behind forest patterns. In highland forests, a smaller pool (SR) of distantly related species (ses.PD) can establish with similar traits due to adaptations to environmental conditions. Moreover, in the Southern Brazilian

Atlantic Forest, functional trait variation is unrelated to phylogenetic information, at least for leaf area and wood density, as there is limited overlap between the phylogeny and the specific components of these traits. Divergences or convergences in the functional structure were not associated with the pattern of phylogenetic information of traits. These variations may reflect processes that extend beyond evolutionary history and encompass factors within the recent environment. Regarding the diversity of seed mass, the relationships with environmental gradients were primarily influenced by recent trait adaptations, becoming evident only after removing the phylogenetic influence on the trait information. Our findings provide evidence of the complex processes that influence the assembly of long-lived species over evolutionary timescales and across diverse environmental gradients, such as trees in the Southern Brazilian Atlantic Forest region.

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Data availability statement

The data used in this study is available in the supplementary information.

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Supplementary Material

SM Table 1: List of communities and their respective information concerning longitude (Long), latitude (Lat), sampling effort (m^2), altitude, mean annual precipitation (MAP), cation exchange capacity (CEC), soil pH (*10), rarefied species richness (465 individuals considered), phylogenetic (ses.PD) and functional diversity metrics (ses.FD and ses.FDs). Plant functional traits used were fresh leaf area (LA- cm^2), wood density (WD- $g.cm^3$), and seed mass (g). The diversity metrics measured to each community were functional diversity from overlapping components (FD), functional diversity from specific components (FDs), and phylogenetic diversity (PD). To run the analysis, we calculated FDs and PD using 1000 phylogenetic trees and we extracted the mean value of diversity metrics measured in each community to measure the standardized effect size (independent swap). The analyses were conducted in R version 3.6.3 Statistical Environment, using the 'vegan' (Oksanen et al., 2017) and 'FD' (Laliberté et al., 2015) packages.

Long	Lat	Sampling Effort	Elevation	MAP	CEC	pH	Species Richness	ses.PD	ses.FD LA	ses.FDs LA	ses.FD WD	ses.FDs WD	ses.FD SM	ses.FDs SM
-50.15	-29.71	10000	88	1528	21	53	58.51	-0.51	2.41	1.28	0.38	-0.06	-0.48	1.84
-50.17	-29.48	2100	819	1936	25	52	40.24	-0.61	-0.77	-0.68	0.35	0.59	-0.49	-0.22
-50.37	-29.61	10000	824	2004	20	51	58.33	0.37	-0.40	-0.55	0.16	-0.47	-0.62	-0.16
-48.87	-28.44	4000	143	1469	13	51	73.07	-0.63	0.46	1.82	-0.60	0.53	-0.44	0.32
-49.5	-28.71	4000	41	1321	13	51	52.77	-0.24	1.93	1.55	0.65	0.68	0.07	0.70
-49.3	-28.37	10000	157	1445	13	48	78.25	-0.51	2.66	2.08	1.04	0.66	-0.31	2.93
-49.95	-29.16	4000	244	1523	18	51	65.2	-0.65	1.15	1.16	0.63	0.44	-0.53	1.23
-49.55	-28.6	10000	140	1373	17	51	71.51	-0.02	2.55	2.54	-0.43	-0.76	-0.70	1.15
-49.41	-28.62	4000	68	1360	12	51	62	0.05	0.56	0.14	0.75	0.76	0.20	2.73
-49.83	-28.73	10000	728	1606	22	51	97.36	-0.61	1.29	2.48	0.18	-0.08	-0.63	0.07
-50.39	-29.41	10000	913	2086	17	51	47.18	0.88	-0.99	-0.93	0.44	0.49	1.18	-0.37
-50.4	-28.35	4000	988	1511	21	51	27.08	0.95	-0.74	-0.69	-0.80	-0.72	0.30	-0.37
-49.95	-28.44	4000	1148	1591	20	52	16.98	-0.01	-0.80	-0.73	1.36	1.60	1.06	-1.09
-50.22	-28.35	4000	907	1484	18	51	35	1.54	-0.99	-0.48	1.16	1.23	0.89	-0.83
-49.49	-28.01	4000	1045	1600	19	51	24.85	0.35	-0.92	-0.93	-0.80	-0.63	0.35	-0.65
-50.93	-28.42	10000	899	1636	18	50	23.97	0.42	0.00	0.01	1.02	0.53	-0.42	-0.25
-50.12	-29.35	2000	785	1880	20	54	16.78	0.23	-0.42	-0.22	-0.13	-0.53	-0.41	-0.33
-49.48	-28.13	10000	1752	1824	28	49	6.65	0.17	-0.09	-0.11	1.21	-0.05	-0.26	-0.81
-49.55	-28.39	10000	1374	1759	28	49	9.3	0.29	-0.43	-0.36	-0.22	0.05	-0.23	-0.79
-50.23	-27.84	9600	896	1428	16	43	45.31	-0.39	-0.32	-0.06	1.48	1.58	-0.28	-0.49
-49.38	-27.73	4000	821	1621	15	50	64.73	-0.50	-0.96	-0.63	-0.26	-0.55	-0.37	-0.38
-50.75	-28.19	10000	730	1527	19	52	41.07	-1.02	-0.70	-0.45	0.39	0.17	-0.73	-0.87
-51.16	-27.58	10000	765	1592	19	54	65.99	0.24	-0.30	-0.42	-0.60	-0.35	1.45	-0.41
-50.31	-28.12	10000	1102	1499	18	47	45.36	0.80	-0.93	-0.72	1.48	1.47	0.80	-0.79
-50.43	-27.75	10000	940	1464	22.97	48	51.82	0.09	-1.04	-0.78	0.05	0.34	0.07	-0.71
-50.32	-27.85	10000	949	1420	19.37	48	60.75	1.43	-0.15	-0.25	0.92	0.70	1.22	-0.75
-49.63	-28.07	10000	1536	1767	23	38	22.17	-0.49	-0.80	-0.73	-1.10	-0.66	-0.36	-0.76
-50.35	-27.79	10000	935	1426	24	38	57.27	0.22	-0.98	-0.58	0.18	0.59	0.07	-0.51
-49.5	-28.09	2000	1599	1799	23.5	44	21.87	-1.11	-0.44	-0.33	-0.12	-0.86	-0.60	-0.83

-49.61	-28.16	2000	1678	1781	24	44	10.93	0.46	-0.22	-0.03	0.25	1.10	-0.33	-0.64
-50.19	-27.86	10000	975	1449	23.66	48	63.57	1.42	-0.61	-0.48	0.62	1.07	0.98	-0.82
-50.17	-27.85	10000	1062	1478	17	48	48.06	1.49	-1.04	-0.67	0.75	1.51	1.02	-0.91
-50.96	-27.55	9600	724	1627	26.42	45	46.88	0.38	-0.42	0.24	1.06	1.08	1.00	-0.54
-49.98	-29.36	10000	460	1453	16.7	51	78.2	-0.65	0.69	1.03	-0.07	-0.43	-0.56	1.06
-50.24	-29.44	1200	934	2006	17	51	18	0.71	-0.66	-0.49	0.90	0.36	0.69	-0.10
-50.24	-29.38	1200	898	1995	18	51	21.99	0.98	-0.77	-0.59	0.42	-0.03	0.97	-0.43
-50.26	-29.36	1200	920	2003	17	50	14	1.09	-0.58	-0.48	0.99	0.34	0.73	-0.44
-50.18	-29.62	1200	555	1795	21	52	28.9	-0.26	0.45	0.07	0.92	0.37	-0.39	1.29
-50.19	-29.61	1200	392	1704	23	54	57.79	0.74	0.74	0.40	-0.40	-0.44	-0.47	0.90
-50.19	-29.54	1200	588	1810	21	58	34	-0.11	1.45	1.62	-0.47	-0.62	-0.22	0.28
-50.18	-29.55	1200	434	1726	21	58	32.55	0.97	0.12	0.21	-0.28	-0.21	-0.29	1.10
-50.1	-29.17	1200	947	1876	26.64	40	22.91	0.48	-0.82	-0.63	0.13	-0.35	0.71	-0.58
-50.12	-29.16	1200	959	1881	26.95	41	19.98	0.46	-0.71	-0.62	0.06	-0.12	0.66	-0.54
-50.09	-29.15	1200	1003	1877	30.38	38	22	0.00	-0.78	-0.49	-0.32	-0.55	-0.13	-0.70
-50.21	-29.48	1200	919	1989	19	51	28.83	-0.23	-0.78	-0.74	0.51	-0.47	-0.08	-0.08
-50.19	-29.48	1200	909	1982	19	52	22.95	-0.20	-0.58	-0.47	0.84	0.10	-0.32	-0.09
-50.22	-29.48	1200	904	1990	18	49	24.97	0.50	-0.70	-0.61	0.01	-0.39	0.40	-0.30
-50.14	-29.64	2400	667	1846	22.33	57	73.85	0.48	-0.06	0.04	-0.17	-0.24	-0.61	0.45
-50.13	-29.64	2400	277	1624	24.4	50	60.09	-0.55	0.17	0.37	-0.07	-0.16	-0.52	0.63
-50.14	-29.64	2400	424	1702	32.43	43	73.19	-0.22	0.13	0.22	0.04	-0.05	-0.60	0.54

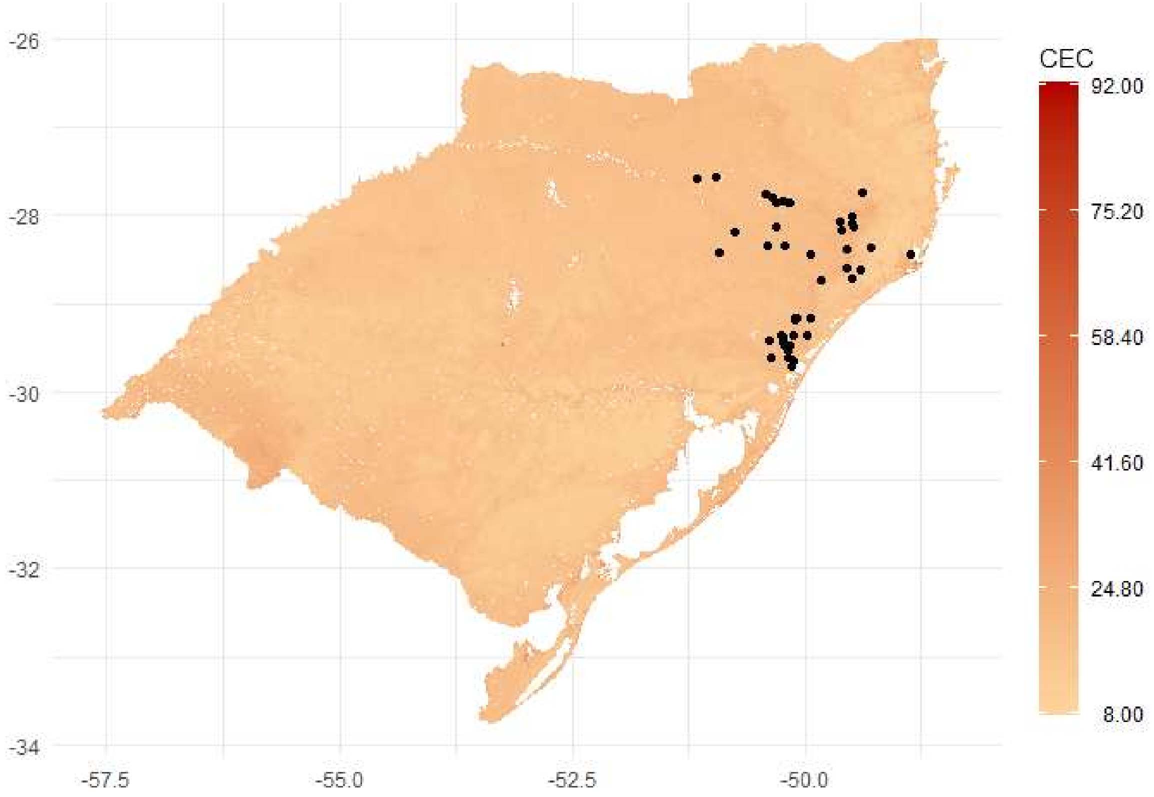
SM Table 2: Correlation between the species functional traits used in this study. Plant functional traits measured were fresh leaf area (LA, cm^2), wood density (WD, $g.cm^3$), and seed mass (g). Correlation values above 0.7 were considered correlated ($p < 0.05$).

	LA	WD	SM
LA	1		
WD	-0.13	1	
SM	-0.04	0.02	1

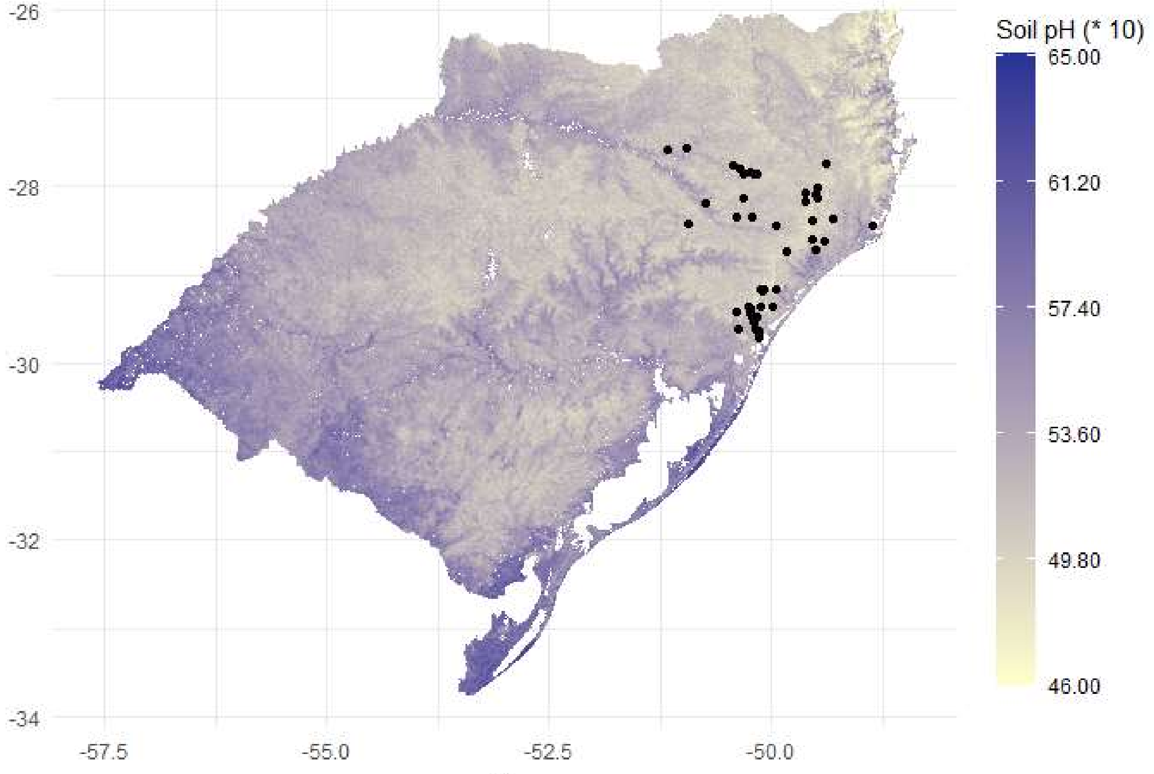
SM Table 3: Correlation between the variables used in this study: altitude, annual mean temperature (MAT), temperature seasonality (TS), minimum temperature of coldest month (MT), mean annual precipitation (MAP), precipitation seasonality (PS), clay content, cation exchange capacity (CEC), soil pH, bulk density, and soil nitrogen (N). Variables with correlation values above 0.7 were considered correlated.

	Altitude	MAT	TS	MT	MAP	PS	Clay	CEC	Ph	Bulk Density	N
Altitude	1										
MAT	-0.98	1									
TS	-0.73	0.77	1								
MT	-0.95	0.91	0.55	1							
MAP	0.38	-0.52	-0.51	-0.26	1						
PS	-0.3	0.4	0.22	0.15	-0.74	1					
Clay Content	0.57	-0.54	-0.44	-0.46	0.23	-0.36	1				
CEC	0.52	-0.58	-0.6	-0.34	0.4	-0.42	0.4	1			
pH	-0.37	0.3	0.18	0.5	0.14	-0.38	-0.25	0.19	1		
Bulk Density	-0.82	0.87	0.68	0.72	-0.64	0.54	-0.49	-0.57	0.16	1	
N	0.63	-0.74	-0.57	-0.57	0.88	-0.67	0.34	0.46	-0.06	-0.77	1

(a)


-26
-28
-30
-32
-34
-57.5
-55.0
-52.5
-50.0
CEC
92.00
75.20
58.40
41.60
24.80
8.00

(b)


-26
-28
-30
-32
-34
-57.5
-55.0
-52.5
-50.0
Soil pH (* 10)
65.00
61.20
57.40
53.60
49.80
46.00

SM Figure 1: Location of the 50 tree communities' surveys along the subtropical Brazilian Atlantic Forest showing the distribution patterns of cation exchange capacity (a) and soil pH (b) in the background.

SM Table 4: Seed mass values documented (SM- raw data) for the species from our study area, and SM values using two methods of filling missing data: missForest algorithm and average trait value of the species with SM values documented. Our analysis showed the same patterns using SM values from both methods.

Species	SM (raw data)	SM (missForest algorithm)	SM (average trait value)
Abarema langsdorffii	NA	0.304609179	0.260589
Acca sellowiana	0.004629496	0.004629496	0.004629496
Actinostemon concolor	0.38	0.38	0.38
Aegiphila brachiata	NA	0.121312611	0.260589
Aegiphila integrifolia	0.0263	0.0263	0.0263
Aegiphila sellowiana	NA	0.135411096	0.260589
Aiouea acarodomatifera	NA	0.602195444	0.260589
Aiouea pseudoglaziovii	0.41369	0.41369	0.41369
Aiouea saligna	NA	0.654089808	0.260589
Albizia edwallii	NA	0.286558833	0.260589
Albizia niopoides	NA	0.255948389	0.260589
Alchornea glandulosa	0.05	0.05	0.05
Alchornea triplinervia	0.021111111	0.021111111	0.021111111
Allophylus edulis	0.047277778	0.047277778	0.047277778
Allophylus guaraniticus	NA	0.123760766	0.260589
Allophylus petiolulatus	0.07	0.07	0.07
Alseis floribunda	0.0003	3.00E-04	0.0003
Alsophila setosa	NA	NA	0.260589
Amaioua guianensis	0.008	0.008	0.008
Aniba firmula	2.17	2.17	2.17
Annona cacans	0.238948626	0.238948626	0.238948626
Annona neosalicifolia	0.43405	0.43405	0.43405
Annona neosericea	0.05	0.05	0.05
Annona rugulosa	0.46255	0.46255	0.46255
Annona sylvatica	0.2515	0.2515	0.2515
Araucaria angustifolia	5.487804878	5.487804878	5.487804878
Aspidosperma australe	0.2	0.2	0.2
Aspidosperma olivaceum	0.2	0.2	0.2
Aspidosperma parvifolium	0.2	0.2	0.2
Aspidosperma tomentosum	0.47	0.47	0.47
Azara uruguayensis	NA	0.1371198	0.260589
Baccharis oblongifolia	NA	0.127708002	0.260589
Baccharis semiserrata	NA	0.21348422	0.260589
Banara parviflora	NA	0.10168815	0.260589

Banara tomentosa	0.00083	0.00083	0.00083
Bathysa australis	0.00033264	0.00033264	0.00033264
Bauhinia forficata	0.08	0.08	0.08
Blepharocalyx salicifolius	0.015946297	0.015946297	0.015946297
Boehmeria caudata	0.0007	7.00E-04	0.0007
Brosimum glaziovii	0.263157895	0.263157895	0.263157895
Brosimum lactescens	NA	0.196686333	0.260589
Buchenavia kleinii	NA	0.397781899	0.260589
Butia eriospatha	NA	1.722619736	0.260589
Byrsonima ligustrifolia	0.959230769	0.959230769	0.959230769
Byrsonima niedenzuiana	0.1789	0.1789	0.1789
Cabralea canjerana	0.4992	0.4992	0.4992
Calyptranthes concinna	0.03795	0.03795	0.03795
Calyptranthes grandifolia	0.095238095	0.095238095	0.095238095
Calyptranthes lucida	0.0728	0.0728	0.0728
Campomanesia guaviroba	0.1351	0.1351	0.1351
Campomanesia guazumifolia	0.037727273	0.037727273	0.037727273
Campomanesia rhombea	0.00945	0.00945	0.00945
Campomanesia xanthocarpa	0.053431818	0.053431818	0.053431818
Casearia decandra	0.0162	0.0162	0.0162
Casearia obliqua	0.38	0.38	0.38
Casearia sylvestris	0.011904762	0.011904762	0.011904762
Cecropia glaziovii	0.000021739	2.17E-05	0.000021739
Cedrela fissilis	0.027964988	0.027964988	0.027964988
Celtis iguanaea	0.134860715	0.134860715	0.134860715
Cestrum bracteatum	NA	0.073987075	0.260589
Cestrum intermedium	0.0115	0.0115	0.0115
Chionanthus filiformis	NA	0.143840568	0.260589
Chionanthus micranthus	NA	0.13821708	0.260589
Chionanthus trichotomus	NA	0.120840551	0.260589
Chrysophyllum gonocarpum	0.2513	0.2513	0.2513
Chrysophyllum inornatum	0.19	0.19	0.19
Chrysophyllum marginatum	0.181818182	0.181818182	0.181818182
Chrysophyllum viride	0.524666667	0.524666667	0.524666667
Cinnamodendron dinisii	0.3571	0.3571	0.3571
Cinnamomum amoenum	NA	0.434838428	0.260589
Cinnamomum glaziovii	0.161290323	0.161290323	0.161290323
Cinnamomum pseudoglaziovii	NA	0.67981567	0.260589
Citharexylum montevidense	0.0526	0.0526	0.0526
Citharexylum myrianthum	0.42185	0.42185	0.42185
Citharexylum solanaceum	0.484518889	0.484518889	0.484518889
Citronella gongonha	0.2057	0.2057	0.2057
Citronella paniculata	0.666666667	0.666666667	0.666666667
Clethra scabra	0.00025	0.00025	0.00025
Clusia criuva	0.241	0.241	0.241
Copaifera trapezifolia	1.626	1.626	1.626
Cordia americana	0.17375	0.17375	0.17375
Cordia ecalyculata	0.185185185	0.185185185	0.185185185

Cordia silvestris	0.065232692	0.065232692	0.065232692
Cordia trichotoma	0.028409091	0.028409091	0.028409091
Cordiera concolor	NA	0.156705763	0.260589
Cordyline spectabilis	NA	0.442474687	0.260589
Coussapoa microcarpa	0.0006	6.00E-04	0.0006
Coussarea contracta	NA	0.090457224	0.260589
Coutarea hexandra	0.0003	3.00E-04	0.0003
Crinodendron brasiliense	NA	0.280474124	0.260589
Croton macrobothrys	NA	0.120422732	0.260589
Cryptocarya aschersoniana	1.337994445	1.337994445	1.337994445
Cryptocarya mandioccana	NA	0.893568208	0.260589
Cryptocarya moschata	NA	0.791599079	0.260589
Cupania vernalis	0.1573	0.1573	0.1573
Cyathea atrovirens	NA	NA	0.260589
Cyathea corcovadensis	NA	NA	0.260589
Cyathea delgadii	NA	NA	0.260589
Cyathea phalerata	NA	NA	0.260589
Cybistax antisyphilitica	0.036	0.036	0.036
Dalbergia frutescens	NA	0.261616345	0.260589
Daphnopsis fasciculata	0.03805	0.03805	0.03805
Dasyphyllum brasiliense	0.0005	5.00E-04	0.0005
Dasyphyllum spinescens	0.0005	5.00E-04	0.0005
Dicksonia sellowiana	NA	NA	0.260589
Diospyros inconstans	0.249865217	0.249865217	0.249865217
Drimys angustifolia	0.003897297	0.003897297	0.003897297
Drimys brasiliensis	0.0031	0.0031	0.0031
Duguetia lanceolata	0.625	0.625	0.625
Duranta vestita	0.0198	0.0198	0.0198
Endlicheria paniculata	0.67275	0.67275	0.67275
Enterolobium contortisiliquum	0.1802	0.1802	0.1802
Erythrina falcata	0.6452	0.6452	0.6452
Erythroxylum cuneifolium	0.01445	0.01445	0.01445
Erythroxylum deciduum	0.05	0.05	0.05
Escallonia bifida	0.0005	5.00E-04	0.0005
Esenbeckia grandiflora	NA	0.09359734	0.260589
Eugenia bacopari	NA	0.238868266	0.260589
Eugenia beaurepairiana	NA	0.579949527	0.260589
Eugenia brasiliensis	NA	0.371408094	0.260589
Eugenia brevistyla	NA	0.379321401	0.260589
Eugenia burkartiana	0.045	0.045	0.045
Eugenia chlorophylla	NA	0.589862179	0.260589
Eugenia handroana	NA	0.424214691	0.260589
Eugenia handroi	0.4	0.4	0.4
Eugenia involucrata	0.155161539	0.155161539	0.155161539
Eugenia multicostata	0.4574	0.4574	0.4574
Eugenia neoverrucosa	NA	0.280831739	0.260589
Eugenia oeidocarpa	0.6615	0.6615	0.6615
Eugenia paracatuana	NA	0.763702839	0.260589

Eugenia platysema	NA	0.838551332	0.260589
Eugenia pluriflora	NA	0.214900723	0.260589
Eugenia pruinosa	5.2379	5.2379	5.2379
Eugenia pyriformis	0.8547	0.8547	0.8547
Eugenia ramboi	0.1923	0.1923	0.1923
Eugenia rostrifolia	0.13	0.13	0.13
Eugenia stigmatosa	NA	0.496421102	0.260589
Eugenia subterminalis	0.133448276	0.133448276	0.133448276
Eugenia ternatifolia	NA	0.572260051	0.260589
Eugenia uniflora	NA	0.406849169	0.260589
Eugenia uruguayensis	0.28063125	0.28063125	0.28063125
Eugenia verticillata	NA	0.283714021	0.260589
Euterpe edulis	0.6504	0.6504	0.6504
Faramea montevidensis	0.05885	0.05885	0.05885
Ficus adhatodifolia	0.00121935	0.00121935	0.00121935
Ficus cestrifolia	0.0006	6.00E-04	0.0006
Ficus eximia	NA	0.085034664	0.260589
Ficus luschnathiana	0.0002	2.00E-04	0.0002
Garcinia gardneriana	2.9	2.9	2.9
Gochnatia polymorpha	0.005	0.005	0.005
Guapira opposita	0.0725	0.0725	0.0725
Guarea macrophylla	0.187966667	0.187966667	0.187966667
Guatteria australis	NA	0.43262741	0.260589
Guazuma ulmifolia	0.0063	0.0063	0.0063
Gymnanthes klotzschiana	NA	0.276264695	0.260589
Handroanthus albus	0.0117	0.0117	0.0117
Handroanthus chrysotrichus	0.0107	0.0107	0.0107
Handroanthus pulcherrimus	NA	0.063061246	0.260589
Handroanthus umbellatus	0.0186	0.0186	0.0186
Heisteria silvianii	0.5128	0.5128	0.5128
Helietta apiculata	0.0177	0.0177	0.0177
Hennecartia omphalandra	0.494	0.494	0.494
Hieronyma alchorneoides	0.0208	0.0208	0.0208
Hirtella hebeclada	0.51282051	0.51282051	0.51282051
Ilex brevicuspis	0.0020125	0.0020125	0.0020125
Ilex dumosa	0.00313529	0.00313529	0.00313529
Ilex microdonta	0.002608163	0.002608163	0.002608163
Ilex paraguariensis	0.007657143	0.007657143	0.007657143
Ilex taubertiana	NA	0.058494405	0.260589
Ilex theezans	0.0019	0.0019	0.0019
Inga	0.24	0.24	0.24
Inga lentiscifolia	NA	0.265999057	0.260589
Inga marginata	0.250875	0.250875	0.250875
Inga sessilis	NA	0.252234264	0.260589
Inga striata	0.251669912	0.251669912	0.251669912
Inga virescens	0.2382	0.2382	0.2382
Jacaranda micrantha	0.008	0.008	0.008
Jacaranda puberula	0.00496902	0.00496902	0.00496902

Jacaratia spinosa	0.0081	0.0081	0.0081
Kaunia rufescens	NA	0.148163098	0.260589
Lamanonia ternata	0.0007	7.00E-04	0.0007
Laplacea acutifolia	0.0034	0.0034	0.0034
Leandra dasytricha	NA	0.176779761	0.260589
Leandra salicina	NA	0.164352117	0.260589
Licaria armeniaca	NA	1.213348556	0.260589
Lithraea brasiliensis	0.0392	0.0392	0.0392
Lonchocarpus campestris	NA	0.209693544	0.260589
Lonchocarpus cultratus	0.1639	0.1639	0.1639
Lonchocarpus grazielae	NA	0.213917304	0.260589
Luehea divaricata	0.002733333	0.002733333	0.002733333
Machaerium paraguariense	0.3517	0.3517	0.3517
Machaerium stipitatum	0.0915	0.0915	0.0915
Magnolia ovata	0.19635	0.19635	0.19635
Margaritaria nobilis	NA	0.438123976	0.260589
Marlierea excoriata	NA	0.275046247	0.260589
Marlierea sylvatica	NA	0.304175418	0.260589
Matayba elaeagnoides	0.145949333	0.145949333	0.145949333
Matayba intermedia	1.20714286	1.20714286	1.20714286
Maytenus	0.02	0.02	0.02
Maytenus aquifolia	0.1505	0.1505	0.1505
Maytenus boaria	NA	0.084611826	0.260589
Maytenus dasyclada	NA	0.108602329	0.260589
Maytenus evonymoides	0.023302778	0.023302778	0.023302778
Maytenus ilicifolia	0.0308	0.0308	0.0308
Maytenus schumanniana	NA	0.106028305	0.260589
Meliosma sellowii	0.8315	0.8315	0.8315
Meliosma sinuata	NA	0.444768702	0.260589
Miconia cabussu	0.0013	0.0013	0.0013
Miconia cinerascens	0.001843262	0.001843262	0.001843262
Miconia cinnamomifolia	0.0004	4.00E-04	0.0004
Miconia cubatanensis	NA	0.111472401	0.260589
Miconia eichleri	NA	0.129203389	0.260589
Miconia latecrenata	NA	0.097769032	0.260589
Miconia pusilliflora	NA	0.07947317	0.260589
Mimosa bimucronata	0.0112	0.0112	0.0112
Mimosa scabrella	0.0182	0.0182	0.0182
Mollinedia	0.06	0.06	0.06
Mollinedia fruticulosa	0.05	0.05	0.05
Mollinedia schottiana	0.084	0.084	0.084
Mollinedia triflora	NA	0.201367986	0.260589
Monteverdia floribunda	NA	0.107203638	0.260589
Moquiniastrum polymorphum	0.0003625	0.0003625	0.0003625
Muellera campestris	0.08	0.08	0.08
Myrceugenia alpigena	NA	0.35124965	0.260589
Myrceugenia euosma	NA	0.303997477	0.260589
Myrceugenia foveolata	0.011195833	0.011195833	0.011195833

Myrceugenia glaucescens	NA	0.312978748	0.260589
Myrceugenia mesomischa	0.012247368	0.012247368	0.012247368
Myrceugenia miersiana	0.01269	0.01269	0.01269
Myrceugenia myrcioides	0.029884906	0.029884906	0.029884906
Myrceugenia ovalifolia	NA	0.193662797	0.260589
Myrceugenia ovata	NA	0.232503918	0.260589
Myrceugenia oxysepala	NA	0.137822858	0.260589
Myrceugenia regnelliana	NA	0.075336356	0.260589
Myrcia	0.029	0.029	0.029
Myrcia aethusa	NA	0.128501638	0.260589
Myrcia brasilensis	NA	0.074655218	0.260589
Myrcia catharinensis	NA	0.068024289	0.260589
Myrcia dichrophylla	NA	0.158213312	0.260589
Myrcia glabra	NA	0.078159182	0.260589
Myrcia guianensis	0.02	0.02	0.02
Myrcia hartwegiana	NA	0.152022986	0.260589
Myrcia hatschbachii	NA	0.161287779	0.260589
Myrcia lajeana	NA	0.079275103	0.260589
Myrcia oblongata	NA	0.173179829	0.260589
Myrcia oligantha	0.0382625	0.0382625	0.0382625
Myrcia palustris	0.0179	0.0179	0.0179
Myrcia pubipetala	NA	0.138655254	0.260589
Myrcia retorta	NA	0.186604186	0.260589
Myrcia richardiana	NA	0.058743406	0.260589
Myrcia selloi	0.0165	0.0165	0.0165
Myrcia spectabilis	0.1046	0.1046	0.1046
Myrcia splendens	0.140410715	0.140410715	0.140410715
Myrcia tijucensis	0.38	0.38	0.38
Myrcia undulata	NA	0.08544927	0.260589
Myrcianthes gigantea	NA	0.277183364	0.260589
Myrcianthes pungens	0.31315	0.31315	0.31315
Myrciaria cuspidata	NA	0.152491687	0.260589
Myrciaria delicatula	0.047654545	0.047654545	0.047654545
Myrciaria floribunda	0.1415	0.1415	0.1415
Myrciaria plinioides	0.3096	0.3096	0.3096
Myrocarpus frondosus	0.0524	0.0524	0.0524
Myrrhinium atropurpureum	0.009055661	0.009055661	0.009055661
Myrsine	0.01	0.01	0.01
Myrsine coriacea	0.011963044	0.011963044	0.011963044
Myrsine gardneriana	NA	0.050231384	0.260589
Myrsine guianensis	0.026	0.026	0.026
Myrsine hermogenesii	NA	0.056769457	0.260589
Myrsine loefgrenii	NA	0.047574086	0.260589
Myrsine lorentziana	0.014933333	0.014933333	0.014933333
Myrsine umbellata	0.300425	0.300425	0.300425
Nectandra grandiflora	1.11	1.11	1.11
Nectandra lanceolata	0.52134	0.52134	0.52134
Nectandra megapotamica	0.40816327	0.40816327	0.40816327

Nectandra membranacea	0.1845	0.1845	0.1845
Nectandra oppositifolia	0.7692	0.7692	0.7692
Nectandra puberula	NA	0.564747397	0.260589
Neomitranthes gemballae	NA	0.107004206	0.260589
Ocotea bicolor	0.06903333	0.06903333	0.06903333
Ocotea catharinensis	0.83333333	0.83333333	0.83333333
Ocotea corymbosa	0.2597	0.2597	0.2597
Ocotea diospyrifolia	0.5556	0.5556	0.5556
Ocotea elegans	0.35545	0.35545	0.35545
Ocotea indecora	0.19	0.19	0.19
Ocotea laxa	NA	0.377036063	0.260589
Ocotea mandioccana	NA	0.445043264	0.260589
Ocotea nectandrifolia	NA	0.467436792	0.260589
Ocotea odorifera	0.3003	0.3003	0.3003
Ocotea porosa	0.54466	0.54466	0.54466
Ocotea puberula	0.177755357	0.177755357	0.177755357
Ocotea pulchella	0.0863	0.0863	0.0863
Ocotea pulchra	NA	0.466467197	0.260589
Ocotea riedeliana	NA	0.453976378	0.260589
Ocotea silvestris	0.235	0.235	0.235
Oreopanax fulvus	0.0281	0.0281	0.0281
Ormosia arborea	1.25	1.25	1.25
Ouratea parviflora	NA	0.477204815	0.260589
Pachystroma longifolium	0.7692	0.7692	0.7692
Parapiptadenia rigida	0.0299	0.0299	0.0299
Pausandra morisiana	NA	0.170298549	0.260589
Pera glabrata	0.0196	0.0196	0.0196
Persea major	NA	0.723334511	0.260589
Persea willdenovii	NA	0.698155502	0.260589
Phytolacca dioica	0.0056	0.0056	0.0056
Picramnia parvifolia	NA	0.365373899	0.260589
Pilocarpus pennatifolius	0.044930953	0.044930953	0.044930953
Pimenta pseudocaryophyllus	0.11	0.11	0.11
Piptadenia gonoacantha	0.0625	0.0625	0.0625
Piptocarpha angustifolia	0.0082333	0.0082333	0.0082333
Piptocarpha axillaris	0.00076759	0.00076759	0.00076759
Pisonia ambigua	0.1471	0.1471	0.1471
Pisonia zapallo	0.1471	0.1471	0.1471
Plinia peruviana	0.182857143	0.182857143	0.182857143
Plinia pseudodichasiantha	NA	0.697232181	0.260589
Podocarpus lambertii	0.01425	0.01425	0.01425
Posoqueria latifolia	0.432366667	0.432366667	0.432366667
Pouteria venosa	NA	0.216942395	0.260589
Protium kleinii	0.38	0.38	0.38
Prunus myrtifolia	0.08325	0.08325	0.08325
Prunus subcoriacea	NA	0.208816238	0.260589
Pseudobombax grandiflorum	0.117	0.117	0.117
Psidium cattleianum	0.0137	0.0137	0.0137

Psidium longipetiolatum	NA	0.614021682	0.260589
Psidium myrtoides	1.3699	1.3699	1.3699
Psychotria carthagenensis	0.007183333	0.007183333	0.007183333
Psychotria suterella	0.02504	0.02504	0.02504
Psychotria vellosiana	0.38	0.38	0.38
Quillaja brasiliensis	0.0038	0.0038	0.0038
Randia ferox	0.2	0.2	0.2
Recordia reitzii	NA	0.104629915	0.260589
Rhamnus sphaerosperma	0.018155556	0.018155556	0.018155556
Rollinia rugulosa	NA	0.414572913	0.260589
Roupala brasiliensis	0.02	0.02	0.02
Roupala montana	0.02	0.02	0.02
Roupala rhombifolia	NA	0.182530339	0.260589
Rudgea jasminoides	NA	0.237860862	0.260589
Ruprechtia laxiflora	0.05	0.05	0.05
Sapium glandulosum	0.037946154	0.037946154	0.037946154
Schefflera angustissima	0.0088	0.0088	0.0088
Schefflera calva	0.0364	0.0364	0.0364
Schinus	0.01	0.01	0.01
Schinus lentiscifolius	NA	0.115105419	0.260589
Schinus terebinthifolius	0.0274	0.0274	0.0274
Schizolobium parahyba	NA	0.250692676	0.260589
Scutia buxifolia	0.13	0.13	0.13
Sebastiania brasiliensis	0.021	0.021	0.021
Sebastiania commersoniana	0.0043	0.0043	0.0043
Senna multijuga	0.0128	0.0128	0.0128
Siphoneugena reitzii	NA	0.27594053	0.260589
Sloanea guianensis	0.2	0.2	0.2
Sloanea hirsuta	NA	0.218790289	0.260589
Sloanea lasiocoma	NA	0.224373453	0.260589
Sloanea monosperma	NA	0.241040364	0.260589
Solanum	0.003	0.003	0.003
Solanum johannae	0.001571557	0.001571557	0.001571557
Solanum mauritianum	NA	0.063251782	0.260589
Solanum pabstii	NA	0.054120813	0.260589
Solanum pseudoquina	0.0035	0.0035	0.0035
Solanum sanctaecatharinae	0.005070136	0.005070136	0.005070136
Solanum variabile	NA	0.04347113	0.260589
Sorocea bonplandii	0.159525	0.159525	0.159525
Strychnos brasiliensis	0.198603448	0.198603448	0.198603448
Styrax acuminatus	NA	0.136948005	0.260589
Styrax leprosus	0.125	0.125	0.125
Syagrus romanzoffiana	3.52	3.52	3.52
Symphyopappus itatiayensis	NA	0.154222822	0.260589
Symplocos tenuifolia	NA	0.152743969	0.260589
Symplocos tetrandra	NA	0.206625508	0.260589
Symplocos uniflora	0.109728571	0.109728571	0.109728571
Tabernaemontana catharinensis	0.0553	0.0553	0.0553

Tetrorchidium rubrivenium	0.0149	0.0149	0.0149
Tibouchina sellowiana	2.77778E-05	2.78E-05	2.77778E-05
Trema micrantha	NA	0.137399597	0.260589
Trichilia claussenii	0.4251	0.4251	0.4251
Trichilia elegans	NA	0.23525464	0.260589
Trichilia lepidota	0.3809	0.3809	0.3809
Trichilia pallens	0.147058824	0.147058824	0.147058824
Urera baccifera	0.0007	7.00E-04	0.0007
Vernonanthura discolor	0.00051642	0.00051642	0.00051642
Vernonanthura puberula	NA	0.116226637	0.260589
Virola bicuhyba	1.2957	1.2957	1.2957
Vitex megapotamica	0.2602	0.2602	0.2602
Weinmannia humilis	NA	0.220257727	0.260589
Weinmannia paulliniifolia	0.008	0.008	0.008
Xylopia brasiliensis	0.073	0.073	0.073
Xylosma ciliatifolia	NA	0.117419905	0.260589
Xylosma pseudosalzmannii	0.008310938	0.008310938	0.008310938
Xylosma tweediana	NA	0.108137571	0.260589
Zanthoxylum astrigerum	NA	0.103736251	0.260589
Zanthoxylum caribaeum	NA	0.104460086	0.260589
Zanthoxylum fagara	0.01622	0.01622	0.01622
Zanthoxylum kleinii	NA	0.117163439	0.260589
Zanthoxylum rhoifolium	0.0066	0.0066	0.0066
Zanthoxylum riedelianum	NA	0.09269589	0.260589
Zollernia ilicifolia	0.8333	0.8333	0.8333

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Conclusão geral

Concluding remarks

No esforço de compreender os intricados padrões de desempenho, coexistência e distribuição das árvores da Mata Atlântica, esta tese foi elaborada, explorando diferentes escalas: desde a perspectiva individual (capítulo 1) até as interações em nível local (capítulo 2) e as influências regionais (capítulos 3 e 4). Nesse sentido, esta tese representa uma tentativa de aliar conhecimentos prévios adquiridos ao longo da minha formação acadêmica a novos conhecimentos e ideias que adquiri durante esses anos de doutorado, sempre tendo em visto o entrelace entre assembleia de comunidades, florestas e biodiversidade.

Após vários anos de trabalho de campo nas parcelas de longa duração na região subtropical da Mata Atlântica, iniciamos a avaliação do desempenho das árvores por meio de suas taxas de crescimento e começamos a refletir sobre uma possível relação entre esse desempenho e a arquitetura das árvores, em particular, a estrutura de suas copas, bem como o impacto que as árvores vizinhas podem exercer sobre o crescimento de uma determinada árvore. Iniciamos a coleta de dados referentes ao tamanho de copa para todos os indivíduos nas parcelas permanentes mantidas pelo laboratório, buscando compreender como essa informação aparentemente simples pode ser utilizada como preditor do crescimento das árvores. Além disso, coletamos dados de todos os indivíduos arbóreos em um raio de 5 metros ao redor de árvores focos que aleatoriamente selecionamos.

Nosso estudo indica que a área da copa, representada como uma elipse e integrada como a massa fotossintética total da árvore em nível individual, influencia positivamente as taxas de crescimento anual das árvores. Notavelmente, essa influência depende muito menos da massa foliar por área do que da área da copa em si. Árvores com copas maiores e com mais massa foliar por área voltada para a interceptação da luz, mas ao mesmo tempo mantendo folhas por mais tempo, tendem a ter taxas de crescimento individual mais rápidas. Em conjunto, essas características estão intimamente relacionadas à interceptação de luz no dossel, mas também à manutenção eficiente de suas folhas a longo prazo. Além disso, a formação de copas estruturalmente compartimentadas pelas árvores também pode aumentar a interceptação de luz em nível de comunidade, aumentando assim a produtividade da comunidade de árvores. Desta maneira, identificamos a importância da incorporação de medidas da copa em estudos e trabalhos de campo que aprimoram nossa compreensão da dinâmica de crescimento das árvores e do desempenho dos ecossistemas.

Para investigar a influência das árvores vizinhas sobre o crescimento de uma árvore específica (ou foco), examinamos vários fatores, incluindo medidas de interações bióticas, como diferenças hierárquicas e absolutas nos atributos funcionais das árvores foco e seus vizinhos, índice de aglomeração do entorno, estrutura funcional da comunidade e distância filogenética. Nossos resultados indicaram que as distâncias funcionais e filogenéticas, bem como a estrutura funcional da comunidade, contribuem para os padrões de crescimento das árvores focais, mas fazem isso de maneira diferente para as árvores altas e as do sub-bosque. Especificamente, para essas árvores altas e as do sub-bosque, os resultados específicos variaram dependendo dos atributos considerados, enfraquecendo assim os efeitos gerais dos vizinhos em todas as espécies focais consideradas. No geral, nossos resultados indicaram que o crescimento relativo e os resultados competitivos entre as árvores subtropicais são influenciados por múltiplos fatores, como diferenças no custo de construção das folhas, condutância hídrica, tamanho das árvores e a distância filogenética entre a árvore focal e suas árvores vizinhas. Concluímos que as interações entre as espécies em termos de suas diferenças ecológicas podem variar de acordo com sua posição competitiva dentro de uma comunidade, refletida pelas habilidades de captura de luz em nosso sistema de estudo.

No sul do Brasil, florestas subtropicais formam mosaicos com campos naturais. Os mosaicos de campos e florestas geralmente representam habitats contrastantes para plantas lenhosas. Isso significa que a densidade e a composição de espécies lenhosas podem variar entre as florestas e as áreas adjacentes de campo, já que muitas espécies lenhosas desenvolveram estratégias adaptativas para sobreviver em um ou em ambos os habitats. Essas estratégias adaptativas estão ligadas à história evolutiva das espécies e às características, que também podem variar entre as espécies e em nível individual. Portanto, a integração de informações funcionais em diferentes escalas ecológicas pode oferecer *insights* valiosos sobre como as espécies lenhosas se adaptam a esses habitats contrastantes. Com o objetivo de investigar como as espécies lenhosas se distribuem em ambientes contrastantes, aqui entendido como gradiente espacial, exploramos a influência da variabilidade intraespecífica e interespecífica de atributos foliares, e mudanças nas diversidades funcionais e filogenética.

Neste estudo, observamos que as comunidades de plantas lenhosas são filogeneticamente semelhantes entre os habitats de campo e floresta. No entanto, ao considerar as mudanças na diversidade funcional e na composição funcional na transição entre floresta e campo, nossos resultados indicam que a floresta contrasta com o campo em termos da montagem das comunidades de plantas lenhosas. Nas florestas, as comunidades tinham uma menor diversidade na área foliar, com predominância de folhas grandes. Por outro lado, havia uma maior diversidade em características estruturais das folhas, que predominantemente exibiam uma estratégia de aquisição de recursos. Esse padrão foi corroborado pelos resultados das comparações entre espécies com diferentes preferências de habitat. As espécies especialistas em florestas apresentavam características mais relacionadas à aquisição de recursos, enquanto as espécies especialistas em campos tinham valores de características mais associados à conservação de recursos. No entanto, as espécies generalistas exibiram valores de características que se alinhavam com o habitat onde foram amostradas, com variabilidade intraespecífica suficiente para se adaptar tanto a habitats de floresta quanto de campo. As mudanças consistentes nas características das folhas intraespecífica e interespecífica nas transições entre floresta e campo, sem mudanças na diversidade filogenética (ou seja, sem substituição de linhagens), reforçam o papel da plasticidade fenotípica na estrutura das comunidades e populações de plantas lenhosas.

No âmbito da investigação da distribuição de espécies arbóreas em gradientes ambientais, conduzimos uma análise abrangente das mudanças em diversas facetas da diversidade ao longo de gradientes de altitude, precipitação e condições edáficas na região subtropical da Mata Atlântica. Uma característica distintiva deste estudo reside na nossa consideração da informação específica dos atributos funcionais. Isso significa que retiramos o legado evolutivo dos atributos funcionais ao calcular a diversidade funcional, o que nos permitiu avaliar a adaptação evolutiva recente. Além disso, integramos a informação filogenética aos atributos funcionais para obter uma visão mais completa.

Estudos que investigam a montagem de comunidades ao longo de gradientes ambientais frequentemente utilizam análises de riqueza de espécies, filogenéticas e funcionais, mas raramente avaliam essas facetas da diversidade juntas e muitas vezes não consideram a sobreposição entre informações funcionais e filogenéticas. Neste estudo, demonstramos padrões em diferentes aspectos da diversidade (riqueza de espécies, diversidade filogenética e funcional), sugerindo que processos mistos impulsionam os padrões de montagem de comunidades arbóreas ao longo do gradiente altitudinal, e o componente filogenético e de características específicas revelam diferentes mecanismos por trás dos padrões florestais. Em florestas de altitude, um conjunto menor de espécies pode se estabelecer com características similares devido a adaptações às condições ambientais. Além disso, na Mata Atlântica do Sul do Brasil, a variação de características não está relacionada a informações filogenéticas, pelo menos para a área foliar e densidade da madeira, pois há pouca sobreposição entre a filogenia e os componentes específicos dessas características. Divergências ou convergências na estrutura funcional não estavam associadas ao padrão de informações filogenéticas das características. Essas variações podem refletir processos que se estendem além da história evolutiva e englobam fatores do ambiente recente. No que diz respeito à diversidade da massa das sementes, as relações com gradientes ambientais foram principalmente influenciadas por adaptações recentes de características, tornando-se evidentes somente após remover a influência filogenética nas informações de características. Nossos resultados fornecem evidências dos processos complexos que influenciam a montagem de espécies de longa vida ao longo de escalas de tempo evolutivas e gradientes ambientais diversos, como as árvores na região da Mata Atlântica do Sul do Brasil.

Reconhecendo o imenso potencial de informação que a Mata Atlântica abriga, ciente de que apenas arranhamos a superfície desse vasto conhecimento e levando em consideração a velocidade com que essa floresta tropical é fragmentada, enfatizo a necessidade de unir uma rede de pesquisadores com o objetivo de vincular o conhecimento teórico às medidas práticas de conservação. Além disso, a analogia que fiz com título desta tese e com sinfonia não é apenas metafórica, mas também evoca a complexidade e a interconexão que caracterizam tanto a música quanto a biodiversidade. Compreender esse ecossistema é fundamental para manter a harmonia da vida, fortalecendo assim os esforços na área de conservação, a fim de assegurar que as gerações futuras tenham a oportunidade de apreciar, aprender e viver com a diversidade que a Mata Atlântica abriga.