UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
Instituto de Biociências
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Tese de Doutorado

Estrutura e dinâmica de florestas no continente americano
Forest structure and dynamics across the American continent

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Porto Alegre, setembro de 2022.

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Você é meu maior exemplo de vida.

“Comes the summer rain
Cue the lighting and far-off thunder again
Projecting through the clouds
And meditations, lifting out in the sound
The more mistakes the more resolve
It's gonna take much more than ordinary love
To lift this up
Stars align they say when things are better than right now
Feel the retrograde spin us round, round
Seven seas are rising, forever future's fading out
Feel the retrograde all around, round
Accelerate the change
Feeling equal, and opposite all the same
Momentum rearranged
Shout the echo, turning back but now changed
The rusted shapes refuse to fall
It's gonna take much more than ordinary love
To lift this up
Stars align they say when times are better than right now
Feel the retrograde spin us round, round
Seven seas are rising, forever future's fading out
Feel the retrograde all around, round
Hear the sound, in the distance now
Could be thunder, or a crowd

Hear the sound”
Retrograde, Pearl Jam

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Mas claro, também teve muita coisa boa. Essa jornada linda, intensa e deliciosa só foi possível porque em 2011 as políticas para ingresso e permanência no ensino superior eram efetivas e assertivas. No meu caso, foi através do FIES (financiamento estudantil), mas muitos outros colegas se beneficiaram de políticas de cotas ou auxílio financeiro. Não posso deixar de agradecer àqueles que lutam e atuam por um mundo mais justo e inclusivo, pois do contrário eu não teria conseguido seguir no ensino superior.

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Resumo

Ecossistemas florestais representam a maior parte da estocagem e sumidouro de carbono do planeta. Infelizmente, estas florestas vêm sofrendo uma drástica redução em área, dada especialmente pelo avanço do desmatamento e outros distúrbios antrópicos. Assim, é necessário conhecer o potencial das florestas de outras regiões para além dos trópicos na estocagem de carbono, capacidade de sumidouro de carbono, e consequente contribuição para mitigar emissões globais de CO_2. Esta tese abordará o papel das florestas subtropicais do sul do Brasil com este enfoque. Além disso, tendo em vista a importância dos elementos estruturais da comunidade sobre a dinâmica de espécies, também avaliaremos relações de *trade-off* entre crescimento e mortalidade e como atributos funcionais influenciam o desempenho de espécies temperadas nos Estados Unidos da América. Desta forma, esta tese pode ser compreendida como uma avalição geral de acerca da estrutura e dinâmica de florestas ao longo do continente americano. A tese está organizada em três capítulos, cujos objetivos principais são: (1) Determinar os estoques de biomassa e os *drivers* desses estoques em florestas subtropicais no sul da América; (2) Determinar o balanço líquido de carbono em florestas subtropicais na Mata Atlântica Brasileira, bem como as relações desse balanço com a biodiversidade arbórea; e (3) Determinar a probabilidade anual de morte de espécies temperadas em crescimento zero, além das relações de *trade-off* entre crescimento e mortalidade, e o efeito preditivo de atributos funcionais sobre a probabilidade anual de morte dessas espécies. Encontramos que (1) as florestas subtropicais têm uma alta capacidade de estocar biomassa (246,5 Mg/ha), e esses estoques são influenciados positivamente pela proporção de árvores grandes e negativamente pela variação anual de temperatura; (2) observamos que o balanço líquido de carbono é positivo (indicando que estas florestas atuam como sumidouro de carbono), porém esse sumidouro não é relacionado a métricas de biodiversidade; e (3) estimamos a probabilidade de morte para 71 espécies temperadas, as quais demonstraram uma fraca relação de *trade-off* entre crescimento e mortalidade, porém a probabilidade de morte foi positivamente relacionada ao nitrogênio foliar. Esta tese avaliou diferentes processos associados à dinâmica de florestas, abrangendo desde a espacialização e dinâmica de carbono em florestas subtropicais, bem como seus determinantes, até a estimativa da probabilidade de mortalidade de espécies temperadas em crescimento zero, refletindo suas tolerâncias à ausência de recursos. Estas avaliações só foram possíveis devido à avaliação temporal dos indivíduos que compõem essas comunidades. Deste modo, a manutenção de parcelas permanentes é crucial para que estudos de dinâmica de florestas sejam conduzidos, especialmente diante de mudanças no clima onde não sabemos como estas florestas irão reagir.

Palavras-chave: dinâmica de carbono; estoque de biomassa; florestas subtropicais; mortalidade em crescimento zero; mudanças climáticas; parcelas permanentes.

Abstract

Forest ecosystems correspond to the greatest part of the overall carbon storage and sink. Unfortunately, these forests have been suffering a drastic reduction in area due to illegal harvesting and anthropogenic disturbances. Thus, to understand the potential of forests out of tropics for carbon storage and sink are fundamental comprehend their contribution to mitigate CO_2 emissions. This thesis will address the subtropical forests in southern Brazil with this emphasis. Additionally, due to the remarkable importance of community structural parameters on species dynamics, we also evaluate the between species growth and mortality trade-offs, and how functional traits affect the species performance in temperate US forests. Thus, this thesis can be summarised as a general evaluation about the structure and dynamics of forests in the American continent. The thesis is organised in three chapters, and the aims are (1) to determine the biomass stocks and drivers of biomass storage across South American subtropical forests; (2) to determine the net carbon change in subtropical Brazilian Atlantic Forests, as well as the relationship between net carbon change and biodiversity metrics; and (3) to determine the annual mortality probability at zero growth, the growth-mortality trade-offs, and the predictive power of functional traits in driving the annual mortality probability of temperate species. We found that (1) subtropical forests store large amounts of biomass (246.5 Mg/ha), and these stocks are driven positively by the proportion of large trees, and negatively by the annual temperature range; (2) the net carbon change is positive, meaning that these forests are acting as carbon sinks, but this carbon sink is not related to biodiversity metrics; (3) we estimated the mortality probability for 71 species, and they have a weak growth-mortality trade-offs, and the mortality probability is positively related to leaf nitrogen. This thesis evaluated different process associated with the forest dynamics, from the spatial and temporal distribution of carbon across subtropical forests and its drivers to the mortality probability at zero growth for temperate species, reflecting their tolerances to absence of resources. These evaluations were only possible due to the long-term monitoring of the stems across forests. Thus, to maintain long-term plots is fundamental to allow forest dynamics' studies, especially in a scenario of global changes.

Keywords: carbon dynamics; biomass stocks; subtropical forests; mortality at zero growth; climate change; permanent plots.

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Introduction

1. As florestas no mundo: importância e perspectivas

Reconhecidos pela biodiversidade e importância para os serviços ecossistêmicos, os ecossistemas florestais respondem pela maior parte da estocagem de carbono do planeta (Pan et al. 2011). Florestas são sistemas complexos, com dinâmica temporal e sucessional lentas e características altamente associadas às condições ambientais regionais. Os fatores ambientais influenciam não apenas a composição e diversidade de espécies em florestas, mas também o desempenho destas espécies, como taxas de crescimento e mortalidade. Dentre os ecossistemas floreats, florestas as tropicais representam a maior extensão de área florestal observada e, consequentemente, são responsáveis pela maior parte da estocagem de carbono (Sullivan et al. 2020). Além disso, historicamente, as florestas tropicais são mais estudadas quanto aos padrões e processos associados à ciclagem de carbono, o que está relacionado principalmente à representatividade espacial e marcada importância para a manutenção da biodiversidade.

Ao longo das últimas décadas as florestas tropicais e subtropicais vêm sofrendo uma drástica redução em área, dada especialmente pelo avanço do desmatamento e outros distúrbios antrópicos (Ribeiro et al. 2009; Rosa et al. 2021). Como consequência, essa redução tem levado a efeitos negativos sobre o desempenho dessas florestas diante da ciclagem global de carbono (Brinck et al. 2017), bem como a capacidade de sumidouro de carbono nesses locais (Hubau et al. 2020; Gatti et al.

2021). Florestas de outras regiões, para além dos trópicos, vêm sendo cada vez mais avaliadas quanto à sua capacidade de estocagem e sumidouro de carbono, fornecendo informações sobre a contribuição dessas florestas para o fluxo de carbono no planeta (Bordin and Müller 2019; Capellesso et al. 2020, 2021; Duque et al. 2021).

O conhecimento sobre o potencial de florestas além dos trópicos na estocagem de carbono, a capacidade de sumidouro de carbono, e consequente contribuição para mitigar emissões globais de carbono, ainda é incipiente. Esta tese abordará o papel das florestas subtropicais do sul do Brasil com este enfoque. Além disso, tendo em vista a dinâmica e coexistência de espécies diante de estresses ambientais e mudanças na disponibilidade de recursos, também avaliaremos relações de *trade-offs* entre crescimento e mortalidade e como atributos funcionais influenciam o desempenho de espécies em florestas temperadas nos Estados Unidos da América. Desta forma, esta tese pode ser compreendida como uma avalição geral acerca da estrutura e dinâmica temporal de florestas ao longo do continente americano.

2. Estrutura e dinâmica de comunidades florestais: abordagens diferentes, mas complementares

A análise da estrutura e dinâmica de florestas pode ser feita a partir de diferentes metodologias, que vão do trabalho de campo ao uso de sensoriamento remoto e modelagens computacionais. A busca pelo entendimento de como as florestas são organizadas iniciou-se a partir de trabalhos de campo realizados em um único momento no tempo, com inventários florísticos e fitossociologia (i.e., obtenção de diâmetro e altura das árvores) (Mueller-Dombois & Ellenberg 1974). Estes parâmetros permitem analisar a estrutura da floresta, respondendo perguntas pontuais sobre o potencial de estocagem de carbono ou diversidade de espécies, por exemplo. Por outro lado, atualmente vêm se investindo muitos esforços na marcação permanente de parcelas para avaliação em longo prazo, as quais permitem avaliar essas comunidades florestais ao longo do tempo, e assim, estudar a dinâmica desses ecossistemas (Phillips et al. 1998; ForestPlots et al. 2021). Desta forma, torna-se possível conhecer taxas médias de crescimento e mortalidade de indivíduos, espécies, e comunidades, além de ganhos e perdas de carbono ao longo do tempo, revelando assim, as mudanças temporais nesses ambientes.

2.1 O que determina os fluxos de carbono em florestas?

Uma vez conhecida a capacidade de estoque de biomassa, produtividade e perda de carbono via mortalidade nas florestas, a pergunta seguinte geralmente é relacionada a quais fatores influenciam essas variáveis. De modo geral, dentre os fatores conhecidos como potencialmente determinantes do estoque de carbono é possível destacar fatores abióticos, como o clima (Poorter et al. 2017) e condições edáficas (van der Sande et al. 2017a), além de fatores bióticos como a diversidade (Poorter et al. 2015) e composição (tanto de espécies quanto funcional) (van der Sande et al. 2017c), e a própria estrutura da floresta em termos de área basal ou biomassa (Lohbeck et al. 2015; Ali et al. 2019). Além disso, estes fatores também são importantes preditores de ganhos e perdas de carbono ao longo do tempo (van der Sande et al. 2017b).

De modo geral, fatores climáticos estão relacionados principalmente à temperatura (Sullivan et al. 2020) e precipitação (Vilanova et al. 2018), e o impacto desses fatores vêm se tornando cada vez mais intenso (via extremos climáticos) devido às mudanças climáticas globais (Aleixo et al. 2019). Com relação aos fatores edáficos, as relações exploradas são principalmente devido à fertilidade (van der Sande et al. 2017a) e textura do solo (Quesada et al. 2012; Bordin & Müller 2019). Solos mais férteis tendem a ter maior disponibilidade de nutrientes para utilização pelas plantas, enquanto solos mais argilosos tendem a ter maior capacidade de reter água.

Com relação aos fatores bióticos, relações entre fluxos de carbono em florestas com a diversidade tendem a ser mais facilmente encontradas em escalas espaciais menores (Chisholm et al. 2013), enquanto em escalas maiores essas relações não são observadas (Poorter et al. 2015; Sullivan et al. 2017). Dentre as métricas de diversidade já avaliadas quanto ao seu efeito sobre a estocagem de carbono estão a taxonômica (Mori et al. 2021), funcional (Ali & Yan 2017) e filogenética (de Aguiar-Campos et al. 2021). Relações entre diversidade e componentes do ciclo do carbono são frequentemente exploradas porque maior diversidade geralmente implica em uma melhor utilização dos recursos nos ambientes, uma vez que maior diversidade está relacionada à maior disponibilidade de nichos para serem ocupados (Diaz & Cabido 2001). Além disso, o efeito da composição taxonômica, funcional ou filogenética se dá principalmente através da dominância de algumas espécies (Slik et al. 2010; Banin et al. 2014), clados (de Aguiar-Campos et al. 2021), ou atributos funcionais (Prado-Junior et al. 2016; Ali & Yan 2017). Por exemplo, espera-se que locais onde haja a dominância de determinado táxon que possua a capacidade de estocar grandes quantidades de carbono, a exemplo de espécies da família Dipterocarpaceae em florestas asiáticas, tenham em média uma maior estocagem de carbono em relação a outras florestas (Sullivan et al. 2020).

Associar os fluxos de carbono em florestas a medidas estruturais da própria floresta, em um primeiro momento, pode parecer redundante. No entanto, diversos estudos vêm indicando o forte poder preditivo de causalidade entre métricas como área basal, densidade de caules e proporção de árvores grandes sobre a estocagem de carbono (Lohbeck et al. 2015; Ali et al. 2019) e dinâmica do carbono em florestas, os quais estão ligados principalmente ao efeito dessas variáveis sobre à mortalidade de árvores (Iida et al. 2014; Bennett et al. 2015). Existem evidências de que florestas com maior proporção de árvores grandes estocam mais carbono, mas ao longo do tempo essas grandes árvores tendem a morrer, e assim impactar a capacidade de sumidouro dada a perda de carbono via mortalidade (Bordin & Müller 2019).

Embora a contribuição e determinantes dos estoques e fluxos de carbono nas florestas tropicais – especialmente na Amazônia, sejam relativamente conhecidos, essas informações para florestas além dos trópicos ainda são incipientes. Dada a heterogeneidade apresentada por estes diferentes tipos de florestas, o efeito das variáveis bióticas e abióticas acima mencionados pode ser diferente. Por exemplo, as florestas subtropicais sul-americanas, encontradas na região sul do Brasil, são caracterizadas por apresentarem um filtro climático diferente da porção tropical da Mata Atlântica e Amazônia, por exemplo. Dentre esses filtros, há a presença de uma marcada sazonalidade, a qual é relacionada à temperatura, mas não à precipitação (Oliveira-Filho & Fontes 2000; Rosenfield et al. 2019). Nesta região, é possível observar uma alta amplitude de temperaturas ao longo do ano, o que potencialmente influencia a dinâmica interna dessas florestas.

2.2 Qual o papel da diversidade e as estratégias de conservação?

Tendo em vista que as condições climáticas são diferentes na região subtropical em relação à região tropical, também é possível que as relações bióticas que determinam a estrutura dessas florestas sejam diferentes. Por exemplo, florestas subtropicais no sul do Brasil possuem espécies originadas nas regiões Austral-Antárticas e Andinas (Rambo 1953), o que leva à composição de espécies com a presença de coníferas (como a *Araucaria angustifolia* e *Podocarpus lambertii*), e deste modo, além de alta diversidade taxonômica, também alta diversidade funcional e filogenética (Duarte et al. 2014). Por consequência, torna-se necessário avaliar se e como a variação biótica também influencia os fluxos de carbono nessa região.

De modo geral, variação temporal e estocagem de carbono em florestas devem ser tratadas como funções ecossistêmicas diferentes (Chisholm et al. 2013), pois representam medidas distintas e potencialmente não correlacionadas. Consequentemente, o efeito de variáveis bióticas e abióticas pode ser diferente para cada uma das métricas associadas ao fluxo de carbono (e.g., estoque e sumidouro de carbono), e diante da crescente necessidade de conservar estes ameaçados ecossistemas florestais, entender as relações entre esses fluxos e a biodiversidade é urgente. Conforme mencionado anteriormente, florestas tropicais e subtropicais são ambientes altamente diversos, e com (potencialmente) alta estocagem e sumidouro de carbono (Sullivan et al. 2017; Bordin & Müller 2019). Neste sentido, muitos são os co-benefícios encontrados em investir esforços de conservação nesses ambientes, pois gerariam resultados de ganho em ambas as situações (Capellesso et al. 2021). No entanto, assim como as métricas relacionadas ao fluxo de carbono, as relações entre biodiversidade e esses fluxos podem ser fracas ou ausentes (Ferreira et al. 2018), levando-as a serem consideradas diferentes alvos para em estratégias de conservação.

3. Conhecer as espécies para entender as comunidades

Comunidades vegetais são compostas por vários conjuntos de espécies co-ocorrendo no mesmo espaço e tempo, e cada uma dessas espécies pode apresentar diferentes estratégias de vida (Chesson 2000). De modo geral, as estratégias de vida das espécies de árvores são associadas à forma como alocam seus recursos, e estas estratégias se traduzem em capacidade competitiva. Por exemplo, espécies com maior dependência de luz tendem a investir na aquisição de recursos, e consequentemente apresentam maiores taxas de crescimento, mas também maiores taxas de mortalidade (Brienen et al. 2020). Em contraste, espécies tolerantes à sombra geralmente têm maior longevidade, mas menores taxas de crescimento e mortalidade (Sterck et al. 2006; Iida et al. 2014), e geralmente são caracterizadas por serem espécies com atributos conservativos.

Uma vez conhecidas as estratégias de vida que as espécies possuem, espera-se que essa gama de estratégias encontradas no espectro de aquisição e conservação de recursos esteja ligada a valores de atributos funcionais, os quais estão alinhados a um espectro contínuo que vai do mais rápido ao mais lento (*"fast-slow continuum"*) (Reich 2014). Esse espectro rápido-lento tende a influenciar o desempenho demográfico das árvores (Poorter and Bongers 2006; Poorter et al. 2008), de modo que uma espécie de crescimento rápido, muitas vezes alinhada a estratégias aquisitivas, pode ter menor probabilidade de mortalidade em ambientes ricos em recursos (Adler et al. 2014; Russo et al. 2021). Por outro lado, uma espécie de crescimento lento (e muitas vezes alinhada a estratégias conservadoras) pode ser mais tolerante em ambientes hostis (Adler et al. 2014; Reich 2014), sendo mais resistente a períodos com taxas de crescimento baixas ou inexistentes (Russo et al. 2021).

A estratégia de alocação de espécies pode ser avaliada através da probabilidade de mortalidade quando uma espécie para de crescer, o que mostra sua tolerância à limitação de recursos (Russo et al. 2021). Além disso, também se espera que a mortalidade das espécies esteja ligada à sua taxa de crescimento, refletindo em um *trade-off* entre crescimento e mortalidade. Compreender a extensão dos *trade-offs* entre espécies é importante pois se reflete em um tópico central para a compreensão dos mecanismos de coexistência entre as espécies (Silvertown 2004). A existência de *trade-offs* entre crescimento-mortalidade e sua relação com estratégias de vida é consistente em florestas tropicais e subtropicais (Rüger et al. 2020; Russo et al. 2021; Kambach et al. 2022). As florestas temperadas têm presença marcante de espécies de angiospermas e gimnospermas, mas também mostram essa relação entre crescimento e mortalidade (McMahon et al. 2011; Brienen et al. 2020). No entanto, as relações entre estratégias de vida e estratégias funcionais são pouco compreendidas e testes empíricos para confirmar relações entre características funcionais e desempenho das espécies ainda são necessários (Shipley et al. 2016). Sendo assim, compreender a força dos trade-offs em diferentes conjuntos de espécies, bem como relações entre atributos funcionais e probabilidade de morte de espécies é fundamental para entendermos a estruturação de comunidades florestais, assim como as potenciais respostas dessas espécies em cenários de mudanças globais.

4. Estrutura da tese e objetivos

Esta tese está organizada em três capítulos, compreendendo aspectos relacionados aos pontos acima mencionados:

Capítulo 1: Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests

Objetivos: Determinar os estoques de biomassa em florestas subtropicais no sul da América, bem como os potenciais determinantes desses estoques de carbono na região.

Capítulo 2: No relationship between biodiversity and forest carbon sink across the subtropical Brazilian Atlantic Forest

Objetivos: Determinar o balanço líquido de carbono (ganhos via crescimento e recrutamento menos as perdas via mortalidade) em florestas subtropicais na Mata Atlântica Brasileira, bem como as relações desse balanço líquido com a biodiversidade arbórea (i.e., diversidade taxonômica, funcional e filogenética).

Capítulo 3: Growth-mortality strategies across temperate tree species and their relationship with functional traits

Objetivos: Determinar a probabilidade anual de morte de espécies temperadas quando as espécies param de crescer, além das relações de trade-off entre crescimento e mortalidade, e o efeito preditivo de atributos funcionais sobre a probabilidade anual de morte dessas espécies.

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

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Capítulo 1

Chapter 1

Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests

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Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests

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Abstract

Subtropical forests certainly contribute to terrestrial global carbon storage, but we have limited understanding about the relative amounts and of the drivers of above-ground biomass (AGB) variation in their region. Here we assess the spatial distribution and drivers of AGB in 119 sites across the South American subtropical forests. We applied a structural equation modelling approach to test the causal relationships between AGB and environmental (climate and soil), structural (proportion of large-sized trees) and community (functional and species diversity and composition) variables. The AGB on subtropical forests is on average 246 Mg ha^{-1}. Biomass stocks were driven directly by temperature annual range and the proportion of large-sized trees, whilst soil texture, community mean leaf nitrogen content and functional diversity had no predictive power. Temperature annual range had a negative effect on AGB, indicating that communities under strong thermal amplitude across the year tend to accumulate less AGB. The positive effect of large-sized trees indicates that mature forests are playing a key role in the long-term persistence of carbon storage, as these large trees account for 64% of total biomass stored in these forests. Our study reinforces the importance of structurally complex subtropical forest remnants for maximising carbon storage, especially facing future climatic changes predicted for the region.

Keywords: Brazilian Atlantic Forest; carbon stocks; climate change; functional diversity; functional traits; soil texture; structural equation model; temperature annual range.

1. Introduction

Forests are an essential component of the global carbon cycle, being responsible for storing a substantial amount of carbon as living above-ground biomass (hereafter, AGB) (Fahey et al. 2010; Pan et al. 2013). However, carbon storage capacity varies greatly across forests. Tropical forests are able to stock ca. 56% of global plant biomass (Pan et al. 2011; Sullivan et al. 2020), two times more than temperate forests (Fotis et al. 2017). In order to predict the future of the global carbon stocks, we need to understand the drivers behind this variation in AGB. Forest biomass is expected to be affected direct and indirectly by climatic conditions and soil, through effects of forest structure, and species composition and traits (Fig. 1; Poorter et al., 2017, 2015). Ground-based studies on forest structure are still limited for particular ecosystems, hampering our understanding of the distribution and mechanism behind the variation in AGB. This is the case for subtropical forests, one of the most threatened ecosystems in the world (FAO and UNEP 2020), found in China and the Neotropics. AGB in these forests have been assessed only by a few studies (Ali and Yan 2017a; Li et al. 2018), and never in South America.

Climate effects on AGB are largely observed across many forest ecosystems (Vilanova et al. 2018; Sullivan et al. 2020). Within tropical forests temperature seems to be negative related to AGB (Ali et al. 2019a), due to the negative effects of high temperatures on plant metabolism, by increasing respiration rates (Álvarez-Dávila et al. 2017; Sullivan et al. 2020). Thus, it may represent a stressful condition, especially when accounting for the minimum temperatures or higher temperature annual ranges. In addition to temperature, water availability is also an important driver of AGB, which tends to peak under intermediate rainfall conditions, as a combination of the absence of extreme droughts, and low levels of light limitation due to cloud cover under high rainfall conditions (Poorter et al. 2015; Vilanova et al. 2018).

Soil texture and fertility are the main edaphic factors for limiting AGB and forest dynamics in the tropics, especially due to the importance of soil texture for water retention, and fertility due to soil phosphorous content (Quesada et al. 2012; van der Sande et al. 2017b). Soil fertility was found to be negatively related to AGB in Asian subtropical forests, acting as an environmental filter for nutrient-poor tolerant species (Ali and Yan 2017a), and modulating the structure and dynamics in South American subtropical forests (Bordin and Müller 2019). Soil texture is strongly related to water holding capacity, which is greater in clay-rich soils (Quesada et al. 2012), also playing a key role in maintaining ecosystem processes and AGB stocks (Castilho et al. 2006).

Variation in climatic and edaphic conditions are also expected to affect the tree sizes in forest ecosystems (Slik et al. 2013). For instance, large-sized trees are more often exposed to higher solar radiation (Pinho et al. 2020), and are sensitive to water deficit (Bennett et al. 2015). Large trees are an important driver of forest structure (Slik et al. 2013; Bastin et al. 2015, 2018; Lutz et al. 2018), and account for the largest amount of AGB in forest communities, potentially overruling the effect of remaining trees (Ali et al. 2019b). Large-diameter trees are often related to old-growth forests, as they take a longer time to grow and develop (Lindenmayer et al. 2012). Therefore, mature forests have an essential function in maintaining carbon stocks due to the higher proportion of large-sized trees.

Climatic and edaphic conditions may also have indirect effects on AGB by acting as environmental filters for community structuring (Slik et al. 2010; Quesada et al. 2012; Rezende et al. 2015; Ali et al. 2019c), and by imposing physiological limitations to the distribution of species (Peña-Claros et al. 2012; Esquivel-Muelbert et al. 2017; Marcilio-Silva et al. 2017). These limitations are then translated in variations in species composition and their functional trait values across climatic gradients (Asefa et al. 2017; Bruelheide et al. 2018). Functional traits are morpho-physio-phenological features of plants that affect their fitness (Violle et al. 2007). The dominant trait value within an ecological community is expected to be related to the environmental conditions experienced by that community varying along the acquisitive-conservative spectrum of strategies (Lavorel and Garnier 2002; Garnier et al. 2004). An acquisitive strategy is frequently represented by investments on leaf traits to improve light assimilation, via higher mean values of specific leaf area (SLA) or leaf nitrogen content (LNC) (Wright et al. 2004), while a conservative strategy is often represented by greater investments in structures, via higher values of leaf dry-matter content (LDMC) and wood density (WD) (Wright et al. 2004; Chave et al. 2009). Following the mass-ratio hypothesis (Grime 1977; Garnier et al. 2004), the functional composition of the dominant species often influence AGB by improving in resources acquisition in tropical rain forests (van der Sande et al. 2017a), or resources conservation in drier forests (Prado-Junior et al. 2016). However, subtropical forests have a mixture of distinct elements of tree species (e.g. seasonal and evergreen, tropical and austral origins), which often co-dominate the ecological communities, thus the effect of functional composition on biomass is still poorly understood (Ali and Yan 2017b; Souza and Longhi 2019).

Diversity of species and functional traits are also expected to have a positive effect on AGB (Cardinale et al. 2007; Poorter et al. 2015, 2017). Diversity is thought to affect biomass stocks as a consequence of niche complementarity, where a greater number of species allow for greater partitioning in resources use among coexisting species (Diaz and Cabido 2001). However, the relationship between diversity and carbon stocks has not been observed across large spatial scales (Chisholm et al. 2013; Finegan et al. 2015; Sullivan et al. 2017). Moreover, species and functional diversity are related to community species composition, thus increasing complexity in relationships between diversity and biomass across spatial and temporal scales. For instance, forests with the high dominance of one or a few species may have greater AGB despite lower observed niche complementarity (Marimon et al. 2014).

In the Neotropical region in particular, we have a limited understanding of what drives the biomass variation at higher latitudes (Alves et al. 2010; Vieira et al. 2011; Rosenfield and Souza 2013; Poorter et al. 2017). The South American subtropical forests correspond to the second largest remnant of this forest type (FAO 2012). These subtropical forests differ from tropical forests in terms of climatic seasonality, which is characterised by great temperature variations across the year with hot summer and cold winters (Rosenfield et al. 2019), while precipitation is well distributed across the year without the presence of marked dry period (Oliveira-Filho et al. 2014). This region experiences high biotic and abiotic heterogeneity, due to high environmental variation and diverse floristic origins that influence plant strategies (Rezende et al. 2015), even along short distances (Rosenfield et al. 2019). Therefore, we expect AGB within these forests to be driven by a different set of drivers when compared to those controlling the variation of AGB at lower latitudes, with temperature playing a greater role than precipitation. The lack of understanding of the ecological patterns within these unique highly diverse forests makes studying subtropical forests crucial for understanding the role of this climate in determining AGB.

In this study, we determined the above-ground biomass stocks of subtropical forests in Southern Brazil. We further tested the predictive power of climatic variables, edaphic conditions, large-sized trees, composition, and diversity in driving AGB in subtropical forests. To evaluate the drivers of biomass stocks we used a conceptual model (Fig. 1), and tested whether (1) climatic conditions are able to predict - directly or indirectly - AGB; (2) edaphic factors are determining AGB in terms of texture or fertility, directly limiting the biomass or filtering out species or traits which in turn affect AGB; (3) large-sized trees determine biomass stocks; (4) community composition and diversity, in terms of species and functional traits, affect AGB in subtropical forests.

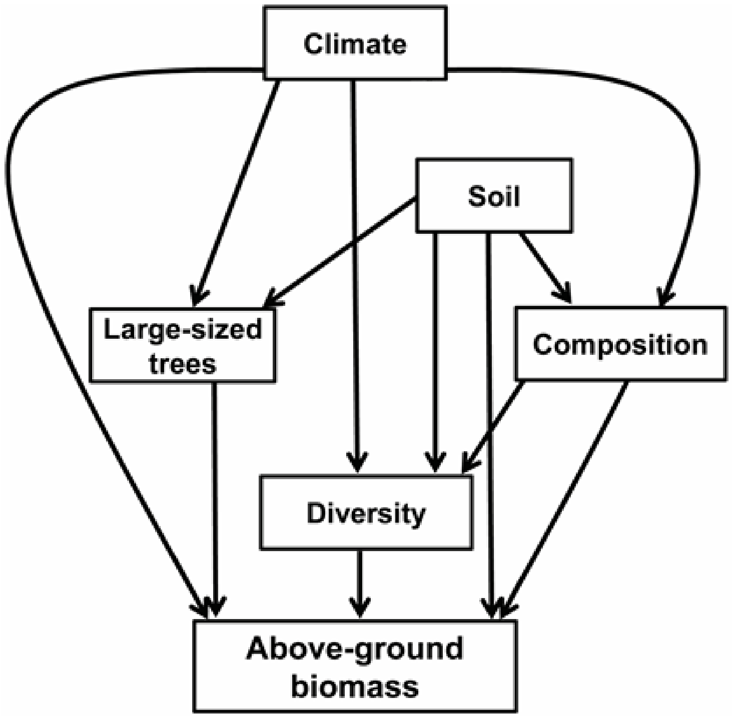

Fig. 1: Conceptual framework showing the expected relationships of distinct sets of factors – climate, soil, large-sized trees, diversity, and composition – on above-ground biomass. Climate is represented by temperature and rainfall variables. Soil is represented by fertility and texture variables. Large-sized trees represent a proportion of large trees in the forest communities. Diversity is represented by both species and functional diversity. Composition is represented by tree species and functional composition.

2. Material and Methods

2.1 Study area

We investigated trends in above-ground biomass by analysing forest inventories in subtropical forests in Southern Brazil. Our database comprehends 119 sites with different sampling efforts (mean sampled area: 0.25 ha; see Appendix A for details), established in old-growth forests, with some minor level of past human disturbances, such as cattle grazing and potential selective logging (but not clear cutting; Fig. 2). The sites cover different forest types across the subtropical forests in the southern portion of Brazilian Atlantic Forest and Pampean forests (Holdridge 1947; Oliveira-Filho et al. 2014), including the Araucaria forests (mixed forests with large dominance of the Gymnosperm Araucaria angustifolia), Seasonal forests and Atlantic moist forests (see Fig. 2; Appendix B). The Pampean forests are located in a grassland matrix (often called Pampa biome), with forested areas along riverine and hillslope areas. For our study, we selected just forest plots along hillslope areas, which have similar species composition to Seasonal forests (Oliveira-Filho et al. 2014). All sites are distributed along a climatic and edaphic gradient (Appendix C).

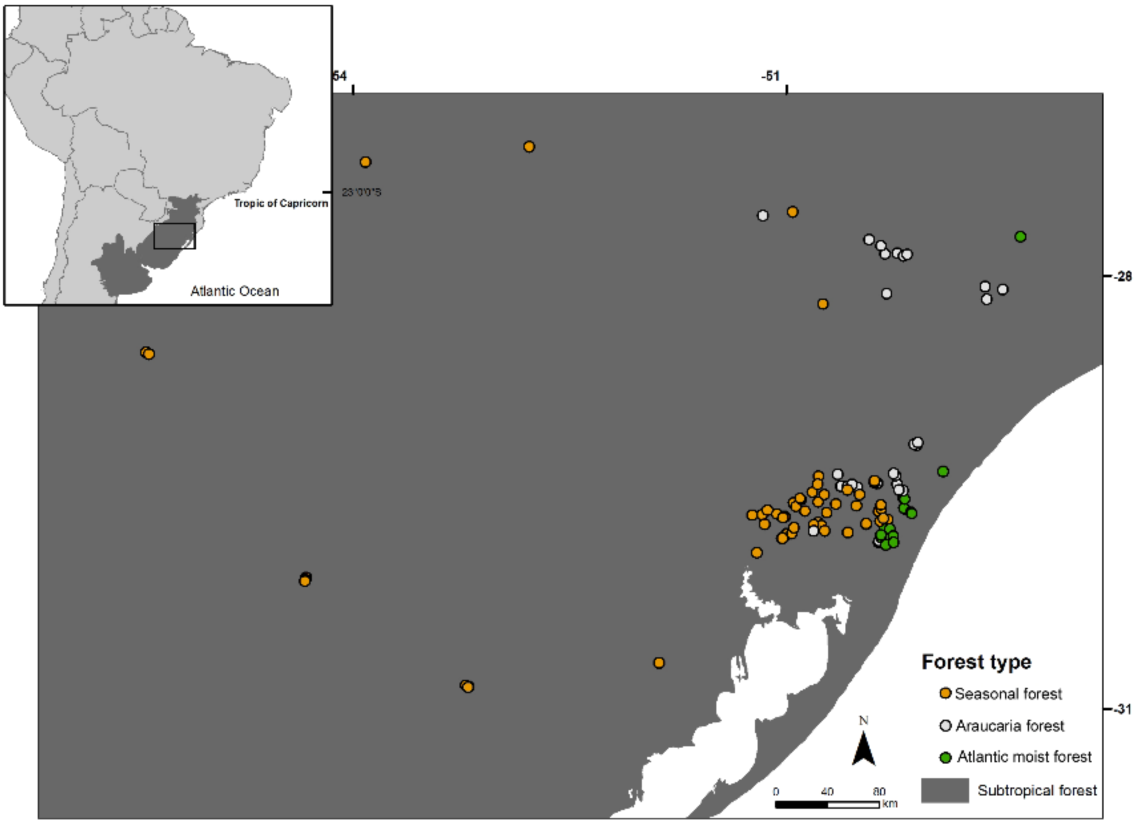

Fig. 2: Distribution of South American subtropical forests, with the location of the 119 study sites. The forest types (i.e. Atlantic moist forest, Araucaria and Seasonal forests) are also shown as the color of points.

2.2 Forest inventory data and AGB estimations

In each of our sampling sites, all alive trees with 10 cm of diameter at breast height (dbh) or greater had their diameter measured and their height estimated by eye, or laser tap. All trees were identified to the species level.

To estimate AGB we used the pantropical allometric equation proposed by Chave et al. (2014) (Eq. 1):

AGB = 0.0673 (WD dbh2 H)0.976 (Eq. 1)

where H represents tree height (m), and WD represents the wood density of the species (g cm^{-3}). Wood density information was obtained from regional (Missio et al. 2017; Oliveira et al. 2019) and global databases (Chave et al. 2009; Zanne et al. 2009). Total AGB per hectare was calculated as the sum of the above-ground biomass of all trees in each site and dividing by the area of the site in hectares (AGB, Mg ha-1). In order to obtain an accurate measure per site, we used the average AGB across multiple censuses whenever possible (see Appendix A). Biomass was estimated by using the ‘computeAGB’ function, package BIOMASS (Réjou-Méchain et al. 2017).

Analysis related to above-ground biomass in inventory plots with different sample sizes, especially smaller plots, may present a large variation to the overall biomass estimates. We tested the need for corrections and further implementation of weights in our analysis following the protocol from Lewis et al. (2009). This analysis showed the need to account for the plot area in our analyses by including the cubic root of the sampling area as weights in our models (Appendix A).

2.3 Climatic and edaphic variables

All climatic variables were obtained at the WorldClim database (grid cells of 30’, i.e. 1 km resolution) (Fick and Hijmans 2017). The climatic variables selected for predictive analysis were the minimum temperature of the coldest month (°C), temperature annual range (°C) and mean annual precipitation (mm). We selected these variables based on Rezende et al. (2015), which describes the strong climatic filter in subtropical forests, mainly related to high humidity and low winter temperatures. Across our study sites, the mean annual precipitation varies from 1704 to 2206 mm yr-1, the minimum temperature of the coldest month varies between 6 and 9.4 °C, the mean annual temperature varies from 11 to 20 °C, and the temperature annual range varies between 16.3 to 23.2 °C.

Information on edaphic conditions were based on clay content (%) and cation exchange capacity (CEC, cmolc/kg, both at 15 cm depth), which were available at the global soil database SoilGrids (grid cells of 1 km resolution) (Hengl et al. 2017). Soil clay content characterises the soil texture, and CEC is a proxy for soil fertility, as it provides information on available ions for plant use. The study sites show soil CEC ranging from 16 to 24 cmol kg^{-1}, while soil clay content ranged from 33 to 44%.

2.4 Functional traits

Functional traits were collected and measured following standardized protocols (Pérez-Harguindeguy et al. 2013). The traits measured in our study were specific leaf area (SLA, cm^2 g^{-1}), leaf dry-matter content (LDMC, mg g^{-1}), leaf nitrogen content (LNC, %), and wood density (WD, g cm^{-3}). Both high values of SLA and LNC are related to species that invest in resources acquisition, while higher values of LDMC and WD are related to species that invest in resources conservation (see Appendix D for details). We used species leaf trait values for 90% of species; when species value was unavailable, we used genus or family means. Species trait values are derived from regional collections, from the database of Plant Ecology Lab of the Federal University of Rio Grande do Sul (also available at TRY database; Kattge et al., 2020) and from specialized databases (Chave et al. 2009; Missio et al. 2017; Oliveira et al. 2019).

2.5 Diversity and composition metrics

We used metrics associated with species and functional traits described above. We described taxonomic richness using rarefied species richness, to control for the different number of stems found in our sites. Thirty-nine individuals was our reference for the rarefied richness, as it was the minimum number of individuals found amongst our plots. For each site, we determined the number of tree species in the stand and based on the number of individuals we calculated the Simpson's species diversity index. The species composition was represented by the first axis of an ordination analysis, obtained through a non-metric multidimensional scaling (NMDS) on a species basal area matrix, after Hellinger transformation (Appendix E). These analyses were performed using the functions 'rarefy', 'diversity' and 'metaMDS', package vegan (Oksanen et al. 2019).

Functional diversity was obtained using Rao's quadratic entropy (Botta-Dukát 2005) considering the Euclidean distance among species using the four traits (SLA, LDMC, LNC, and WD). Functional composition was estimated using community-weighted mean (CWM, Garnier et al. (2004)) for each trait. Both CWM and functional diversity were calculated using the community matrix described by species basal area. We calculated both metrics using 'dbFD' function, FD package (Laliberté et al. 2015).

2.6 Large-sized trees

Our conceptual model included the proportion of large-sized trees as a driver of above-ground biomass in subtropical forests. Within each plot, medium-large diameter trees (trees ≥ 30 cm dbh) were selected and turned into a proportion, representing the state of each site in terms of the large-sized trees.

2.7 Data analysis

We developed structural equation models (SEMs) to evaluate the multiple relationships of biotic and abiotic factors and above-ground biomass, based on the conceptual framework presented in Fig. 1. This approach allows us to estimate direct and indirect correlations among variables, and also to select the best statistically accepted model (Shipley 2016). We evaluated the direct and indirect effects of climatic and edaphic variables and the direct effect of large-sized trees, composition, and diversity on AGB. Indirect effects were quantified through the interaction between the direct effect of a given predictor (e.g., climatic variable) on a mediator (e.g., diversity metric), and the direct effect of a given mediator on above-ground biomass (Fig. 1).

Prior to applying the SEM, we used multiple regression analyses followed by model selection, to pre-select the best subset of variables from the diversity and composition components. The model selection was performed using the 'dredge' function (MuMIn package, Bartón (2012)), and all subset models with the Akaike Information Criterion (AIC) ≤ 2 were selected (Burnham and Anderson 2002). When models were equally supported, we selected the model with the higher AIC weight (see Appendix F for model selection results). We also evaluated the presence of spatial autocorrelation on AGB, by using generalized least-squares models (Beale et al. 2010), applying the maximum likelihood fitting method ('gls' function, nlme package (Pinheiro et al. 2020). We fitted models (AGB ~ predictor variables) among sites with and without spherical autocorrelation structure (i.e. local X and Y coordinate), and selected the model with the lowest AIC (Chisholm et al. 2013; Ali and Yan 2017a). This diagnosis showed no significant spatial structure on AGB; therefore, this was not included in the SEM analyses (Appendix F).

After the composition and diversity variable selection previously described, we tested between 18 candidate SEM models considering climatic variables (minimum temperature of the coldest month, temperature annual range or mean annual precipitation), soil variables (fertility: CEC or texture: clay content), large-sized trees, functional diversity, and CWM of traits (SLA, LNC and LDMC). As we were interested in characterising the general patterns across the region, we controlled for the effect of the different forest types (i.e., Atlantic moist forest, Seasonal, or Araucaria forest), by including it as random effect (Appendix G). The candidate SEMs were developed using the 'psem' function from the piecewiseSEM package (Liefecheck 2015), which allows for evaluation of both fixed and random factors on the response variable. In order to access the potential differences in biomass stocks among forest types in subtropical forests (i.e. Atlantic moist forest, Araucaria and Seasonal forests), we fitted an Analysis of Variance (ANOVA), using 'aov' function.

For each endogenous variable in SEM, we evaluated the R^2 marginal (R2m, related to fixed effect variance), and R^2 conditional (R^2c; related to both fixed and random effect variance). All variables were standardized to mean zero and unit variance to allow direct comparisons ('decostand' function, vegan package). All well-fitted SEM models ($P \geq 0.05$) were subjected to a model selection following the lowest AIC value. All analyses were conducted at R environment for statistical computing (R Core Team 2021).

3. Results

The above-ground biomass stocks across the subtropical forests evaluated in this study were on average 246.5 Mg ha^{-1} (± sd 105.1 Mg ha^{-1}; weighted mean AGB: 231.6 Mg ha^{-1}), ranging from 80.9 Mg ha^{-1} to 539.5 Mg ha^{-1}. When analysing by forest types, we found no difference between the AGB stocks (Fig. 3).

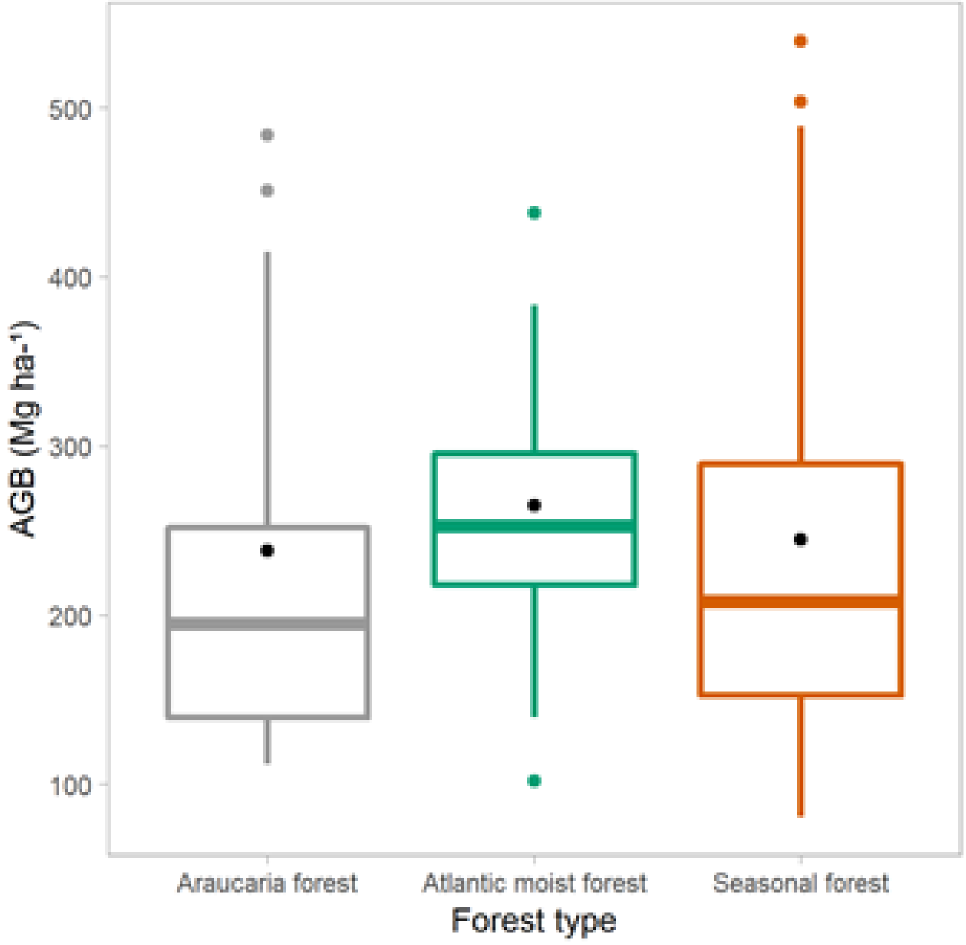

Fig 3: Above-ground biomass (AGB) among forest types across South American subtropical forests (i.e. Atlantic moist forest, Araucaria forest, and Seasonal forest). Boxplots show the AGB variation, and the black points inside the boxplots show the weighted mean values of AGB per forest type.

The best SEM to understand the drivers of biomass stocks across subtropical forests includes temperature annual range, soil texture, large-sized trees, functional diversity, and CWM of leaf nitrogen content (LNC) (Fig. 4). Large-sized trees and temperature annual range are the two most important variables explaining AGB (significant correlations of 0.62 and -0.28, respectively; Fig. 4, Figs. 5d and 5e). On the other hand, soil texture, LNC and functional diversity have no effect in AGB (Fig. 4). However, functional diversity is positively predicted by temperature annual range, leaf nitrogen content and soil texture (indirectly, via LNC; Figs. 5a, 5b, and 5c, see Appendix H for details). All the relationships established according to SEM are shown in Fig. 4, and the corresponding explained variance is presented in Table 1. The random effect, expressed through R2c indicates the potential influence spread throughout the forest types, by controlling the relationship among the predictor variables, but not overall AGB.

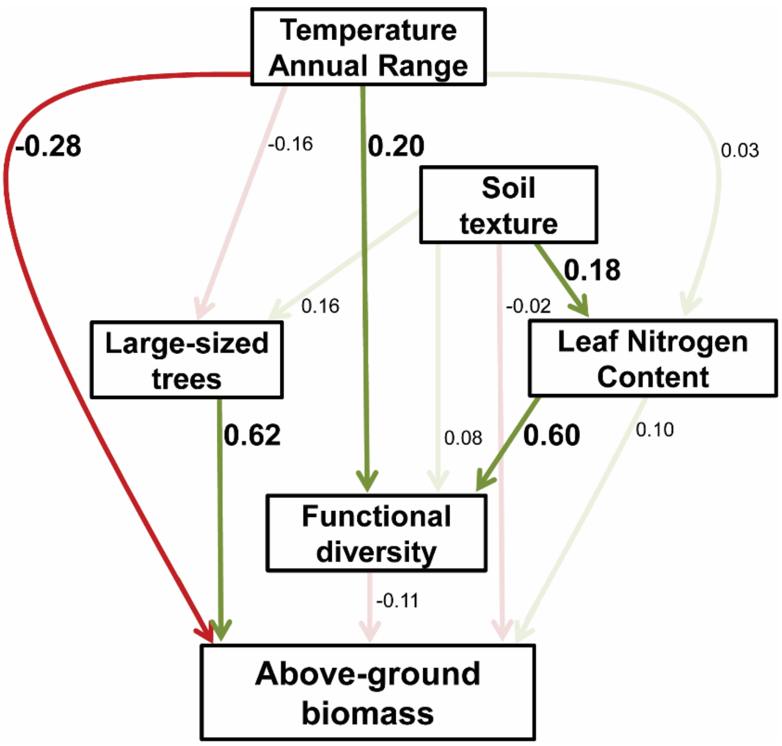

Fig 4: Structural equation model explaining the above-ground biomass across South American subtropical forests. Here we show effects of temperature annual range, soil texture, large-sized trees, functional composition (CWM of leaf nitrogen content), and functional diversity on AGB of subtropical forests. Standardized coefficients with significant levels are

represented by green or red colours (positive and negative effect, respectively), non-significant relationships are expressed by light green or red colours, and no arrows mean that the relationship was not included in the model.

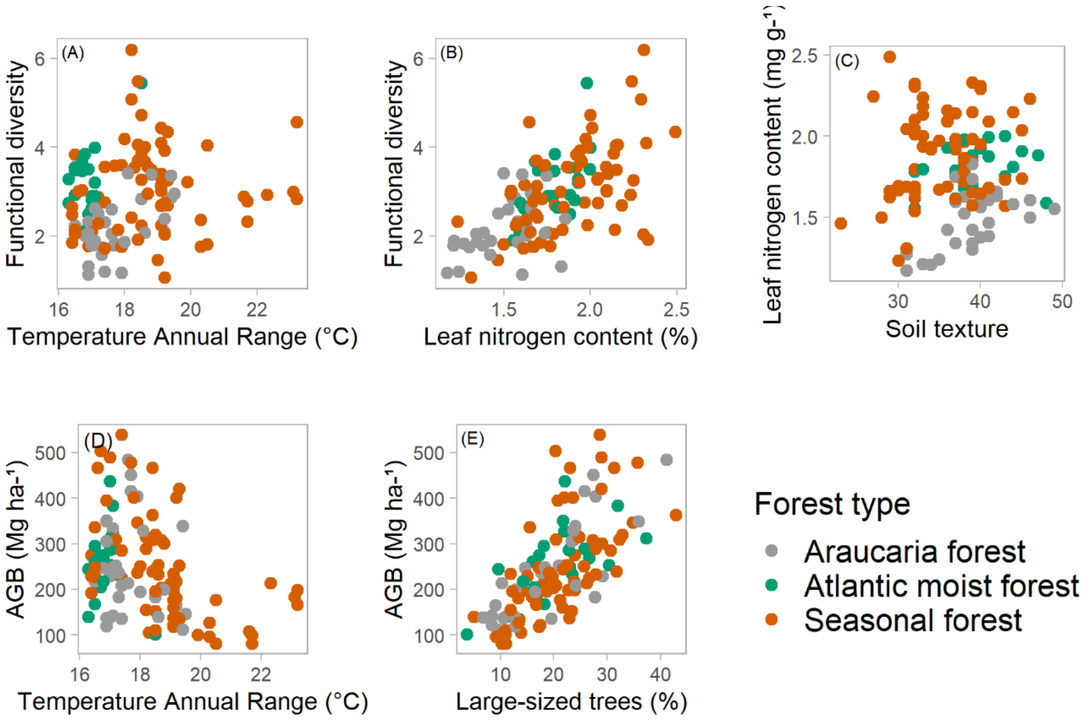

Fig 5: Significant bivariate relationships for hypothesized causal paths used in the structural equation model shown in Figure 4.

Table 1: Variance explained by fixed (R^2m) and fixed + random (R^2c) effects of relationships established in the structural equation model presented in Fig 1.

Response variable	R^2m	R^2c
Large-sized trees	0.05	0.07
Functional diversity	0.27	0.29
Leaf nitrogen content	0.01	0.34
Above-ground biomass	0.36	0.36

4. Discussion

The South American subtropical forests have the capacity of storing a great amount of biomass, equivalent to tropical forests, but here the climatic drivers of AGB stocks differ from those observed in lower latitudes. Above-ground biomass was strongly explained by the proportion of large-sized trees (≥ 30 cm dbh) in forest communities, and temperature annual range. The importance of such forest structural feature on biomass stocks reinforces the needs for protection of the old-growth remnants across these endangered subtropical forests.

4.1 Above-ground biomass stocks in subtropical forests

Our results support the great capacity of subtropical forests in storing biomass. The AGB stocked in South American subtropical forests here studied is within the range of tropical dry forests in Brazil (Prado-Junior et al. 2016), higher than temperate forests (Fotis et al. 2017), but lower than tropical Amazon forest and pan-tropical estimations (Castilho et al. 2006; Sullivan et al. 2020). We highlight that South American subtropical forests store twice as much AGB than Asian subtropical forests (Zhang et al. 2019).

Field estimations shown here are a valuable contribution to our understanding of global estimates of biomass stocks. Avitabile et al. (2016), in a great effort for providing global estimations of above-ground biomass, developed a pan-tropical biomass map combining two locally calibrated and high-resolution biomass maps. However, no field-based AGB information was used for the estimations in this region. It led to an underestimation of AGB stocks in these forests (about half of the mean AGB estimated for the same areas in this study, i.e., 140 Mg ha^{-1}). Our findings should be used to improve future global biomass estimates, providing a broader cover of distribution of AGB in subtropical forests.

The mean AGB stored in these forests does not vary across forest types (i.e., Atlantic moist forest, Araucaria and Seasonal forests), indicating the major influence of large-sized trees and temperature annual range over the geographical gradient marked by significant differences in floristic, structure, and plant strategies between these forest types (Oliveira-Filho et al. 2014; Rosenfield et al. 2019). Moreover, as the

Brazilian Atlantic Forest experienced historical devastation (Ribeiro et al. 2009), related to deforestation for timber products, crop plantations and pastures (Fonseca 1985), and also selective logging, the structure and AGB stocks of current remnants are potentially distinct from former pristine forests. Nevertheless, the key role of these forests in maintaining carbon stocks, by preventing emissions derived from deforestation and forest degradation, reinforces the priority for habitat protection and sustainable management of the complex and heterogeneous subtropical forests (Bergamin et al. 2017).

4.2 Temperature annual range and large-sized trees drive AGB variation

Temperature annual range is an important variable associated to biomass stocks in subtropical climatic conditions, as shown for AGB in our results. Temperature is frequently associated with plant metabolism, which is related to growth and respiration rates, further affecting forest productivity and carbon storage (Ballantyne et al. 2017; Vilanova et al. 2018). Recent reports have indicated the thermal sensitivity of tropical forests, which is closely related to higher maximum temperatures, which affects the potential carbon stocks of these forests (Sullivan et al. 2020). The negative effect of temperature annual range on above-ground biomass observed in the present study may be related to a stressful environmental condition for trees, associated with the great thermal amplitude along the year (Oliveira-Filho and Fontes 2000; Oliveira-Filho et al. 2014). For instance, these tree species must invest more resources to tolerate the environmental change instead of biomass storage. This is likely to be related to Seasonal forest’s species, which are subjected to a deciduous condition during the winter time and to high transpiration rates during hot summers, leading to a higher investment in leaves and metabolism maintenance than AGB. Additionally, Araucaria forests are under the influence of cold winters with frequent frost and cloud conditions, which limit productivity through photosynthesis constrains, contrasting with hot summer periods.

We show that large-size trees are an important predictor of AGB, as expected. Similarly to our results, large-sized trees are related to higher AGB stocks in tropical forests (Slik et al. 2013; Poorter et al. 2015), reflecting their capacity for storing great amounts of biomass per stem. Also, large trees account for 64% of the AGB in these forests, about 158 Mg ha^{-1} on average (see Appendix I), reinforcing their importance for the global carbon cycle. This result further reflects the importance of the conservation of large-diameter trees, and the maintenance and conservation of old-growth forests (Lutz et al. 2018). Large trees also play a key role in creating habitat conditions for epiphytic flora, contributing for litter production, nesting sites, and microclimatic environments for arthropod species (Lindenmayer et al. 2012; Lohbeck et al. 2015). Therefore, conserving old-growth forests not only guarantees greater carbon stocks (due to large-sized trees protection), but also promotes the conservation of biodiversity at the most diverse trophic levels.

Large trees are often more susceptible to atmospheric drought (Ali et al. 2019b), due to higher evaporative demands (Bennett et al. 2015), especially in higher temperatures. Such relationship of large trees and temperature annual range shed light on the importance of climatic variables in subtropical forests structure (Ali et al. 2019c), and on biomass storage, as evidenced here. On the other hand, potential extreme climatic events derived from future climate changes in this subtropical region, such as increasing in temperature, precipitation and extreme events, may have a strong negative impact on the forest biomass stocks and accumulation capacity (Baker et al. 2004; Souza and Longhi 2019). These changes in climate may lead to higher tree mortality rates, and the further consequences in forest dynamics are related to faster carbon sequestration of young trees, but an overall lower carbon storage due to the increase in mortality rates in extreme events (Brienen et al. 2015; Aleixo et al. 2019).

4.3 Soil, diversity, and composition do not predict AGB in subtropical forests

We did not find a relationship between soil texture and AGB for the set of studied subtropical forests, but soil texture is positively related to AGB in tropical forests (Castilho et al. 2006). As our result is associated with clay content, it may indicate that AGB is not constrained by soil moisture in subtropical forests. Nevertheless, temperature annual range and soil texture (indirectly via LNC), positively affects functional diversity of these forest communities. This result indicates that environmental conditions imposed by higher temperature variability and potential soil water availability on species traits shape the diversity of traits in these forest communities (Bruelheide et al. 2018). Such conditions may maximise trait values for resources acquisition strategies in this condition (e.g., more photosynthetically efficient leaves, as there was a positive relationship between LNC and diversity). Regardless of the influence of soil, climate and LNC on functional diversity, diversity itself did not explain the AGB in subtropical forests, as previously reported for tropical forests (Finegan et al. 2015; Sullivan et al. 2017). This might be related to a potential saturation of niche complementarity effects in old-growth forests (Lasky et al. 2014).

Despite of the absence of relationship among functional traits and AGB, these variables are often good predictors of forest dynamics and AGB stocks (Finegan et al. 2015; Prado-Junior et al. 2016). For instance, higher mean LNC values in communities is potentially related to investments in resources acquisition, which may in turn lead to higher AGB along the time (Wright et al. 2004). Also, wood density is an important component to account for forest AGB (Baker et al. 2004). Surprisingly, we found that WD had no influence on the spatial variation of AGB across subtropical forests. This might be explained by the negative relationship between large-sized trees and community mean wood density (Appendix S9), with sites that had a greatest proportion of large trees also having lower community means of WD. For instance, these trees may be old and senescent trees, being remaining in old-growth forests. However, these large trees might be replaced along local forest dynamics (e.g., gap dynamics), as higher mortality rates are associated to big trees in subtropical forests (Ma et al. 2016; Bordin and Müller 2019), influencing the biomass stocks in the long-term ecosystem functioning. Our data also show a negative relationship between mean individual basal area and stem density (Appendix I), suggesting that we have a range in the development characteristics of studied forest remnants, which can be related to the historical selective logging experienced by these forests in the past (Fonseca 1985). Thus, some of these subtropical forests may have stocked more biomass in the past and, if competition processes are acting now on communities with high density of trees (i.e., self-thinning, see Pillet et al. (2018)), they have a greater potential for storing biomass in the future, when achieving a more mature state.

5. Conclusions

The South American subtropical forests have a great capacity to store AGB, which is strongly influenced by the climate and forest structure. The negative effect of temperature annual range shows that forest communities experiencing stable temperatures throughout the year contribute greatly to the AGB stocks in this region. Additionally, structurally complex forests with large-sized trees play a key role in the long-term persistence of carbon storage, and ecosystem processes maintenance. It reinforces the importance of preserving old-growth forests (Pyles et al. 2018), and of protecting regenerating secondary forests (Capellesso et al. 2020), by allowing them to achieve complex structures in order to maximize the carbon stocks in these forests, especially facing future climatic changes predicted for this region.

Quantifying the biomass stocks in subtropical forests is essential for understanding the potential of these forests to mitigate future carbon emissions. Future work based on long-term monitoring, should assess how these stocks vary over time. The maintenance of long-term plots is crucial for understanding forest dynamics and the potential carbon sink of these forest (Phillips et al. 1998), especially in the understudied subtropical forests (Bordin and Müller 2019).

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Authors’ contributions

KMB, AE-M and SCM conceived the ideas and designed methodology; KMB, RSB, JK, RCP, MAF, KJZ, JAJ, CFJ, MM, PH and ACS collected the data; KMB analysed the data; KMB led the writing of the manuscript with the contributions from AE-M and SCM, and RSB, JK, RCP, MVC, JAJ, CFJ, MM, PH and ACS contributed to the drafts.

Data availability

Part of the forest inventory data can be accessed through ForestPlots database (www.forestplots.net). Data for the analyses are available as a ForestPlots.net data package at http://doi.org/10.5521/Forestplots. net/2021_

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119126 (And after references topic as well)

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Appendix A

Plot information and test for plot sampled area effects in AGB estimates.

Table 1: Plot information used for evaluating the sampling area effect on above-ground biomass of subtropical forests.

Site	Longitude	Latitude	Forest type	Sampled area (ha)	Census number
AF01	-51	-29.6	Seasonal forest	0.1	1
AF02	-51	-29.6	Seasonal forest	0.1	1
Aluv	-50.2	-27.8	Araucaria forest	0.96	2
AR02	-50.9	-29.6	Seasonal forest	0.1	1
AW	-49.4	-27.7	Atlantic moist forest	0.4	1
CA	-50.7	-28.2	Seasonal forest	1	2
CA03	-50.3	-29.7	Atlantic moist forest	0.1	1
CA04	-50.3	-29.8	Atlantic moist forest	0.1	1
CA05	-50.3	-29.8	Atlantic moist forest	0.1	1
CA06	-50.3	-29.8	Atlantic moist forest	0.1	1
CA09	-50.3	-29.8	Atlantic moist forest	0.1	1
CA25	-50.4	-29.8	Atlantic moist forest	0.1	1
CA31	-50.4	-29.8	Araucaria forest	0.1	1
CA33	-50.3	-29.8	Atlantic moist forest	0.1	1
CA44	-50.4	-29.7	Seasonal forest	0.1	1
CA46	-50.3	-29.7	Seasonal forest	0.1	1
CA50	-50.3	-29.8	Atlantic moist forest	0.1	1
CA51	-50.3	-29.8	Atlantic moist forest	0.1	1
CB01	-51.1	-29.7	Seasonal forest	0.1	1
CE03	-50.8	-29.4	Seasonal forest	0.1	1
CE07	-50.6	-29.4	Araucaria forest	0.1	1
CN	-51.2	-27.6	Araucaria forest	1	1
CN02	-51.2	-29.9	Seasonal forest	0.1	1
CR	-50.3	-28.1	Araucaria forest	1	1
EEA-01	-50.2	-29.4	Araucaria forest	0.12	1
EEA-02	-50.2	-29.4	Araucaria forest	0.12	1
EEA-03	-50.3	-29.4	Araucaria forest	0.12	1
EN01	-50.8	-29.7	Seasonal forest	0.1	1
EN05	-50.8	-29.7	Seasonal forest	0.1	1
ENN-01	-50.2	-29.6	Atlantic moist forest	0.12	1
ENN-02	-50.2	-29.6	Atlantic moist forest	0.12	2
Epagri	-50.4	-27.8	Araucaria forest	1	3
EV01	-51.2	-29.7	Seasonal forest	0.1	1
FL01	-50.4	-29.4	Araucaria forest	0.1	1
FL02	-50.4	-29.4	Araucaria forest	0.1	1
FL03	-50.4	-29.4	Araucaria forest	0.1	1

FL04	-50.4	-29.4	Seasonal forest	0.1	1
FNC-01	-52.8	-27.1	Seasonal forest	1.2	3
GA	-50.3	-27.9	Araucaria forest	1	1
HE	-50.1	-29.6	Atlantic moist forest	0.24	1
IG01	-50.8	-29.6	Seasonal forest	0.1	1
IV01	-51.1	-29.6	Seasonal forest	0.1	1
LE	-50.1	-29.6	Atlantic moist forest	0.24	1
MA01	-51	-29.7	Seasonal forest	0.1	1
MA02	-51	-29.7	Seasonal forest	0.1	1
MA03	-51	-29.7	Seasonal forest	0.1	1
MA05	-51	-29.7	Seasonal forest	0.1	1
MA06	-51	-29.7	Seasonal forest	0.1	1
MA07	-51	-29.7	Seasonal forest	0.1	1
MA08	-51	-29.7	Seasonal forest	0.1	1
MA09	-51	-29.7	Seasonal forest	0.1	1
MA10	-51	-29.7	Seasonal forest	0.1	1
MA11	-51	-29.7	Seasonal forest	0.1	1
MA12	-51	-29.7	Seasonal forest	0.1	1
MB01	-51	-29.8	Seasonal forest	0.1	1
MB02	-51	-29.8	Seasonal forest	0.1	1
MD01	-51.2	-29.7	Seasonal forest	0.1	1
ME	-50.1	-29.6	Atlantic moist forest	0.24	1
MFO-01	-50.2	-29.5	Atlantic moist forest	0.12	2
MFO-02	-50.2	-29.6	Atlantic moist forest	0.12	2
MN	-49.6	-28.1	Araucaria forest	1	3
MO01	-50.9	-29.6	Seasonal forest	0.1	1
MW01	-51	-29.7	Seasonal forest	0.1	1
NH02	-51	-29.8	Seasonal forest	0.1	1
OS03	-50.3	-29.9	Atlantic moist forest	0.1	1
OS04	-50.3	-29.8	Atlantic moist forest	0.1	1
Parnamul	-50.3	-27.8	Araucaria forest	1	3
PB04	-50.9	-29.6	Seasonal forest	0.1	1
PB1	-50.2	-27.9	Araucaria forest	1	3
PB2	-50.2	-27.9	Araucaria forest	1	2
PF01	-51	-29.7	Seasonal forest	0.1	1
PNA-01	-50.1	-29.2	Araucaria forest	0.12	2
PNA-02	-50.1	-29.2	Araucaria forest	0.12	2
PNA-03	-50.1	-29.2	Araucaria forest	0.12	2
PO04	-51.2	-29.7	Seasonal forest	0.1	1
PRM-01	-50.2	-29.5	Araucaria forest	0.12	2
PRM-02	-50.2	-29.5	Araucaria forest	0.12	2
PRM-03	-50.2	-29.5	Araucaria forest	0.12	2
PSJ1	-49.5	-28.1	Araucaria forest	0.2	1
PSJ3	-49.6	-28.2	Araucaria forest	0.2	1
RO02	-50.5	-29.6	Seasonal forest	0.1	1
RZ03	-50.4	-29.6	Seasonal forest	0.1	1

RZ04	-50.3	-29.6	Seasonal forest	0.1	1
RZ05	-50.3	-29.6	Seasonal forest	0.1	1
RZ06	-50.3	-29.7	Seasonal forest	0.1	1
SA04	-50.4	-29.7	Seasonal forest	0.1	1
SA05	-50.4	-29.7	Seasonal forest	0.1	1
SA08	-50.6	-29.8	Seasonal forest	0.1	1
SAM_EN_A5	-55.4	-28.5	Seasonal forest	0.5	1
SAM_EN_A5_Sup	-55.4	-28.5	Seasonal forest	0.5	1
SAM_EN_B7	-55.4	-28.5	Seasonal forest	0.5	1
SBV_EN_C3	-53.2	-30.8	Seasonal forest	0.5	1
SBV_EN_C5	-53.2	-30.8	Seasonal forest	0.5	1
SBV_EN_D5	-53.2	-30.9	Seasonal forest	0.5	1
SF01	-50.6	-29.5	Araucaria forest	0.1	1
SF02	-50.6	-29.5	Araucaria forest	0.1	1
SF05	-50.6	-29.5	Araucaria forest	0.1	1
SF08	-50.5	-29.5	Araucaria forest	0.1	1
SF09	-50.5	-29.4	Araucaria forest	0.1	1
SF13	-50.6	-29.5	Seasonal forest	0.1	1
SF14	-50.5	-29.5	Seasonal forest	0.1	1
SG_EN_B2	-54.3	-30.1	Seasonal forest	0.5	1
SG_EN_D2	-54.3	-30.1	Seasonal forest	0.5	1
SG_EN_E3	-54.3	-30.1	Seasonal forest	0.5	1
SG01	-50.9	-29.5	Seasonal forest	0.1	1
ST02	-51	-29.8	Seasonal forest	0.1	1
ST03	-51	-29.8	Seasonal forest	0.1	1
TC02	-50.8	-29.5	Seasonal forest	0.1	1
TC04	-50.7	-29.5	Seasonal forest	0.1	1
TC05	-50.8	-29.4	Seasonal forest	0.1	1
TQ01	-50.7	-29.6	Seasonal forest	0.1	1
TQ03	-50.7	-29.8	Seasonal forest	0.1	1
TQ04	-50.7	-29.6	Seasonal forest	0.1	1
TQ05	-50.8	-29.7	Seasonal forest	0.1	1
TQ07	-50.8	-29.8	Araucaria forest	0.1	1
turvo	-53.9	-27.2	Seasonal forest	1	1
Varg	-51	-27.6	Seasonal forest	0.96	2
Zjar	-49.9	-29.4	Atlantic moist forest	1	1
Zjur	-51.9	-30.7	Seasonal forest	1	1

Test for plot sampled area effects in AGB estimates.

Analysis related to above-ground biomass in inventory plots with different sample sizes, especially smaller plots, may present a large variation to the overall biomass estimates. In these cases, to evaluate the needs of corrections and further implementation of weights for predictive analysis is strongly recommended (Lewis et al. 2009). The effect of sample effort was accessed through the slope of the relationship between above-ground biomass estimate and area (Figure 1a). After that, we tested the relationship between residuals*area vs. sampled area (Figure 1b). A positive relationship was found in this second test, which means a potential bias in AGB estimation, reinforcing the needs for correction in the following analysis. To correct this potential bias we conducted a transformation of the sampled area by the cubic root of the area, and then we tested again the relationship between the residuals *cubic root of the area *vs.* the sampled area (1c). This test showed us that the cubic root of the sampled area is enough for correcting the bias, and we further used this metric as weighting variable in the models.

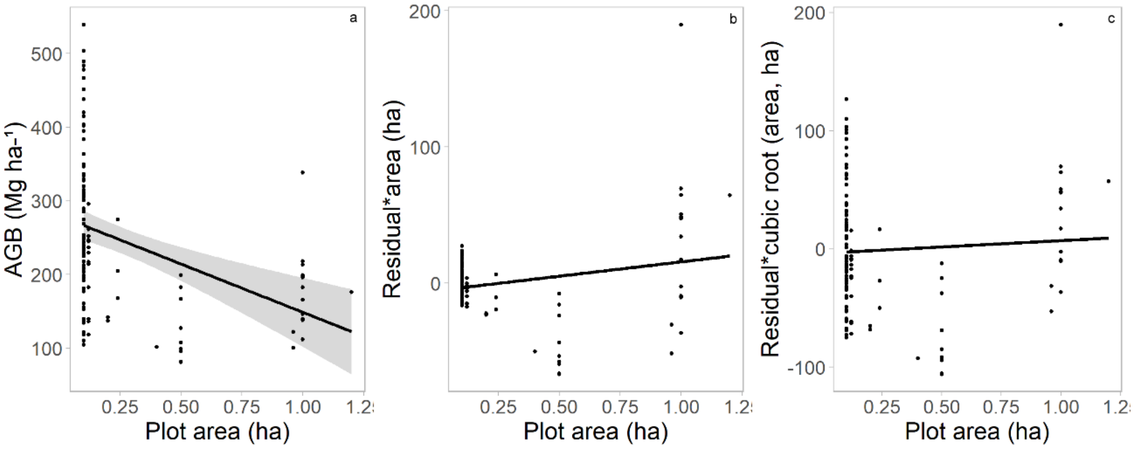
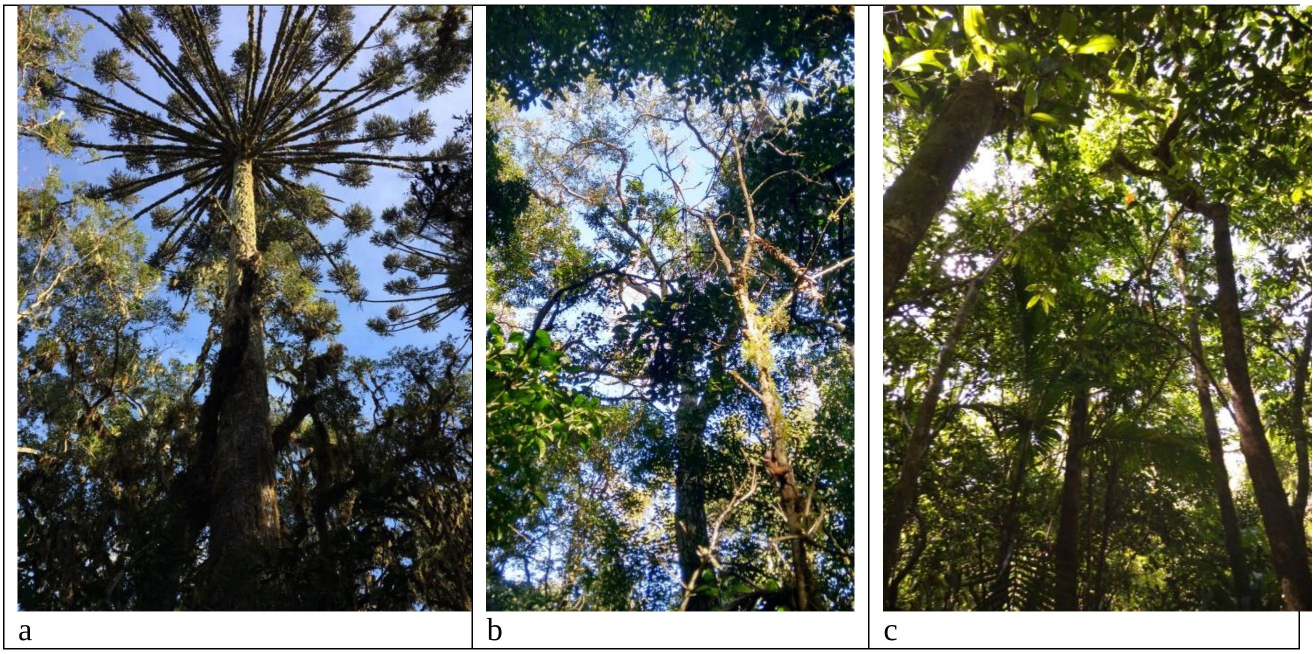


Figure 1: a: Relationship between above-ground biomass estimate and sampled area; b: Relationship between residuals*area *vs.* sampled area; c: Relationship between residuals * cubic root (area) *vs.* sampled area.

Appendix B

Brazilian subtropical forests studied for estimating above-ground biomass. a) Araucaria forest; b) Seasonal forest; and c) Atlantic moist forest. © Kauane Maiara Bordin



a b c

Appendix C

Climatic and edaphic variation across South American subtropical forests.

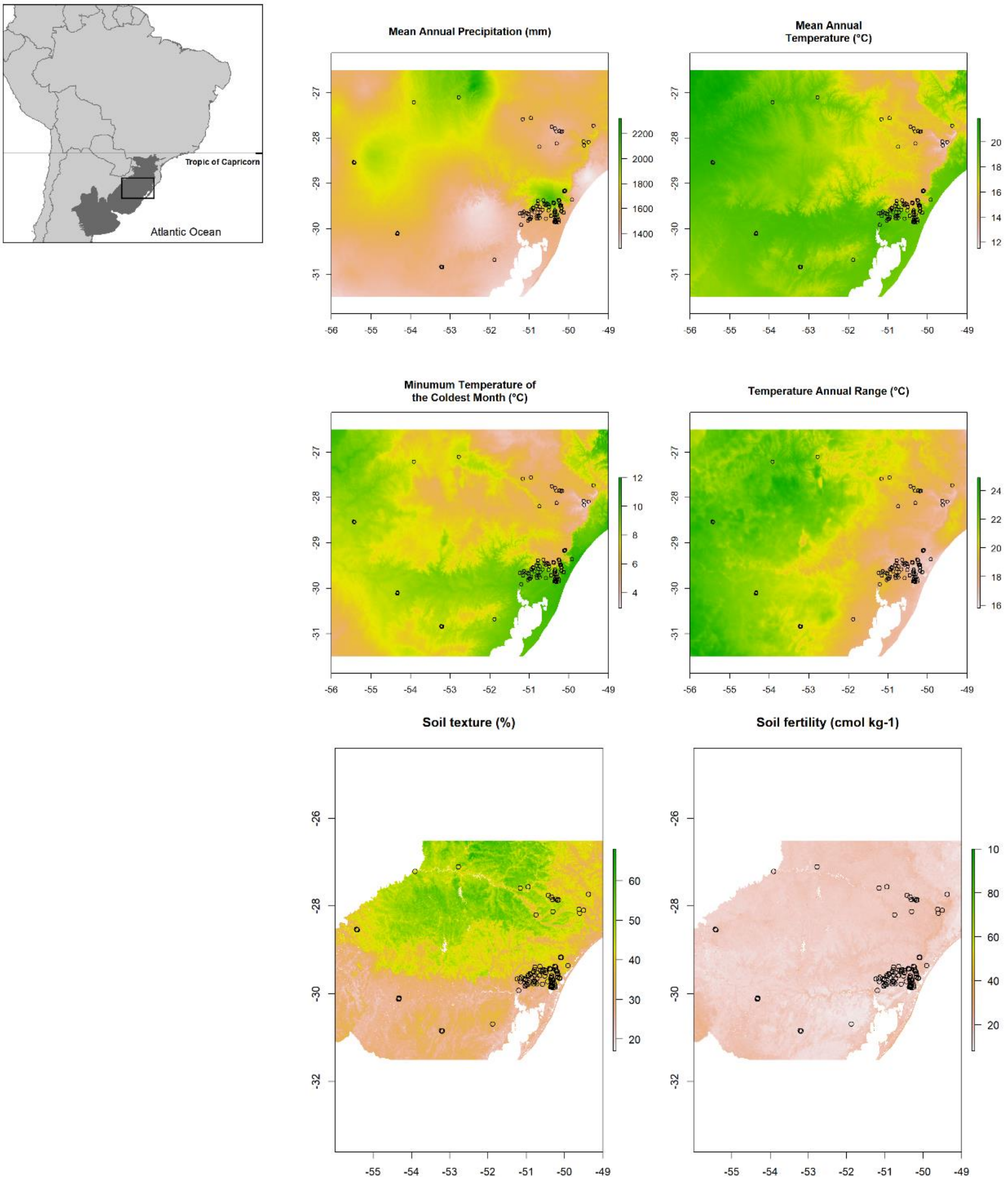


Figure 1: Climatic and edaphic variables across 119 sites in South American subtropical forests. The figures show the mean annual precipitation (mm), mean annual temperature (°C), minimum temperature of the coldest month (°C), temperature annual range (°C), soil texture and soil fertility.

Appendix D

Functional traits and ecological function in tree species.

The leaf functional traits were obtained from our Plant Ecology Lab database (from Universidade Federal do Rio Grande do Sul, Brazil, and also TRY database (Kattge et al. 2020)), and local collections (data obtained since the 2013, following the standardized protocol developed by Pérez-Harguindeguy et al., 2013). Wood density was obtained from wood density database (Zanne et al. 2009; Chave et al. 2014), Missio et al. (2017) and Oliveira, Uller, Klitzke, Eleotério, & Vibrans (2019). Obtaining leaf trait had the following collection procedures: at least five leaves per plant (to obtain the individual mean) and at least three individuals per species (to obtain species trait value). To access leaf area values, the fresh leaves were scanned. All simple leaves selected were measured including petioles, and compound leaves had just the leaflet area measured, without rachis. Leaf nitrogen content was obtained from samples composed by at least three individuals' leaves.

Functional trait	Ecological function	Reference
Specific Leaf Area (SLA, cm^2/g)	Photosynthetic assimilation, leaf nutrient concentration and light interception	(Wright et al. 2004; Poorter et al. 2008)
Leaf Dry Matter Content (LDMC, mg/g)	Leaf stem structures, nutrient cycling, forest productivity	(Fortunel et al. 2009; Smart et al. 2017)
Leaf Nitrogen Content (LNC, %)	Dark respiration and photosynthetic assimilation	(Wright et al. 2004; Rowland et al. 2017)
Wood Density (WD, g/cm^3)	Hydraulic conductance, stem structures	(Poorter et al. 2008; Chave et al. 2009)

Appendix E

Species composition and variable selection

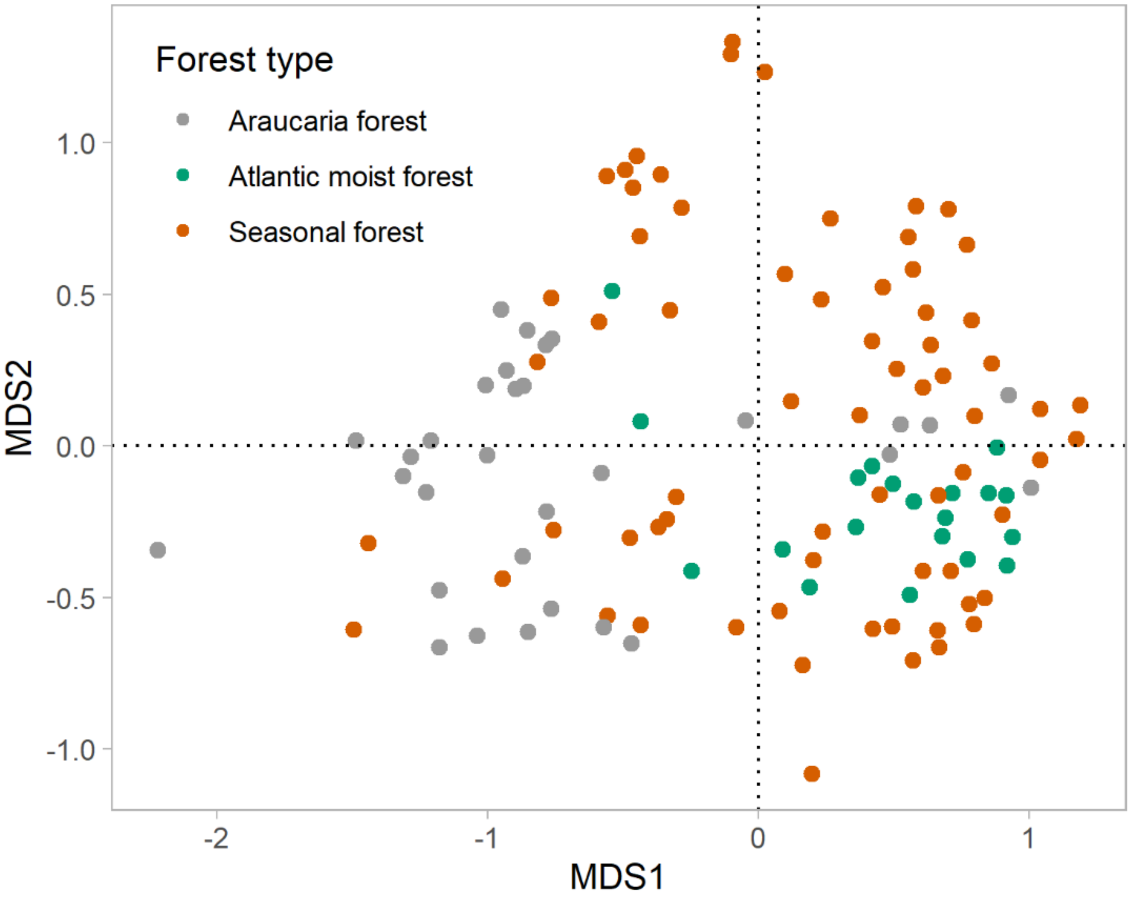


Figure 1: Non-metric multidimensional scaling (NMDS), derived from species basal area matrix. This matrix was Hellinger transformed prior to analysis. The first NMDS axis was used as a proxy for tree species composition influence on above-ground biomass.

Model selection used for diversity and composition variable selection.

Model selection: AGB ~ composition variables					
AGB ~ SLA + LDMC + LNC + WD + NMDS1					
Component models	df	logLik	AICc	delta	weight
124	**5**	**-160.56**	**331.66**	**0**	**0.31**
1245	6	-159.79	332.33	0.67	0.22
245	5	-160.94	332.41	0.75	0.21
1234	6	-160.21	333.16	1.51	0.14
2345	6	-160.41	333.57	1.91	0.12
Term codes:	**LDMC:1**	**LNC:2**	NDMS1:3	**SLA:4**	WD:5
Model averaged coefficients					
Full average	Estimate	SE	Adj. SE	z-value	P- value
(Intercept)	-9.648E-17	0.0870	0.0879	0	1
LDMC	**-0.1211**	**0.1170**	**0.1175**	**1.031**	**0.30273**
LNC	**0.2472**	**0.1091**	**0.1102**	**2.243**	**0.02491**
SLA	**-0.3704**	**0.1117**	**0.1129**	**3.282**	**0.00103**
WD	-0.08115	0.1016	0.1021	0.795	0.42683
NDMS1	0.03005	0.0820	0.0825	0.364	0.71585
Conditional average	Estimate	SE	Adj. SE	z-value	P- value
(Intercept)	-9.648E-17	0.0870	0.0879	0	1
LDMC	**-0.1804**	**0.0984**	**0.0994**	**1.815**	**0.06951**
LNC	**0.2472**	**0.1091**	**0.1102**	**2.243**	**0.02491**
SLA	**-0.3704**	**0.1117**	**0.1129**	**3.282**	**0.00103**
WD	-0.1480	0.0946	0.0955	1.548	0.12153
NMDS1	0.1144	0.1263	0.1277	0.896	0.37001

Model selection: AGB ~ diversity variables					
AGB ~ Functional diversity + Species rarefaction + Simpson index					
Component models	df	logLik	AICc	delta	weight
(Null)	2	-168.35	340.81	0	0.69
1	**3**	**-168.12**	**342.45**	**1.64**	**0.31**
Term codes:	**Functional diversity:1**				
Model averaged coefficients					
Full average	Estimate	SE	Adj. SE	z-value	P- value
(Intercept)	-1.373E-17	0.09173	0.09269	0	1
Functional diversity	**-0.01911**	**0.05859**	**0.05906**	**0.324**	**0.746**
Model averaged coefficients					
Conditional average	Estimate	Std. Error	Adj. Std. Error	z-value	P- value
(Intercept)	-1.373E-17	0.09173	0.09269	0	1
Functional diversity	-0.0625	0.0922	0.09323	0.67	0.503

Appendix F

Test for detecting spatial autocorrelation between above-ground biomass and predictor variables, using generalized least-squares approach and spherical correlation.

Table 1: Generalized Least Squares models testing for spatial autocorrelation.

Response variable	**Predictor variable**	**Intercept**	**SE**	**t-value**	**p-value**	**AIC**
Above-ground biomass	**Specific Leaf Area**	**-0.18**	**0.09**	**-2.06**	**0.04**	**338.45**
	Specific Leaf Area + corr	-0.19	0.09	-2.11	0.03	339.71
	Leaf Nitrogen Content	0.08	0.09	0.89	**0.37**	**341.95**
	Leaf Nitrogen Content + corr	0.08	0.09	0.91	0.36	341.89
	Leaf Dry-Matter Content	**-0.13**	**0.09**	**-1.49**	**0.13**	**340.45**
	Leaf Dry-Matter Content + corr	-0.13	0.09	-1.46	0.14	341.99
	Functional diversity	**-0.06**	**0.09**	**-0.67**	**0.49**	**342.23**
	Functional diversity + corr	-0.05	0.09	-0.64	0.51	343.72
	Large-sized trees	**0.69**	**0.06**	**10.35**	**0**	**265.24**
	Large-sized trees + corr	0.69	0.06	10.39	0	**266.30**
	Mean Annual Precipitation	**0.33**	**0.08**	**3.79**	**0.00**	**328.91**
	Mean Annual Precipitation + corr	0.32	0.08	3.73	0.00	330.74
	Anual Temperature Range	**-0.39**	**0.08**	**-4.61**	**0**	**322.81**
	Anual Temperature Range + corr	-0.38	0.08	-4.58	0	324.52
	Minimum Temperature of the Coldest Month	**0.12**	**0.09**	**1.41**	**0.15**	**340.67**
	Minimum Temperature of the Coldest Month + corr	0.13	0.09	1.49	0.13	341.90
	Soil Texture	**0.17**	**0.09**	**1.87**	**0.06**	**339.17**
	Soil Texture+corr	0.16	0.09	1.80	0.07	340.88
	Soil Fertility	**0.13**	**0.09**	**1.45**	**0.14**	**340.57**
	Soil Fertility + corr	0.12	0.09	1.36	0.17	342.26

Appendix G

Results of the model selection for 12 structural equation models that evaluate the effects of climate, soil, diversity, composition, and forest structure on above-ground biomass of subtropical forests (Table S1). The model selected is also shown in Fig. 4. For the model selected (Table S2, Goodness of fit: Fisher's C = 1.953; P-value = 0.744; DF= 4), the standardized coefficients (Std.Coef.), standard error (SE), and P-value are given for all regressions (i.e., all arrows in Fig. 4). SLA = Specific Leaf Area, LNC = Leaf Nitrogen Content, **LDMC** = Leaf Dry-Matter Content.

Table 1: Model selection results.

Response variable	**Climate**	**Soil**	**Composition**	**Diversity**	**Large-sized trees**	**P-value**	**AIC**
Above-ground biomass	**Temperature Annual Range**	**Texture**	**LNC**	Functional diversity	Large-sized trees	**0.744**	**49.95**
	Temperature Annual Range	Fertility	LNC			0.672	50.35
	Mean Annual Precipitation	Texture	LNC			0.569	50.93
	Mean Annual Precipitation	Texture	LDMC			0.549	51.05
	Temperature Annual Range	Fertility	LDMC			0.533	51.14
	Mean Annual Precipitation	Fertility	LDMC			0.469	51.56
	Minimum Temperature of Coldest Month	Texture	LNC			0.451	51.68
	Temperature Annual Range	Fertility	SLA			0.427	51.85
	Minimum Temperature of Coldest Month	Fertility	LDMC			0.412	51.96
	Temperature Annual Range	Texture	LDMC			0.410	51.97
	Mean Annual Precipitation	Fertility	LNC			0.233	53.58
	Minimum Temperature of Coldest Month	Texture	LDMC			0.164	54.36
	Minimum Temperature of Coldest Month	Fertility	SLA			0.135	55.02
	Minimum Temperature of Coldest Month	Fertility	LNC			0.402	55.03
	Mean Annual Precipitation	Fertility	SLA			0.127	55.17
	Minimum Temperature of Coldest Month	Texture	SLA			0.118	55.37
	Temperature Annual Range	Texture	SLA			0.103	55.70
	Mean Annual Precipitation	Texture	SLA			0.045	57.72

Table 2: Model selected (Fig. 4) using SEM approach. Direct and indirect effects of predictor variables on above-ground biomass. Standard error (SE), P-value, and Standardized coefficient (Std.coef) are presented.

Response variable	**Predictor variable**	**SE**	**P-Value**	**Std.Coef**
Above-ground biomass	Temperature Annual Range	0.084	0.001	**-0.28**
Above-ground biomass	Soil texture	0.074	0.801	-0.02
Above-ground biomass	Large-sized trees	0.070	0.000	**0.62**
Above-ground biomass	Leaf Nitrogen Content	0.086	0.246	0.10
Above-ground biomass	Functional diversity	0.087	0.206	-0.11
Large-sized trees	Temperature Annual Range	0.119	0.181	-0.16
Large-sized trees	Soil texture	0.099	0.117	0.16
Functional diversity	Temperature Annual Range	0.091	0.031	**0.20**
Functional diversity	Soil texture	0.080	0.295	0.08
Functional diversity	Leaf Nitrogen Content	0.080	0.000	**0.60**
Leaf Nitrogen Content	Temperature Annual Range	0.100	0.750	0.03
Leaf Nitrogen Content	Soil texture	0.086	0.042	**0.18**

Appendix H

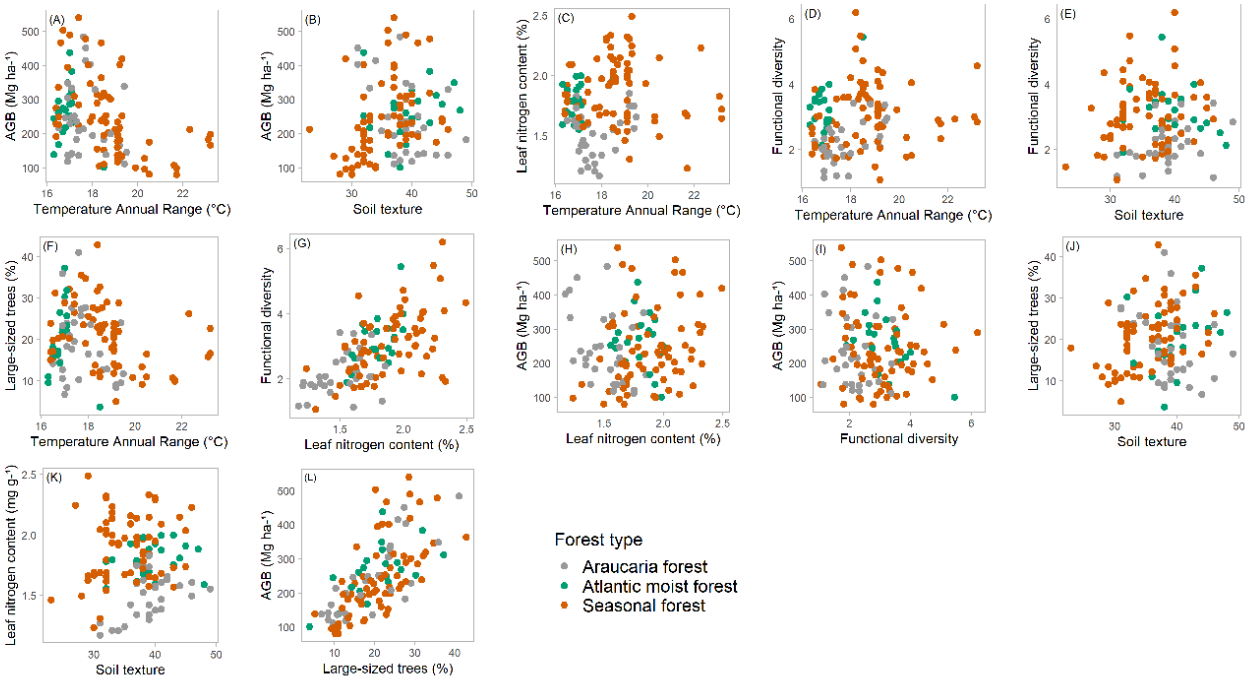


Figure 1: Scatterplots of the bivariate relationships between direct and indirect predictors of above-ground biomass (AGB) stocks. Predicted relationships are established at Fig. 1 from main text.

Appendix L

Biomass corresponding to large-sized trees, relationships of community-weighted mean of wood density with large-sized trees; and individual basal area and stem density per community sites.

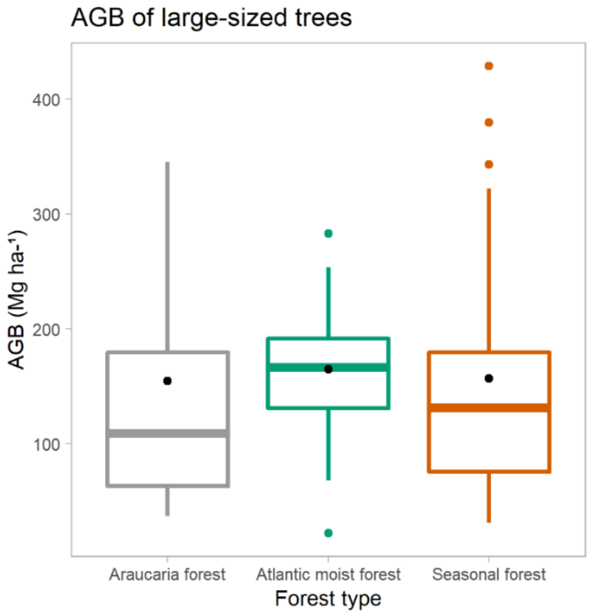


Fig 1: Above-ground biomass of large-sized trees (trees ≥ 30 dbh) in community sites in South American subtropical forests. Back points inside the boxes represent the mean values.

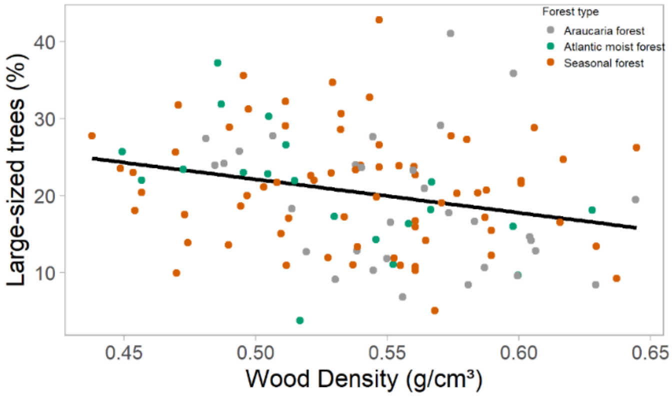


Fig. 2: Relationship between community-weighted mean of wood density and the proportion of large-sized trees in community sites in South American subtropical forests.

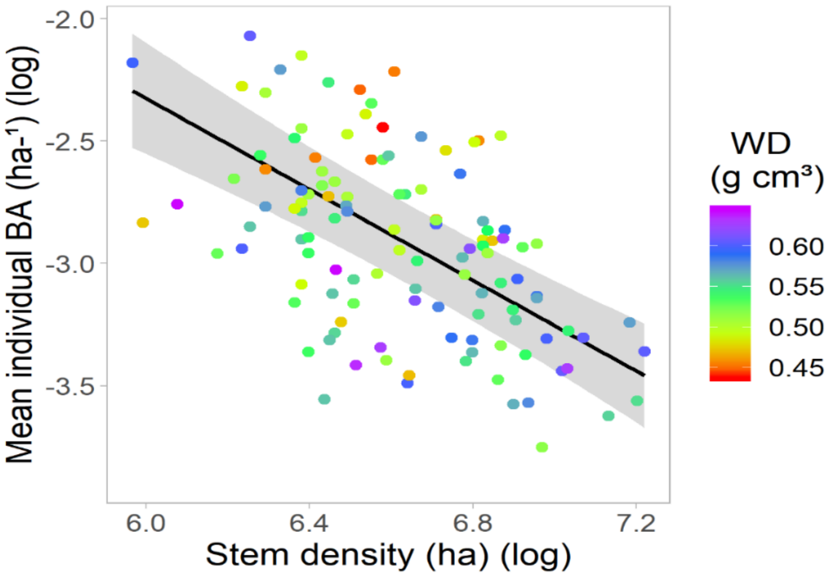


Fig.3: Relationship between the means of individual basal area and stem density per community sites, considering yet the community-weighted means of woody density (WD), following the approach of Pillet et al. (2018) for visually evaluating self-thinning process.

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Capítulo 2

Chapter 2

No relationship between biodiversity and forest carbon sink across the subtropical Brazilian Atlantic Forest

Capítulo em revisão na revista *Perspectives in Ecology and Conservation*

Chapter under review at Journal Perspectives in Ecology and Conservation

No relationship between biodiversity and forest carbon sink across the subtropical Brazilian Atlantic Forest

Running title: Carbon sink capacity across subtropical Brazilian Atlantic Forest

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Abstract

The Brazilian Atlantic Forest (BAF) is a global biodiversity hotspot, but its carbon sink capacity, especially in the subtropical portion, is poorly understood. We aimed to evaluate the relationship between biodiversity measures (i.e., taxonomic, functional, and phylogenetic diversity) and net carbon change across subtropical BAF, testing whether there is a win-win situation in the conservation of biodiversity and carbon sink capacity across forests of distinct ages. We obtained the net carbon change from 55 permanent plots, from early successional to old-growth forests, by combining the carbon gains and losses across two censuses. We found that subtropical BAF are on average acting as a carbon sink, but carbon gains and losses varied a lot across plots, especially within late successional/old-growth forests. The carbon sink was consistent across different forest ages, and we did not find a relationship between biodiversity and net carbon change in subtropical BAF. Therefore, conservation programs should aim at both targets in order to maximize the protection of biodiversity and carbon capture across the secondary and old-growth subtropical BAF, especially in a scenario of global changes.

Keywords: Biodiversity conservation, carbon dynamics, forest dynamics, forest productivity, net carbon change, tree mortality.

Introduction

The Brazilian Atlantic Forest (BAF) is widely recognised as a biodiversity hotspot (Myers et al., 2000), making it a global conservation priority. Under the current context of global changes, preserving forests with high capacity to absorb and store carbon becomes a fundamental conservation goal. However, we have only punctual assessments of the capacity of BAF to absorb carbon (Bordin and Müller, 2019; Capellesso et al., 2020; Maia et al., 2020; Rolim et al., 2005). The BAF suffers with historical deforestation, degradation, recent land-use changes (Ribeiro et al., 2009), and land in large areas of the region have been abandoned, meaning that these forests are a mosaic of successional stages (Rosa et al., 2021). The profound human impact across BAF has led to the loss of biodiversity and carbon stocks (Bergamin et al., 2017; Lima et al., 2020), with potential impacts to the carbon sink capacity of these forests. Most conservation programs in the BAF to date have focused on preserving biodiversity (Grelle et al., 2021). However, whether conservation efforts to preserve biodiversity will also lead to the conservation of the carbon sink capacity resulting in a win-win conservation scenario across these forests is still unknown. A win-win scenario where strategies to preserve biodiversity maintain forests with large carbon capture capacity would be especially welcomed facing current biodiversity and climate emergency (Mori et al., 2021; Reside et al., 2017), but the presence of such relationship is likely to be dependent on scale, forest type and biodiversity metric evaluated (Capellesso et al., 2021; Ferreira et al., 2018; Mori et al., 2021).

Biodiversity is a multifaceted concept that integrates taxonomic, functional, and phylogenetic diversity. Nonetheless, the effects of biodiversity on the carbon sink capacity, or net carbon change (the balance between carbon gains through productivity and recruitment and carbon losses through tree mortality (Phillips et al., 1998)) remains poorly understood (Poorter et al., 2017). For instance, local-scale studies in the subtropical BAF found no relationship between biodiversity and carbon sink capacity and stocks (Bordin and Müller, 2019; Capellesso et al., 2020). However, as forests in the BAF are very heterogeneous, varying in species composition (Bergamin et al., 2017), structure (Bordin et al., 2021), and biodiversity (Lima et al., 2020), local assessments may be unable to capture the regional picture. Thus, regional studies assessing the influence of biodiversity on net carbon change would allow deeper understanding of forest dynamics and their long-term implications for conservation (Ferreira et al., 2018) and restoration of both carbon sink capacity and biodiversity (Matos et al., 2019).

Taxonomic diversity is commonly used to evaluate the relationship between carbon and biodiversity (Ferreira et al., 2018; Mori et al., 2021). Nevertheless, taxonomic diversity is only one of the diversity facets, and may be unable to capture other aspects of diversity, such as functional and phylogenetic diversity. Functional diversity, for instance, quantifies the range of plant forms and strategies, and therefore is expected to capture ecosystem functions due to niche complementarity (Diaz and Cabido, 2001). Additionally, different plant lineages may have different roles in forest carbon cycling (Coelho de Souza et al., 2019), and closely related species often show similar capacity of carbon storage (de Aguiar-Campos et al., 2021). Thus, the presence or absence of certain species may imply in lower or higher phylogenetic diversity, and then affect carbon gains over time. Therefore, distinct diversity measures may have distinct relationships with carbon dynamics and may help understanding such relationship and its implications for conservation.

Old-growth and successional forests are expected to differ in terms of their carbon dynamics and to have different relationship between biodiversity and their carbon sink capacity. In the tropical region, successional forests frequently show larger carbon uptakes than old-growth forests (Heinrich et al., 2021; Poorter et al., 2016). In contrast, old-growth forests in subtropical BAF show higher gains in biomass over time than successional forests (Shimamoto et al., 2014; Souza and Longhi, 2019). These old-growth subtropical BAF are also able to stock large amounts of biomass, equivalent to many tropical forests (Bordin et al., 2021). The subtropical BAF is highly diverse (Bergamin et al., 2017), and is likely to have high carbon accumulation potential (Bordin et al., 2021; Bordin and Müller, 2019; Capellesso et al., 2021; Gross et al., 2018; Souza and Longhi, 2019; Vibrans et al., 2022), but it is currently underrepresented in global net biomass change estimations (Requena Suarez et al., 2019). The carbon sink capacity across successional and old-growth subtropical BAF and their relationship with biodiversity is a powerful and yet missing information to future conservation efforts across this region.

Here we investigated the relationships between the different aspects of biodiversity measured at different levels (i.e., taxonomic, functional, and phylogenetic diversity) and net carbon change across successional and old-growth forests in the subtropical BAF. We aim to quantify the carbon sink capacity of these forests, determine whether there is a relationship between biodiversity and carbon sink capacity and which biodiversity aspect most affects the net carbon change in this region. A positive relationship between biodiversity and net carbon change would imply a win-win scenario in forest conservation.

Material and Methods

1 Study area, forest dynamics, and trait data

The Brazilian Atlantic Forest (BAF) is a biodiversity hotspot, with large latitudinal distribution (from latitude 5° to 30°S) encompassing high heterogeneity of environments (Oliveira-Filho and Fontes, 2000). The mean temperature across subtropical BAF is 18°C, and the mean annual precipitation is 1,800 mm. We used vegetation data from 55 plots distributed across subtropical BAF (Figure 1), where 31 are old-growth forests and 24 are successional forests, with regeneration age varying from 15 to over 80 years after disturbance from pasture or agriculture ceased. Each of these sites contain permanent plots with two censuses over time. All census occurred between the year 2000 and 2020. Most t1 occurred between 2010 and 2016, and most t2 occurred between 2016 a 2020. The mean sampled area is 0.4 ha (0.06 – 1.2 ha) and mean census interval is 6 years (1 – 9 years) (Supplementary Information 1).

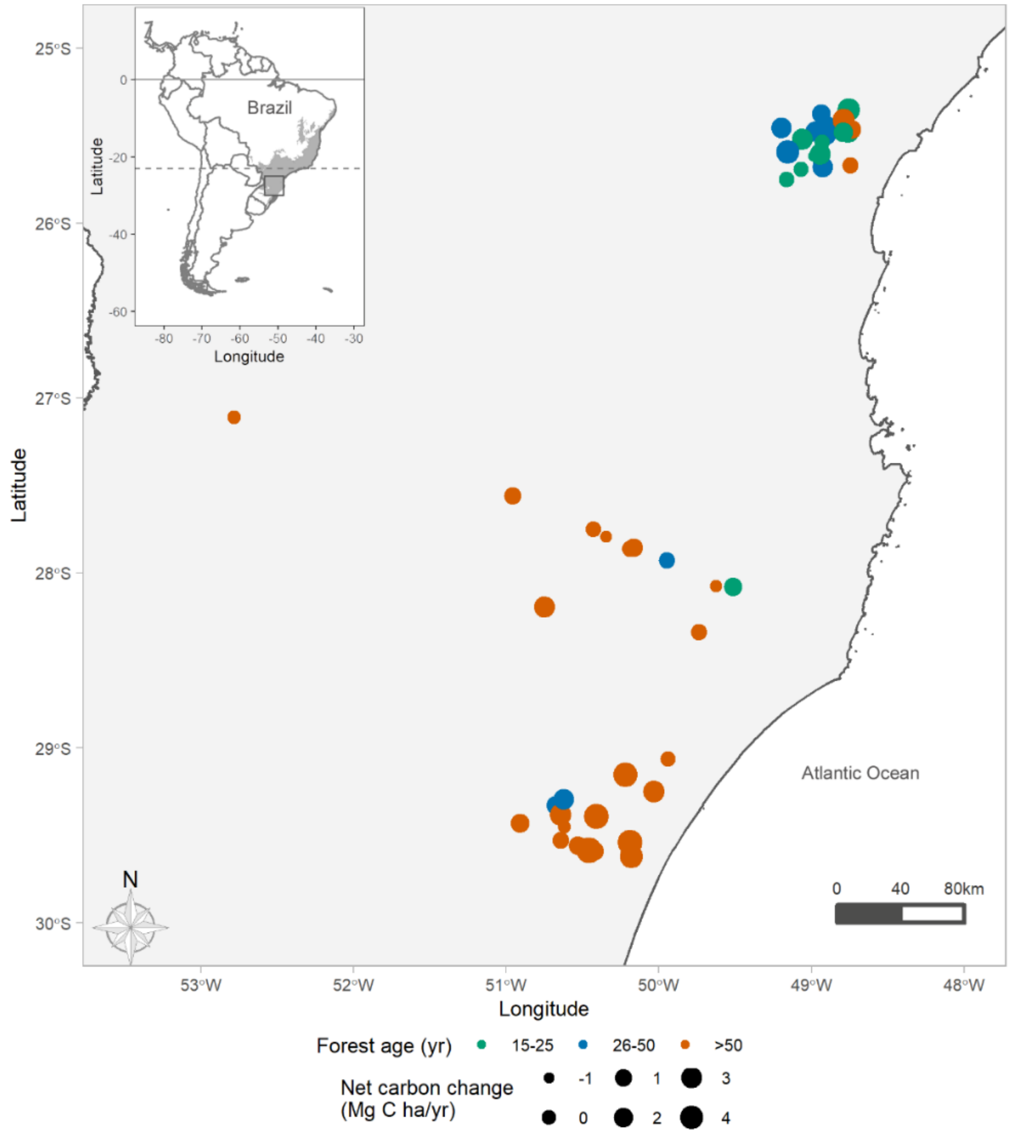

Figure 1: Distribution of sampling points across subtropical Brazilian Atlantic Forest (BAF). The colours represent forest age (green = 15-25 years, blue = 25-50 years, and

orange = >50 years), and point size represents the net carbon change estimates per plot. Distribution of the BAF is detailed in grey. Points show the location of the sampling units at subtropical BAF. For visualization purposes, the position of points is slightly shifted when they overlap.

The forest inventories followed the RAINFOR protocol whenever possible (22 plots) (Phillips et al., 2001). In each plot, all stems ≥ 10 cm of diameter of breast height (dbh) had their diameter measured at 1.3 m above the ground, or 30 cm above buttresses or trunk irregularities using a diameter tape. Stems were tagged with a unique number, were identified at species level, and had tree height (H, m) estimated by eye (0.8 % of stems) or measured using telemetric and laser tapes (99.2 % of stems). This procedure was adopted in the first (t1) and second census (t2). In t2, all surviving stems tagged in t1 were re-measured, new trees (recruits) were measured, tagged, and identified, and dead or absent stems were accounted as dead stems. We maintained palm species in the dataset to account for carbon gains through recruitment and losses through mortality, as palms do not present secondary growth (Supplementary Information 2). Lianas and ferns were excluded from our analyses. For more details, see (Phillips et al., 2001).

We collected information for the following plant traits: specific leaf area (SLA, cm2 g^{-1}), leaf dry-matter content (LDMC, mg g^{-1}), wood density (WD, g cm3), and species maximum height (Hmax, m). These data are also available at TRY database and can be accessed under formal request (Kattge et al., 2020). All data collection followed the standardised protocol developed by (Pérez-Harguindeguy et al., 2013). For leaf traits, we collected at least five leaves per individual and at least three individuals per species. The leaf area values were calculated from scanned fresh leaves. All simple leaves selected were measured including petioles, and compound leaves had just the leaflet area measured, without rachis. Wood density collection also followed the standardised protocol, and species values were obtained from plot (Missio et al., 2017) and regional level (Oliveira et al., 2019), and global databases (Chave et al., 2009; Zanne et al., 2009). Details about the trait collection, measurement, and expected effect of each trait on species fitness and overall community is described at Supplementary Information 3.

2 Carbon estimation

All living stems were used to estimate individual above-ground biomass (AGB) in both censuses, by applying a pantropical biomass equation. This equation considers tree dbh, height, and species wood density ($AGB = 0.0673 (WD\ dbh^2\ H)^{0.976}$, (Chave et al., 2014). We converted all AGB values to above-ground carbon by multiplying AGB by 0.456 (Martin et al., 2018). The tree-level above-ground carbon estimates were summed to obtain the above-ground carbon values for each plot.

Net carbon change was estimated as the balance between above-ground woody carbon productivity and above-ground carbon loss through mortality (Phillips et al., 1998). Total above-ground carbon stocks per plot was obtained as the sum of the above-ground carbon estimations of all living trees in t2. To obtain woody productivity and loss metrics, we used the information of all stems in both t1 and t2 censuses. Then, we obtained the annual rates of above-ground woody carbon productivity by combining carbon estimates for growth of surviving trees (meaning growth, t2-t1) and recruitment (recruited trees from t1 to t2). Carbon losses through mortality were estimated based on the carbon of dead trees between t1 to t2. We evaluated above-ground woody carbon productivity and loss by using the equations 3 and 4 recommended by (Kohyama et al., 2019) (Supplementary Information 2). All carbon dynamics metrics were obtained as annual estimations ($Mg\ C\ ha^{-1}\ yr^{-1}$).

3 Biodiversity metrics

We estimated taxonomic, functional, and phylogenetic diversity to evaluate their effects on the forest carbon sink capacity. These metrics were obtained based on the community matrix per site described by species stem density (number of stems ha^{-1}; Supplementary Information 2) using the data from second census in each plot. Taxonomic diversity was calculated using the Inverse Gini-Simpson index, which gives a greater weight to the common species across the communities. Functional diversity (FD) was estimated using Rao's quadratic entropy to give a greater weight for the functional contribution of the common species across communities. This FD metric is equivalent to the chosen taxonomic diversity metric. Phylogenetic diversity (PD) was evaluated via Mean Pairwise Distance, to obtain the mean phylogenetic relatedness among species. To calculate PD, we constructed an ultrametric phylogeny for tree species using a complete, time-calibrated phylogeny developed by (Smith and Brown, 2018) as a backbone. As our phylogenetic tree does not contain polytomies, no corrections for phylogenetic uncertainty were considered.

5 Data analysis

Plots differed in their area and the length of time they were monitored for (Supplementary Information 1). This is likely to affect carbon estimations, as smaller areas are more sensitive to mortality of larger trees, for instance. To control for these potential biases, we conducted two analyses to detect the effect of plot size and census interval on carbon estimations, following (Lewis et al., 2009). This diagnosis showed the need to account for the effect of monitoring length and plot size in our analyses (Supplementary Information 4). Here, we used the ((cubic root of plot size) + (cubic root of census interval) – 1) as a weighting variable in the models (see Lewis et al., 2009 for details).

We tested for the correlation among the biodiversity variables, which are not correlated (Pearson's correlation < 0.6). We fitted linear mixed models to evaluate the relationship between different biodiversity metrics and net carbon change, accounting for forest age as a random effect (three groups: 15-25, 26-50 and >50 years). We separated forest age into three categories: 15-25 and 26-50 years since clear-cut are characterised as successional forests, and >50 years since clear-cut as late successional/old-growth forests (Chazdon, 2008), as the 50 years' time-frame is enough to recover almost 90% of the forest functioning along succession (Poorter et al., 2021). As we do not intend to test causality among the variables, but their relationship, the Pearson's correlation among the diversity metrics and net carbon change is also shown. To control for spatial autocorrelation detected in our data, we included an exponential correlation structure (corExp) in the model. The model accounting for spatial structure had significantly lower Akaike Information Criterion (AIC) (Burnham and Anderson, 2002) when compared with models not accounting for it (Δ AIC=5 without accounting for spatial variation). All predictor variables were standardised prior to the analyses to allow direct comparisons, and all the mean values are presented as cubic root of plot size weighted means. All analyses were conducted at R statistical programming language, version 4.1.1 (R Core Team, 2021). All the functions and packages used to conduct data analysis are available at Supplementary Information 2.

Results

The above-ground woody carbon stocks in the subtropical Brazilian Atlantic Forest are on average 98.5 Mg C ha^{-1} (± 45.3) across all forest ages. The subtropical BAF are acting as carbon sink, with a positive net carbon change of 1.8 (± 1.75) Mg C ha^{-1} yr^{-1}. This is the balance between the mean annual above-ground woody productivity of 3.3 (± 1.73) Mg C ha^{-1} yr^{-1}, and carbon losses of 1.5 (± 1.04) Mg C ha^{-1} yr^{-1} (Table 1, Figure 2a). Net carbon change does not vary significantly amongst different successional stages, but we observed a great variation in the net carbon change across the late successional/old-growth forests (Table 1, Fig 2a).

Table 1: Mean (± standard deviation) values of carbon dynamics metrics and biodiversity variables for forest communities in the subtropical Brazilian Atlantic Forest grouped into different successional stages (15-25 years, 26-50 years and >50 years). Overall results are highlighted in bold.

Forest age (yr)	Productivity (Mg C ha^{-1} yr^{-1})	Mortality (Mg C ha^{-1} yr^{-1})	Net carbon change (Mg C ha^{-1} yr^{-1})	Carbon stocks (Mg C ha^{-1})	Taxonomic diversity	Functional diversity	Phylogenetic diversity
15-25	2.87 (1.07)	1.31 (1.06)	1.55 (1.37)	50.66 (22.74)	5.37 (3.79)	1.78 (0.79)	1.29 (0.20)
26-50	3.80 (1.57)	1.42 (0.86)	2.38 (1.50)	85.30 (25.72)	10.97 (4.89)	2.85 (1.22)	1.27 (0.15)
>50	3.29 (1.85)	1.62 (1.08)	1.67 (1.85)	109.06 (44.16)	12.68 (4.96)	3.97 (1.24)	1.35 (0.06)
Overall	**3.3 (1.75)**	**1.5 (1.04)**	**1.8 (1.75)**	**98.5 (45.3)**	**10.82 (5.45)**	**3.27 (1.44)**	**1.32 (0.12)**

We found no relationship between diversity metrics and net carbon change (Figure 2 a, b, and c). Both functional, taxonomic, and phylogenetic diversity had no predictive power in determining forest carbon sink, and the models presented very low R²m (i.e., fixed effects). The Pearson's correlation coefficients between biodiversity are low as well: 0.13, -0.11, and -0.13 for FD, taxonomic diversity, and PD, respectively (Figure 2 b-d).

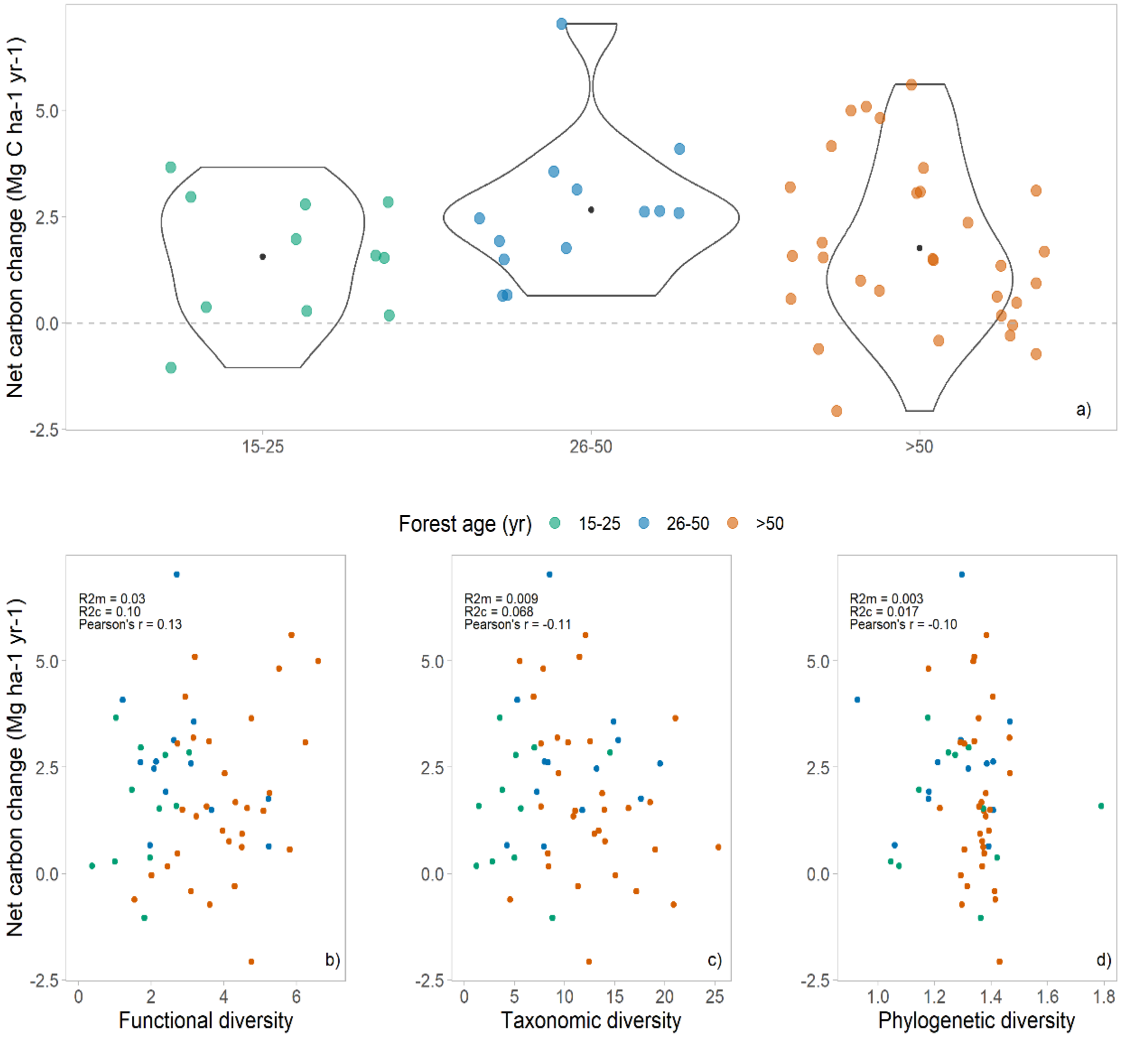

Figure 2: Net carbon change across successional stages and its relationship with different biodiversity metrics. a) Net carbon change estimates across different forest ages (green points = 15-25, blue points = 26-50, and orange points = >50 years) in the subtropical Brazilian Atlantic Forest. The black point shows the mean value across the data. The scatterplots show the relationship of b) functional diversity, c) taxonomic diversity, and d) phylogenetic diversity and forest net carbon changes across the subtropical Brazilian Atlantic Forest.

Discussion

Here we provide the first regional analysis of carbon dynamics across the subtropical Brazilian Atlantic Forest (BAF). We show that these forests are working as carbon sink. However, we did not find significant relationship between biodiversity and carbon capture capacity across the region. This implies that conservation efforts only focusing on carbon sink capacity will fail to protect distinct biodiversity facets (taxonomic diversity, FD, and PD of trees) across these forests. Therefore, management and conservation actions should consider carbon and biodiversity as independent targets to allow both the biodiversity and carbon-related processes conservation.

These subtropical forests have an important contribution to carbon cycling even across different successional stages, acting as carbon sink from initial secondary forests (15-25 years) to late successional and old-growth forests. Local studies previously showed the carbon sink of 0.4 Mg C ha^{-1} yr^{-1} in old-growth forests (Bordin and Müller, 2019). Here, with a broader coverage of evaluation with forest sites of different successional stages, we revealed a greater sink capacity of the subtropical BAF, on average of 1.8 Mg C ha^{-1} yr^{-1}; considering the old-growth forests (1.67 Mg C ha^{-1} yr^{-1}), the estimated sink is higher than Andean (Duque et al., 2021), African (Hubau et al., 2020), and Amazonian forests (Brienen et al., 2015). If this positive carbon sink is maintained over time, this region may represent an important refuge for carbon sequestration, particularly considering the weakening in carbon sink across tropics due to increasing tree mortality after drought periods or deforestation (Brienen et al., 2015; Maia et al., 2020). Thus, it indicates the potential of subtropical forests in capturing atmospheric CO2, to maintain carbon uptake and storage in the future (Duque et al., 2021), therefore making subtropical BAF an important region for forest restoration programs.

Contrary to our expectation, there is no relationship among biodiversity measures and net carbon changes (R^2 and Pearson's correlation near to null). It means that higher diversity of species, functions, and lineages did not imply in higher carbon sink capacity in this region, and the absence of relationship was independent of the forest age (Supplementary Information 5). In tropical forests, the relationship of biodiversity and carbon-related process are scale-dependent, and no relationship is observed across larger spatial grains (i.e., one hectare plots) (Chisholm et al., 2013; Sullivan et al., 2017). This contrasting patterns in different scales may be occurring in subtropical BAF, where there is a positive effect of taxonomic diversity in carbon gains at smaller plots (i.e., 0.05 hectare plots) (Bordin and Müller, 2019). Therefore, to protect biodiversity is in subtropical BAF is crucial, and if managers and policy makers only target carbon-related processes in conservation actions, biodiversity conservation will be neglected (Ferreira et al., 2018; Reside et al., 2017), as these components are not related in this region.

The subtropical BAF forests are highly productive, irrespective of forest ages (Supplementary Information 6). As productivity is an important component to obtain net carbon changes, this result emphasizes the needs of preserving old-growth forests as well restoring young and degraded forest ecosystems. By restoring ecosystems and allowing the secondary succession, subtropical forests may achieve the mature stage, which will be crucial for carbon fluxes in the future (Capellesso et al., 2021; Heinrich et al., 2021; Souza et al., 2021). Additionally, by conserving old-growth forests we will be maintaining not only carbon sink, but a great amount of carbon stored in the large-sized trees across this region (Bordin et al., 2021). Finally, investment in conservation is crucial to maintain both the biodiversity and carbon sink provided by the subtropical Brazilian Atlantic Forest and all the related ecological processes across this important region for carbon mitigation.

Conclusions

There is an urge for efforts to conserve highly productive forests, with a great carbon sink capacity as observed in the subtropical Brazilian Atlantic Forest. These conservation efforts should target both biodiversity protection and carbon storage and fluxes, as efforts focusing solely in one of these make neglect the other. This is especially important when considering the threats from future climatic changes and consequentially carbon losses through tree mortality. For instance, global change is likely to have been causing the decline of the carbon sink capacity in Amazonian forests (Brienen et al., 2015), and potentially leading shifting to carbon source (Maia et al., 2020). Subtropical BAF have been suffering with higher precipitation rates (Souza and Longhi, 2019) and extreme climatic events (Bordin and Müller, 2019; Liebsch et al., 2021) due to global changes. These climatic changes will enhance mortality rates and carbon losses in the near future, thus limiting the currently observed carbon sink capacity (Aleixo et al., 2019). To continue long-term records of forest dynamics from permanent forest inventory plots are crucial to understand the trends of carbon dynamics for this region (ForestPlots et al., 2021) and its potential as a carbon sink and its contribution to the global carbon cycle.

Declarations

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Conflicts of interest

The authors declare no conflict of interests in this work.

Data availability

Part of the original data is available at ForestPlots.net database (ForestPlots et al., 2021). The processed data and R codes used to conduct data analyses will be publicly available after the acceptance of the manuscript.

Authors' contributions

KMB, AE-M and SCM designed the research. KMB, JK, RCP, RSB, ACS, PH, ESC, MCMM, AFS collected the data. KMB analysed the data. KMB led the writing of the manuscript with great inputs and supervision from AE-M and SCM. All authors read and commented on the manuscript, giving final approval for publication.

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Supplementary Information 1: Plot information including plot codes and area, forest ages and census intervals, and weights attributed to each plot. The weights correspond to the ((cubic root of plot area) + (cubic root of census interval) – 1).

PlotCode	Forest sucessional interval yr	Initial census	Final census	Census interval (yr)	Census weight	Plot area (ha)	Plot weight
104	>50	2010	2016	6	1.82	0.06	0.39
110	26-50	2010	2016	6	1.82	0.06	0.39
1537	>50	2000	2009	9	2.08	1	1
1538	26-50	2000	2009	9	2.08	1	1
1539	>50	2000	2009	9	2.08	1	1
1540	>50	2000	2009	9	2.08	1	1
1541	>50	2000	2009	9	2.08	1	1
1542	26-50	2000	2009	9	2.08	1	1
1543	>50	2000	2009	9	2.08	1	1
1544	>50	2000	2009	9	2.08	1	1
1545	>50	2000	2009	9	2.08	1	1
1546	>50	2000	2009	9	2.08	1	1
157FL	26-50	2010	2016	6	1.82	0.06	0.39
158FL	26-50	2010	2016	6	1.82	0.06	0.39
162	26-50	2010	2016	6	1.82	0.06	0.39
25Carbono	>50	2010	2016	6	1.82	0.06	0.39
36	15-25	2010	2016	6	1.82	0.06	0.39
41MFL	15-25	2010	2016	6	1.82	0.06	0.39
80	26-50	2010	2016	6	1.82	0.06	0.39
86	26-50	2010	2016	6	1.82	0.06	0.39
AR03	15-25	2010	2016	6	1.82	0.06	0.39
av1	26-50	2010	2016	6	1.82	0.06	0.39
av2	26-50	2010	2016	6	1.82	0.06	0.39
av3	26-50	2010	2016	6	1.82	0.06	0.39
BJS	>50	2012	2016	4	1.59	1	1
CA	>50	2013	2017	4	1.59	1	1
CA2A	15-25	2010	2016	6	1.82	0.06	0.39
CA2M	26-50	2010	2016	6	1.82	0.06	0.39
CAA3	15-25	2010	2016	6	1.82	0.06	0.39
CAF2	>50	2010	2016	6	1.82	0.06	0.39
CAF3	>50	2010	2016	6	1.82	0.06	0.39
ENN-01	>50	2014	2020	6	1.82	0.12	0.49
ENN-02	>50	2014	2019	6	1.79	0.12	0.49
Epagri	>50	2011	2015	4	1.59	1	1
EW-10	>50	2010	2016	6	1.82	0.06	0.39
EW31	15-25	2010	2016	6	1.82	0.06	0.39
FNC-01	>50	2012	2017	6	1.79	1.2	1.06
GL1A	15-25	2010	2016	6	1.82	0.06	0.39
GL3A	15-25	2010	2016	6	1.82	0.06	0.39

GL3M	15-25	2010	2016	6	1.82	0.06	0.39
LIX01	15-25	2010	2016	6	1.82	0.06	0.39
MFO-01	>50	2014	2020	6	1.83	0.12	0.49
MN	>50	2015	2019	4	1.59	1	1
Painel	26-50	2014	2018	4	1.59	1	1
Parnamul	>50	2015	2019	4	1.59	1	1
PB1	>50	2012	2016	4	1.59	1	1
PB2	>50	2012	2016	4	1.59	1	1
PNA-01	>50	2014	2019	6	1.78	0.12	0.49
PNA-02	>50	2014	2019	6	1.77	0.12	0.49
PNA-03	>50	2014	2019	6	1.78	0.12	0.49
PRM-01	>50	2014	2019	5	1.76	0.12	0.49
PRM-02	>50	2014	2019	5	1.76	0.12	0.49
PRM-03	>50	2014	2019	5	1.74	0.12	0.49
PSJ2	15-25	2016	2020	4	1.59	0.2	0.58
vargem	>50	2014	2015	1	1	0.96	0.99

Supplementary Information 2: Extended material and methods

1 Study area and vegetation data

Concerning the vegetation data, the mean sampled area across 55 plots is 0.36 ha. All plots had at least two censuses across time, and the mean census interval is six years. The vegetation data collection followed the RAINFOR protocols (Phillips et al. 2001).

2 Carbon estimation

The equation used to estimate individual biomass is the following Chave et al. (2014): Individual biomass = 0.0673 (WD dbh^2 H)$^{0.976}$, where H represents the individual tree height (m), and WD represents the wood density of the species (g cm^{-3}). For the palm *Euterpe edulis*, we tested the relationship of this equation and the species-specific equation provided in Uller et al. 2021 (https://doi.org/10.1139/cjfr-2020-0215), which had a correlation of 0.98. Therefore, we used the Chave et al. 2014 equation for all species. Wood density information was obtained from regional (Missio et al. 2017; Oliveira et al. 2019), and global databases (Chave et al. 2009; Zanne et al. 2009). All biomass values were converted into carbon values by multiplying by 0.456 (Martin et al. 2018).

To obtain above-ground wood productivity and carbon loss through mortality, we used the equations 3 and 4 recommended by (Kohyama et al. 2019), see below:

$$\frac{[1-(Bs_0\,/\,B_T)^{1/T}](B_T-B_0)}{T\;[1-(B_0\,/\,B_T)^{1/T}]}$$ Equation to obtain AGWP

$$\frac{[1-(Bs_0\,/\,B_0)^{1/T}](B_T-B_0)}{T\;[(B_T\,/\,B_0)^{1/T}-1]}$$ Equation to obtain carbon loss

Where: T: census interval; B0: total biomass at time t = 0; BT: total biomass at t = T; Bs0: initial biomass at t = 0 for survivors over t = 0 to T.

3 Biodiversity metrics

3.1 Taxonomic diversity

Taxonomic diversity or species diversity is calculated by considering species abundance distribution in a community (a forest plot, for instance). A common index used to represent taxonomic diversity is the Simpson Index (or Inverse Simpson index), which is sensitive to the dominant species in the community (Magurran and McGill 2010). We selected the Inverse Gini-

Simpson index as a taxonomic diversity metric as it is closely related to Rao's quadratic entropy (Botta-Dukát 2005).

3.2 Functional diversity

Functional traits correspond to morpho-physio-phenological features that influence species fitness (Violle et al. 2007). Their effect may also be scaled-up to community levels, due to functional diversity (FD) metrics, such as Rao's quadratic entropy (Botta-Dukát 2005). Functional diversity often corresponds to the value and range of functional traits of the species present in a community, weighting by their abundance, and represents the niche complementarity hypothesis (Diaz and Cabido 2001). According to this hypothesis, the greater niche complementarity in or across communities provides a better use of resources among coexisting species.

3.3 Phylogenetic diversity

Phylogenetic diversity quantifies the diversity of evolutionary lineages in or across communities and is associated with species differences across evolutionary history. For instance, the Mean Pairwise Distance (MPD) is a metric used to quantify phylogenetic dissimilarity among coexisting species (Tucker et al. 2017). Therefore, by assessing the pairwise distance across a group of taxa this metric provides information on the phylogenetic diversity of communities.

Functions and packages used to conduct data analysis

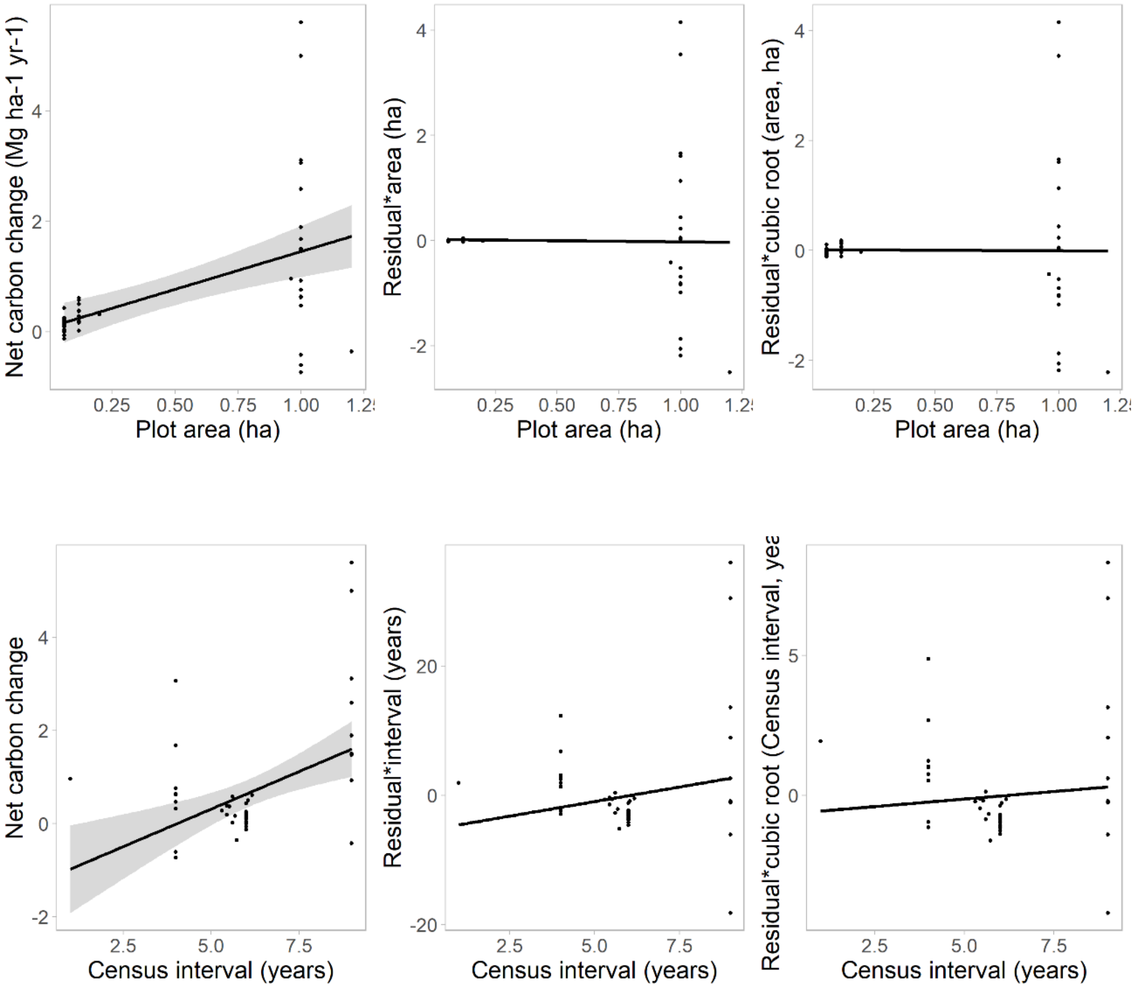
1. Above-ground biomass estimation: AGBChv14 function, available at BiomasaFP package (Sullivan et al. 2020a).
2. Taxonomic diversity: This variable was estimated by using the function diversity, index = "inv", from vegan package (Oksanen et al. 2019), and by using a community matrix described by stem density per plot.
3. Functional diversity: We calculated FD (i.e., Rao's quadratic entropy) with the dbFD function from FD package (Laliberté et al. 2015), and by using a community matrix described by stem density per plot.
4. Phylogenetic tree construction: V.PhyloMaker package (Jin and Qian 2019).
5. Phylogenetic diversity: We calculated PD by using the mpd function from picante package (Kembel et al. 2010), and a community matrix described by stem density per plot.
6. Linear Mixed Models: lme function from nlme package (Pinheiro et al. 2020).
7. Data standardization: function decostand, "standardize" method, vegan package (Oksanen et al. 2019).
8. Original data availability: Part of the original data can be requested at ForestPlots.net database (Lopez-Gonzalez et al. 2011; ForestPlots et al. 2021).

Supplementary Information 3: Tree functional traits and ecological function in forest communities

The leaf functional traits were collected by the Plant Ecology Labs (Universidade Federal do Rio Grande do Sul and Universidade Federal do Paraná, Brazil), and Forestry Department (Universidade do Estado de Santa Catarina, Brazil). These data are also available at TRY database, and can be accessed under formal request (Kattge et al. 2020). All data collection followed the standardised protocol developed by Pérez-Harguindeguy et al. (2013), considering the following collection procedures for leaf traits: at least five leaves per plant (to obtain the individual mean), and at least three individuals per species (to obtain species trait value). The leaf area values were calculated from scanned fresh leaves. All simple leaves selected were measured including petioles, and compound leaves had just the leaflet area measured, without rachis. Wood density collection also followed the standardized protocol (Pérez-Harguindeguy et al. 2013), and species values were obtained from plot (Missio et al. 2017) and regional level (Oliveira et al. 2019), and global databases (Zanne et al. 2009; Chave et al. 2014).

Functional trait	Ecological function	Reference
Specific Leaf Area (SLA, cm^2/g)	Photosynthetic assimilation; low-cost construction	(Westoby 1998; Poorter et al. 2008)
Leaf Dry Matter Content (LDMC, mg/g)	Leaf longevity, forest productivity	(Fortunel et al. 2009; Smart et al. 2017)
Maximum Height (Hmax, m)	Competitive ability to achieve light resources	(Westoby 1998)
Wood Density (WD, g/cm^3)	Hydraulic conductance, stem structures, longevity of carbon stocks	(Poorter et al. 2008; Chave et al. 2009)

Supplementary Information 4: Diagnosis of the effect of plot size and census interval in forest net carbon change estimate, therefore needing to account these variables as weights in the models.

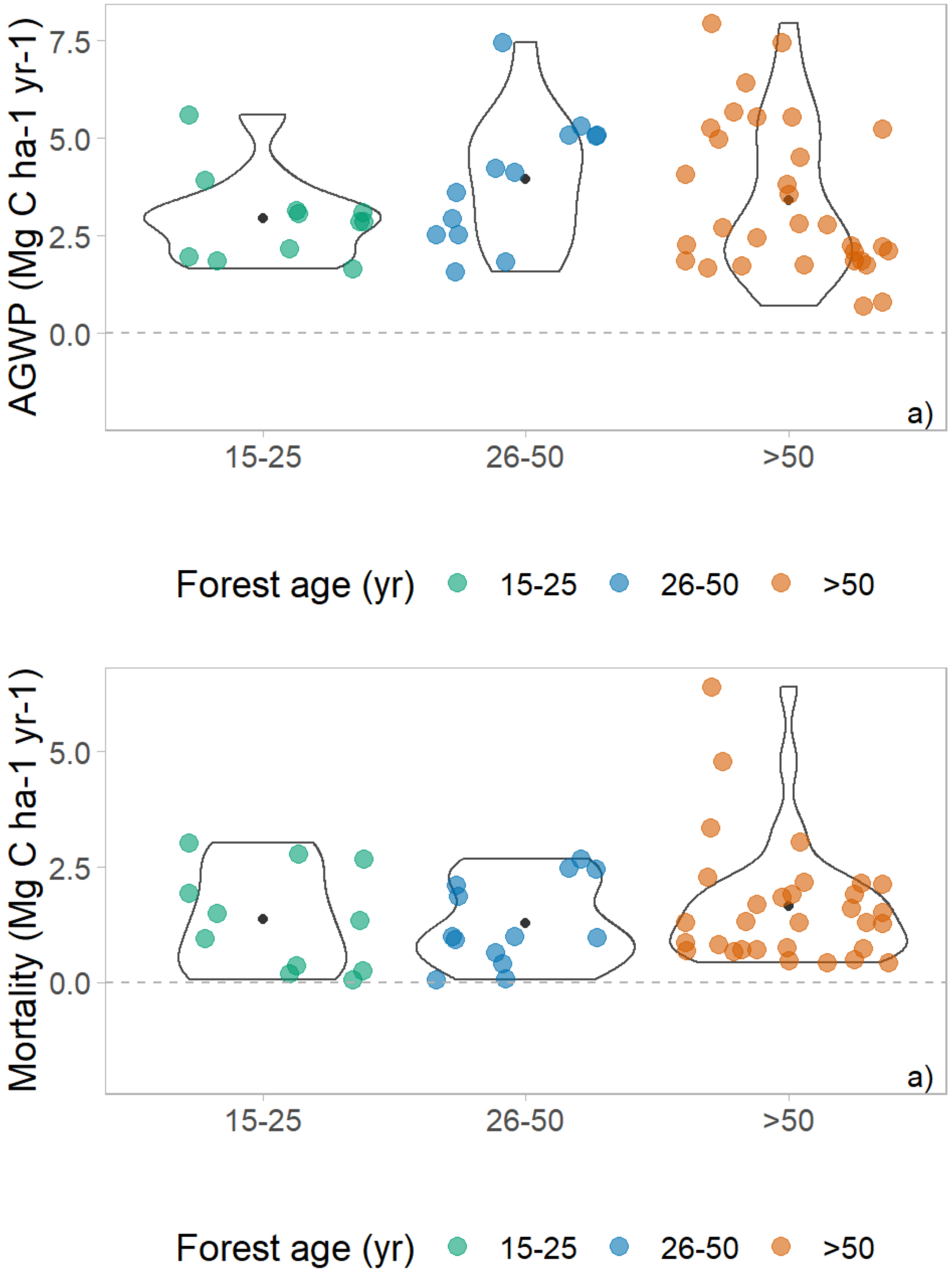


Supplementary Information 5: Results of the generalised least square models among response variable (net carbon change) and predictors (taxonomic, FD, and PD) interacting with forest age. FD = functional diversity; PD = phylogenetic diversity

Net carbon change ~ (taxonomic + FD + PD) * interval				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.83	0.55	3.33	0.00
taxonomic	-0.81	0.39	-2.10	0.04
FD	0.81	0.42	1.92	0.06
PD	-0.53	0.76	-0.70	0.49
interval15-25	1.27	1.44	0.88	0.38
interval26-50	0.64	0.79	0.81	0.42
taxonomic:interval15-25	0.02	1.30	0.02	0.99
taxonomic:interval26-50	1.20	0.83	1.46	0.15
FD:interval15-25	1.66	2.17	0.77	0.45
FD:interval26-50	-1.70	0.82	-2.08	0.04
PD:interval15-25	-0.12	0.99	-0.12	0.91
PD:interval26-50	0.82	0.91	0.90	0.37

Residual standard error: 1.47 on 43 degrees of freedom				

Supplementary Information 6: Comparison of above-ground wood productivity and carbon loss through mortality in different forest ages across subtropical Brazilian Atlantic Forest.



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Capítulo 3

Chapter 3

Growth-mortality strategies across temperate tree species and their relationship with functional traits

Potencial submissão para as seguintes revistas:

Potential submission to:

- ★ Nature Ecology and Evolution
- ★ PNAS
- ★ Ecography

Growth-mortality strategies across temperate tree species and their relationship with functional traits

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Abstract

Species life strategies reflect how plants allocate their resources. These strategies vary from fast growing and high mortality acquisitive species to slow growing and low mortality conservative species. However, it is still unclear how life-history strategies vary across temperate tree species and how these strategies map to the strategies of other organs of the tree. Ultimately, the different life-strategies are importante to shape species coexistence across forests. We used data from 13,756 forest inventory plots to test for the existence of growth-mortality trade-offs amongst 71 North American temperate species, and the relationship of functional traits with species-level life-history strategies. We found a weak growth-mortality trade-off across North American temperate species when testing for the trade-off within Angiosperms, but not for Gynmosperms or when the two groups were analysed together. Species annual mortality probability increased with leaf nitrogen and was not associated with any other leaf or structural fuctional trait. Our results show that the growth-mortality trade-off for temperate species is weaker than expected, indicating for the existence of a more complex set of strategies across temperate tree species.

Keywords: life-history strategies; growth-mortality trade-offs; leaf nitrogen; vital rates.

Introduction

Species life strategies are associated with how plants allocate their resources and how they are translated into competitive ability. Species with higher light dependence tend to invest in resource acquisition, therefore having higher growth rates, but also higher mortality rates (Brienen et al. 2020). In contrast, shade-tolerant species usually have higher longevity, but lower growth and mortality rates (Sterck et al. 2006; Iida et al. 2014) (Figure 1). Differences in allocation strategies amongst species can be assessed through absolute estimates of growth and mortality rates (Poorter et al. 2008), the maximum growth and the mortality rate of slowest growing individuals (Wright et al. 2010), or the maximum growth and the mortality probability of species in the absence of growth (Russo et al. 2021). By considering the last approach (i.e., the mortality probability when a tree growth is equal zero) it is possible to infer about the species tolerance to resource limitation (Russo et al. 2021). This tolerance to low resource availability is linked to the species ability to survive and reduce mortality, which is often related to stress-tolerance (Grime 1977), as slow or absent growth across trees might show a reduction in individual vigour (Chao et al. 2008).

The range of life strategies found across the acquisitive-conservative spectrum is expected to be linked with functional traits' values aligned to a similar axis of variation, known as the fast-slow continuum (Figure 1), since the functional traits can influence tree demographical performance (Poorter & Bongers 2006; Poorter et al. 2008; Reich 2014; Salguero-Gómez et al. 2017). According to the fast-slow continuum, a fast-growing species is aligned to acquisitive strategies, and might have lower mortality in resource-rich environments, while a slow-growing species (with conservative strategies) might be more tolerant in harsh environments (Adler et al. 2014; Russo et al. 2005). Thus, conservative species are expected to be more resistant to periods under resource constraints, with low or near-zero growth rates (Russo et al. 2021).

The relationship between functional traits and life strategies across species depends strongly on the evaluated trait. For instance, leaf traits such as leaf nitrogen are related to photosynthetic process (Rowland et al. 2017), as higher values of leaf nitrogen are linked to investments in resource acquisition (Reich 2014). Wood density and maximum height are traits related to forest structure. While wood density is expected to influence tree growth in tropical (Poorter et al. 2017), but not temperate forests (McMahon et al. 2011), maximum height is related to competitive ability to reach canopy (Chave et al. 2009; Westoby 1998). Higher values of wood density are often linked to conservative strategies (Chave et al. 2009), while of maximum height is linked to acquisitive strategies (Westoby 1998; Wright et al. 2010). Additionally, to assess drought tolerance, some conservative traits such as embolism resistance (lower Ψ50 values) and embolism vulnerability (lower slope values (Choat et al. 2012)) have been explored. Therefore, if there is a coordination between the life-history strategies and the fast-slow continuum within other organs, leaf and structural and drought tolerance traits should be linked to tree demographical performance (Poorter et al. 2008; Reich 2014).

The width of trade-offs allows us to comprehend the mechanisms of species coexistence across forests (Silvertown 2004). The existence of growth-mortality trade-offs and their relationship with life strategies are consistent across tropical and subtropical forests (Rüger et al. 2020; Russo et al. 2021; Kambach et al. 2022; Coelho de Souza et al. 2016), meaning that fast-growing species also have higher mortality rates, while slow-growing species have lower mortality. In temperate regions this relationship between growth and mortality might not be as strong due to the presence of both Angiosperms and Gymnosperm species, which are considered to have different competitive habilities (Bond 1989), due to different characteristics on photosynthesis and water conductance (Lusk et al. 2003; Lusk 2011). Although the growth-mortality relationship in temperate regions has not been tested at biogeographical scales, it has been observed at regional scales (McMahon et al. 2011). However, growth-mortality trade-offs are often stronger for seedlings and saplings (Wright et al. 2010), revealing a size-dependence among life strategies and how they are translated into these trade-offs. The extent of the relationship between fast-slow continuum and life strategies dependes of ontogenetic stage (Paine et al. 2015), tree size class (Iida et al. 2014; McMahon et al. 2011) and evaluated traits (Poorter et al. 2008; Martínez-Vilalta et al. 2010). Therefore, testing the relationships among functional traits and species performance are still necessary (Shipley et al. 2016).

Here we analysed data from 13,756 inventory plots across the United States from Forest Inventory of America (FIA) to understand how species tolerances to resource limitation (measured as their annual mortality probability at zero growth) vary across temperate species. We further test for the existence of a growth-mortality trade-off across 71 dominant species within the data. Finally, we tested the relationship between species life strategies and a range of functional traits.

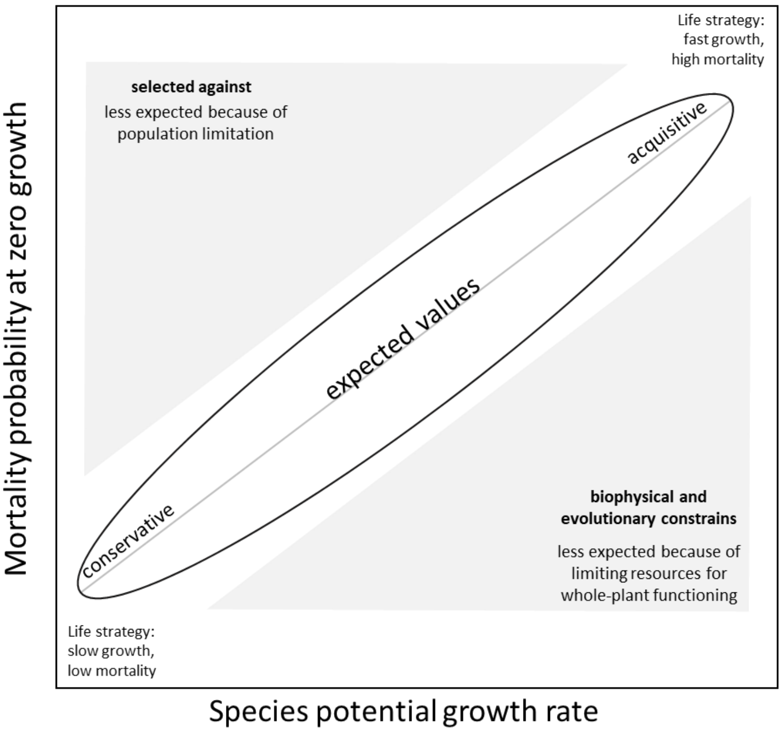

Figure 1: Expected relationships between species potential growth rate and mortality probability at zero growth. Species life strategies vary according to how they allocate resources, along a continuum from slow growth, low investment in growth and high investment in defences, to fast growth, high investment in growth and low investment in defences. Species mortality rates are expected to vary from low to high across this continuum. If following the expected values, these life strategies indicate a trade-off between investment in growth and investment in survival. Additionally, the fast-slow continuum is expected to be related to the acquisitive-conservative axis of variation across other traits. Species that fall within the upper left corner grey triangle would be selected against as it is not successful in the long-term (Russo et al. 2021) and may reduce the population size. The bottom right corner grey triangle indicates a region where species will not be successful in a scenario of environmental stress, as the species would survive less well, with a lower chance of reproduction (Rose et al. 2009; Reich 2014). This figure was adapted from Russo et al. (2021).

Methods

Vegetation data

We used data from the US Forest Inventory and Analysis National Program (FIA, USDA Forest Service - www.fia.fs.usda.gov) (Smith 2002; Bechtold & Patterson 2005).

These data include 13,756 temperate forests plots of 0.06 ha distributed across the US. All stems ≥ 12.7 cm of diameter at breast height (dbh) with three censuses across time were included in our analyses, and those stems harvested or with recognized management records were excluded from the dataset.

Assessment of tree life strategies

To obtain the tree-level annualised growth rate (cm yr $^{-1}$), we used the dbh from the first and second census when the stem was observed within the FIA data. Here, the annual growth rate estimates correspond to the species-level maximum growth rate, quantified as the 95th quantile of distribution of growth rate across all trees within a given species.

Tolerance to resource limitation, represented by the species annual mortality probability at zero growth (p_{ij}), was estimated as the output from a species-specifc model predicting mortality as a function of growth, size, and time. The p_{ij} was estimated using information from survival (0/1) of stem *i* and species *j* at the third census when the stem was observed. As it corresponds to a binary data, p_{ij} is assumed to be Bernoulli distributed. We tested different models to obtain the annual mortality probability estimates across the species (Appendix 1, Eq. 1), which included different combinations of the effect of growth, diameter, and time-census interval (i.e., time between second and third census) (Russo et al. 2021; Baker et al. 2014; Camac et al. 2018). We applied log-transformation for dbh and an exponential to growth (growth ^0.465) to correct homoscedasticity and skewness across the data. In this study, p_{ij} corresponds to the annual mortality probability predicted per species when diameter is 12.7 cm and growth equals zero.

Eq.1: $p_{ij} \sim \beta0 + \beta1\ln(dbh_{ij}) + \beta2\ \mathrm{trans}(growth_{ij}) + \beta3\ time$

where β1= log-transformed diameter, β2 = power-transformed prior growth (in dbh), and β3 = time (census interval between the second and third censuses, in years). This analysis was restricted to species with at least 200 stems alive and 5 dead stems at the third census (Russo et al. 2021), totaling 217,473 stems (approximately 24% of the dataset). Only species-level models of annual mortality probability presenting AUC ≥ 0.6 were considered in the following analyses.

Functional traits: leaf, structural, and drought tolerance

We assess a series of functional traits that are broadly recognized for influencing individual or species performance: wood density (WD, g/cm^{-3}), nitrogen mass per unit leaf mass (LeafN, mg/g), Ψ50 (embolism resistance, xylem water potential at 50% loss of conductivity), slope (almost complete xylem failure, embolism vulnerability curves showing percentage loss of hydraulic conductivity from Ψ50 to Ψ88) (Choat et al. 2012), maximum height (Hmax, m), and deciduousness (with three levels - BT: broadleaf temperature-driven, BE: broadleaf evergreen, and CC: conifer or needle-type). All the regressions considered the plant group (Angiosperms or Gymnosperms) as a covariate in the models. The trait data were obtained from TRY database (Kattge et al. 2020) and from literature review.

Data analysis

To obtain the growth-mortality trade-offs, we used Kendall's τ correlation coefficient. Thus, we tested for the correlation between the species annual mortality probability at zero growth (i.e., tolerance to resource limitation, p_{ij}), and the species 95th quantile of growth.

To test for the relationship between annual mortality probability at zero growth and leaf, structural and drought tolerance traits we used ordinary least square regressions (OLS). However, we first tested the phylogenetic independence between species by considering the Brownian Motion of trait evolution as a correlation in the models. The rooted and time-calibrated phylogeny was built for all tree species with the *V.PhyloMaker* package, based on Smith & Brown (2018) mega-tree as a backbone (Appendix 2). We compared the Akaike Information Criteria (AIC) from models considering the phylogenetic correlation (by using generalised least square models, GLS) with models without phylogenetic correlations (OLS models) (Garamszegi 2014). This diagnosis showed us that there is no phylogenetic dependence (lower AIC for OLS models), and therefore, phylogenetic correlation was not considered in the final models (Garamszegi 2014) (Appendix 2). Traits were standardised to zero mean and unit variance to allow direct comparison of the coefficients of each model. All analyses were conducted at R version 4.2.1 (R Core Team 2022). We performed model diagnostics using the *DHARMa, broom, roc* and *performance* packages.

Results

We estimated the annual mortality probability at zero growth (species tolerance parameter, p_{ij}) for 71 species (on average 3,063 stems per species, Appendix

3). The tolerance to resource limitation varied considerably among species (Figure 2, Appendix 3). Annual mortality probability at zero growth and at 12.7 cm of diameter varied between 74% for *Pinus ponderosa*, and 1% for *Pinus rigida*.

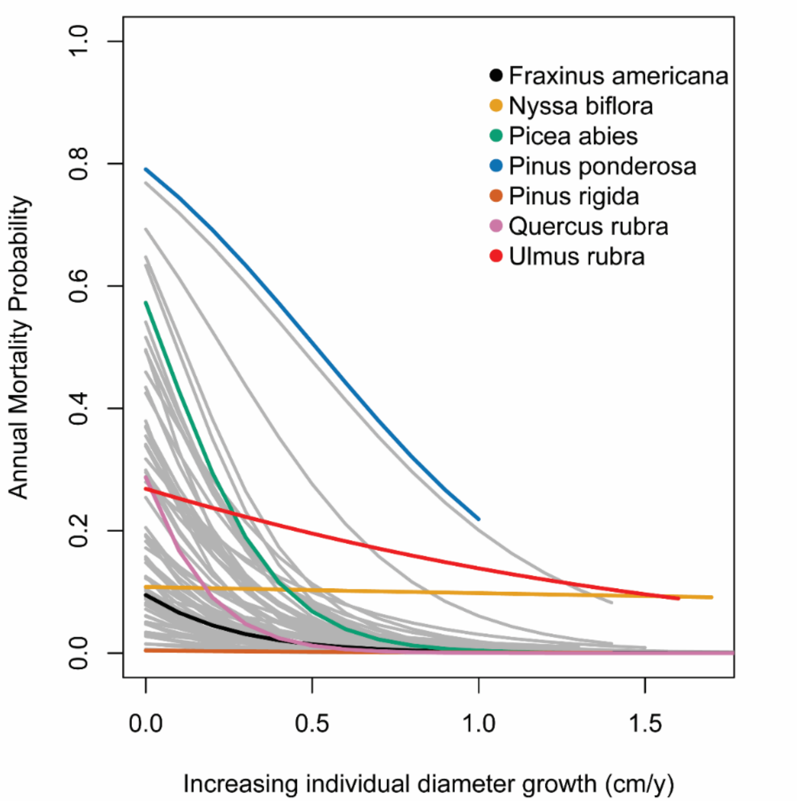

Figure 2: Variation of annual mortality probability with tree diameter growth, showing the model output for 71 North American tree species. The colour lines show a set of the diversity of strategies across temperate species.

We found no significant correlation between species potential growth and their tolerance to resource limitation (Kendall's tau = 0.15, p-value = 0.06), considering the whole set of species. However, these two variables were positively correlated for Angiosperms (53 species, τ = 0.18, p-value = 0.05) but not for Gymnosperms (18 species, τ = -0.05, p-value = 0.76) (Figure 3a).

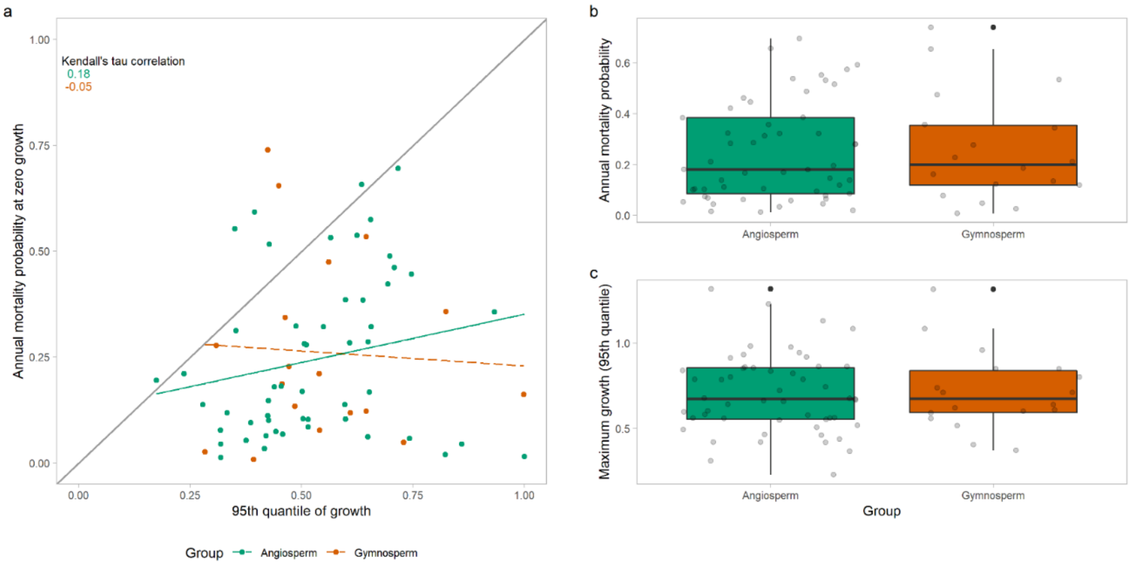

Figure 3: Growth and mortality relationships for Angiosperms and Gymnosperms across temperate species. a) Relationship between 95th quantile of growth and annual mortality probability (tolerance parameter, pij) for 71 temperate species. Lines shows the relationship between the variables (Angiosperms and Gymnosperms), while the grey line shows the theoretical expectation (1:1 line). Continuous line indicates significant relationship, and the dashed line indicates absence of relationship. Under a theoretical expectation of a perfect trade-off observed, relationship would follow the 1:1 line. Kendall's τ correlation coefficient for Angiosperms is 0.18 and for Gymnosperms is -0.05. b) Annual mortality probability for Angiosperms and Gymnosperms. c) Maximum growth (95th quantile) of Angiosperms and Gymnosperms. Angiosperms are highlighted with green colour and Gymnosperms with the orange colour.

By evaluating the effect of functional traits on annual mortality probability at zero growth of temperate species across the US, we found a positive relationship with leaf nitrogen (LeafN) (Appendix 4, Figure 3b). There was no relationship between annual mortality probability and WD, Ψ50, Slope, Hmax, and Deciduousness (Figure 4).

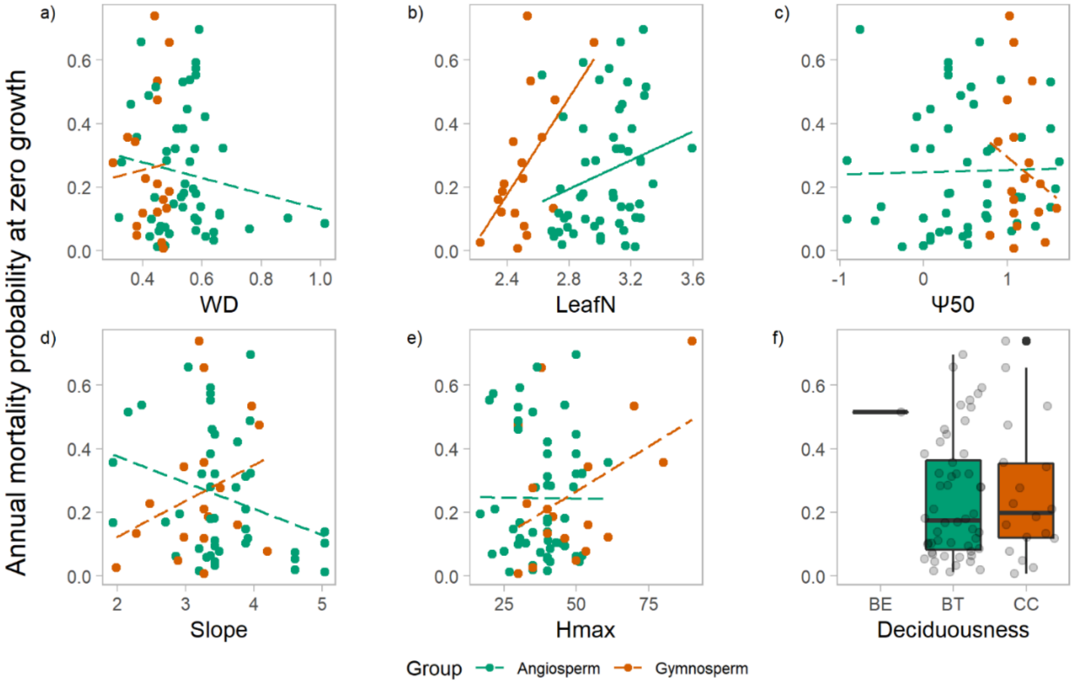

Figure 4: Variation of annual annual mortality probability (tolerance parameter, p_{ij}) across species with different functional traits. Relationship between p_{ij} and different traits: (a) wood density (WD); (b) nitrogen mass per unit leaf mass (LeafN); (c) embolism resistance (Ψ50); (d) embolism vulnerability curves (Slope); (e) maximum height (Hmax). In (f) a comparison of p_{ij} and different deciduousness groups: broadleaf evergreen (BE), broadleaf temperature-driven (BT), conifer and needle-type leaves (CC). Solid lines represent significant relationship whilst relationships that are not significant are shown by the dashed lines. Colors represent different taxonomic groups - green are Angiosperms and orange are Gymnosperms.

Discussion

We show the first assessment of the variation of tolerance to resource limitation across North American temperate species. These probabilities vary greatly across species, ranging from 1% to 76%. The annual mortality probabilities tend to a have a positive correlation to maximum species growth, which is stronger for Angiosperms than Gymnosperms. Additionally, species characterised by higher leaf nitrogen tend to have higher mortality probability at resources limitation, while other traits are not related to mortality probability at zero growth.

The combined effect of previous growth, individual diameter, and time predict the mortality probability (i.e., resources tolerance limitation) of the US temperate species. Overall, the high range of different strategies and tolerances observed for temperate species indicates the different responses of species to absence of resources, and the dependence of local environment to determine species performance (Russo et al. 2021). Ultimatelly, these different strategies may favour species coexistence and resources partitioning in forest communities, therefore contributing to forest resilience (Chesson 2000). Mortality is known to vary with size, and here we show that this is consistent across all species analysed. Some temperate species show great longevity when growing slowly (Di Filippo et al. 2015). Our results show that for most temperate species mortality probability increases under low or zero growth rates, such as *Pinus ponderosa* and *Gleditsia triacanthos*. Other studies from tropical regions show that growth stress, which is expected to reduce vigour (Chao et al. 2008; Esquivel-Muelbert et al. 2020), leads to higher mortality probability.

There is a trade-off between growth and mortality across North American temperate species, but the relationship is weak. This can be explained by the fact that these trade-offs are often stronger for seedlings and saplings (Wright et al. 2010), especially considering that growth and survival are size-dependent. Additionally, it may be linked to higher growth rates observed for temperate species as a consequence of recent climatic changes (McMahon et al. 2010). Most of the species are distributed below the perfect trade-off predicted line. These species distributed in the bottom right region of the trade-off axis allocate resources to functions that favour faster growth, despite having low mortality rates. It would be successful, but if subjected to environmental stress, these species would survive less well, with a lower chance of reproduction (Rose et al. 2009; Russo et al. 2021), and consequently, lower recruitment rates. The general lack of a growth-mortality trade-off amongst these species may be masked by other axis of species strategy trade-off. For instance, the stature-recruitment trade-off (Rüger et al. 2018), which predicts that fast-growing and long-lived species usually have lower investments in recruitment (Rüger et al. 2020). This stature-recruitment axis also predicts that species distributed in the top-left of the growth-mortality space (i.e., slow growing and high mortality), often have higher investments in recruitment (Rüger et al. 2020, 2018), but they potentially might be selected against as this strategy is not successful in the long term (Russo et al. 2021), because it may reduce the population size. As expected, this pattern was rare across our set of temperate tree species.

We found different relationship between growth and mortality for Angiosperms and Gymnosperms. Gymnosperm species show lower annual mortality probability in both resource rich and poor environments, leading to the small and almost null trade-offs, reflecting in potential higher persistence (Bond 1989). On the other hand, Angiosperm species show a significant growth-mortality trade-off, which can be explained by different competitive ability between Angiosperms and conifers (Becker 2000). Angiosperms present a great diversity of strategies and tend to have higher competitive ability (Bond 1989), revealing a consistent relationship between faster growth and high mortality among this group of species.

Leaf nitrogen is positively related to annual species mortality probability, following the expected effect of traits on individual and species fitness (Violle et al. 2007), and species might be acting to maximise resources acquisition and growth across time (Wright et al. 2010). Additionally, it corroborates the association of fast life strategies to the acquisitive spectrum (Adler et al. 2014). Leaf nitrogen is also related to higher leaf herbivory, as it leads to more palatable leaves (Throop & Lerdau 2004; Casotti & Bradley 1991). Leaf herbivory is recognised as a great driver of tree mortality across cold temperate areas (Kambach et al. 2016). Therefore, the combined effect of fast life strategies with higher damage derived from herbivory may be related to the higher mortality probability across temperate tree species. Surprisingly, other traits related to investment in stem structures (e.g., wood density) and resistance to hydraulic failure (e.g., Ψ50 and slope) are not related to mortality probability across temperate trees, despite the fact that wood density tends to be lower for fast-growing small trees (McMahon et al. 2011). The weak relationship between traits and mortality at zero growth at species level is surprising, as theoretical predictions suggest strong links among them (Visser et al. 2016; Wright et al. 2010; Poorter et al. 2008). Future studies should test these relationships at the community level, as growth mortality-trade-offs are expect to influence species coexistence within forest communities (Chesson 2000; HilleRisLambers et al. 2012) and thus different strategies may be more evident.

Conclusions

Temperate species across the US forests have a great range of annual mortality probabilities at zero growth, which is positively related to the leaf nitrogen mass per unit of leaf area. This is translated into a growth-mortality trade-off, but only for Angiosperm species, revealing one aspect of tree life strategies that affect the mechanisms behind species coexistence, which is fundamental to assess the resilience of forests (Chesson 2000; HilleRisLambers et al. 2012). There are evidences that temperate species are facing higher growth rates across time, which is linked to recent climatic changes (McMahon et al. 2010). The positive relationship between fast-acquisitive traits and annual mortality probability alerts for the risks of higher tree mortality across forests, as a consequence of CO_2 enrichment and faster life cicles (Esquivel-Muelbert et al. 2020; Brienen et al. 2020), as these species potentially survive less under zero growth conditions. Thus, the increasing growth and potentially mortality may increase gap dynamics derived from tree falls, change in species composition and lower carbon sink capacity across time (Esquivel-Muelbert et al. 2019; Brienen et al. 2020, 2015). Here, we have charaterised the relationship of life strategies across tree species, but growth-mortality trade-offs are also expected to occur in community level (Russo et al. 2005; Wright et al. 2010). Therefore, future studies should evaluate growth-mortality trade-offs within communities, which will provide an important picture about the responses of forests to the expected global changes.

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Author’s contribution

Kauane Maiara Bordin and Adriane Esquivel-Muelbert designed this study with inputs from Thomas Pugh, Oliver L. Phillips and Sandra Cristina Müller. Adriane Esquivel-Muelbert, Daijun Liu, Julen Astigarraga, Lalasia Bialic-Murphy, and Christopher Woodall compiled and standardised the data. Kauane Maiara Bordin analysed the data. Kauane Maiara Bordin wrote the manuscript with inputs and supervision Adriane Esquivel-Muelbert and Sandra Cristina Müller.

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Appendix 1

Table 1: Models tested to obtain the annual mortality probability at zero growth (p_{ij}). The best model (lower AIC) corresponds to the model which combines log of diameter + transformed growth (growth ^0.456) + time between censuses (second and third census).

Response variable	Tested model	AIC
Mortality (0/1)	**log of diameter + transformed growth + time**	**1250**
	transformed growth + time	1256
	log of diameter + transformed growth	1258
	transformed growth	1264
	time	1418

Appendix 2

Figure 2: Phylogeny obtained for the 71 species derived from the annual mortality probability estimates.

Table 2: Comparison of OLS and GLS models considering the phylogenetic correction (with phylo) and models without phylogenetic correction (without phylo). The lower AIC values were found for models without phylogenetic correction.

Model	Phylogenetic correlation	AIC	Delta AIC
pij ~ LeafN	**without.phylo**	**-14.43**	**0**
pij ~ Hmax	**without.phylo**	**-8.93**	**-5.50**
pij ~ WD	**without.phylo**	**-6.71**	**-7.72**
pij ~ Ψ50	**without.phylo**	**-4.45**	**-9.98**
pij ~ Slope	**without.phylo**	**-1.80**	**-12.64**
pij ~ LeafN	with.phylo	21.32	**-16.34**
pij ~ Ψ50	with.phylo	23.03	6.88
pij ~ Hmax	with.phylo	23.88	8.59
pij ~ WD	with.phylo	25.02	9.45
pij ~ Slope	with.phylo	30.65	10.59

Appendix 3

Table 1: Species identities and the respective families, annual mortality probability per species, 95th quantile of growth rate, functional trait values, number of stems used to estimate species annual mortality probability and goodness-of fit (AUC values). LeafN = leaf nitrogen mass per unit of leaf mass; Ψ50 (embolism resistance); Slope = embolism vulnerability curves showing percentage loss of hydraulic conductivity from Ψ50 to Ψ88; Hmax = maximum height; plant group = Angiosperms or Gymnosperms; Deciduousness = three levels - BT: broadleaf temperature-driven, BE: broadleaf evergreen, and CC: conifer or needle-type.

Species	Family	Annual mortality probability (%)	95th quantile of growth rate (cm/yr)	LeafN	WD	Ψ50	Hmax	Slope	Functional group	Deciduousness	Number of stems to obtain mortality probability	Mortality probability models' AUC
Abies balsamea	Pinaceae	0.47	0.74	2.71	0.45	1.00	30.00	4.08	Gymnosperm	CC	11030	0.75
Acer negundo	Sapindaceae	0.49	0.92	3.29	0.42	0.44	30.00	3.94	Angiosperm	BT	685	0.76
Acer rubrum	Sapindaceae	0.17	0.66	2.87	0.53	1.12	40.00	2.71	Angiosperm	BT	26889	0.81
Acer saccharinum	Sapindaceae	0.02	1.32	3.16	0.48	0.00	40.00	3.20	Angiosperm	BT	487	0.70
Acer saccharum	Sapindaceae	0.09	0.68	3.13	1.02	1.12	41.00	3.20	Angiosperm	BT	15078	0.77
Amelanchier indet	Rosaceae	0.14	0.37	3.19	0.54	1.52	35.00	NA	Angiosperm	BT	281	0.71
Betula alleghaniensis	Betulaceae	0.10	0.68	3.26	0.89	0.77	32.60	3.88	Angiosperm	BT	4727	0.76
Betula lenta	Betulaceae	0.15	0.56	3.25	0.51	0.77	28.20	3.88	Angiosperm	BT	3688	0.78
Betula papyrifera	Betulaceae	0.31	0.46	3.18	0.48	0.77	40.00	3.88	Angiosperm	BT	6742	0.78
Carya alba	Juglandaceae	0.03	0.55	3.00	0.64	0.08	35.05	3.43	Angiosperm	BT	1405	0.69
Carya cordiformis	Juglandaceae	0.32	0.72	3.14	0.58	0.08	52.00	3.43	Angiosperm	BT	801	0.84
Carya glabra	Juglandaceae	0.11	0.56	2.79	0.66	0.74	40.23	3.43	Angiosperm	BT	1914	0.78
Carya ovata	Juglandaceae	0.09	0.51	3.00	0.59	-0.58	46.00	3.43	Angiosperm	BT	1910	0.72
Carya texana	Juglandaceae	0.04	0.42	3.00	0.61	0.08	41.00	3.43	Angiosperm	BT	436	0.62
Celtis occidentalis	Cannabaceae	0.29	0.86	3.26	NA	NA	40.00	NA	Angiosperm	BT	573	0.82
Cornus florida	Cornaceae	0.19	0.23	2.74	0.57	1.58	16.80	2.92	Angiosperm	BT	210	0.70
Fagus grandifolia	Fagaceae	0.28	0.67	3.26	0.56	1.63	49.00	3.37	Angiosperm	BT	5898	0.77
Fraxinus americana	Oleaceae	0.14	0.79	3.14	0.60	-0.51	40.00	5.05	Angiosperm	BT	4044	0.76
Fraxinus nigra	Oleaceae	0.01	0.42	3.22	0.45	-0.26	27.00	5.05	Angiosperm	BT	3267	0.70
Fraxinus pennsylvanica	Oleaceae	0.10	0.79	2.77	0.58	0.00	45.00	5.05	Angiosperm	BT	1596	0.60
Gleditsia triacanthos	Leguminosae	0.70	0.94	3.28	0.59	-0.77	50.00	3.95	Angiosperm	BT	257	0.70
Juglans nigra	Juglandaceae	0.45	0.98	3.12	0.55	0.08	50.00	3.43	Angiosperm	BT	997	0.85
Juniperus virginiana	Cupressaceae	0.13	0.64	2.70	0.48	1.60	40.00	2.28	Gymnosperm	CC	2282	0.69
Larix laricina	Pinaceae	0.65	0.59	2.96	0.49	1.08	38.00	3.27	Gymnosperm	CC	3135	0.65
Liquidambar styraciflua	Altingiaceae	0.06	0.85	2.69	0.46	1.06	50.00	2.86	Angiosperm	BT	1557	0.66
Liriodendron tulipifera	Magnoliaceae	0.36	1.23	3.09	0.38	1.17	61.00	1.93	Angiosperm	BT	3611	0.81
Maclura pomifera	Moraceae	0.07	0.60	NA	0.76	NA	21.00	NA	Angiosperm	BT	416	0.79
Magnolia acuminata	Magnoliaceae	0.17	0.86	3.09	0.44	1.17	30.48	1.93	Angiosperm	BT	239	0.90
Nyssa aquatica	Cornaceae	0.02	1.08	2.75	0.46	0.53	35.05	4.61	Angiosperm	BT	484	0.87
Nyssa biflora	Nyssaceae	0.07	0.58	2.79	0.48	0.53	37.53	4.61	Angiosperm	BT	558	0.71
Nyssa sylvatica	Cornaceae	0.05	0.49	2.83	0.49	0.53	40.00	4.61	Angiosperm	BT	1899	0.62
Ostrya virginiana	Betulaceae	0.21	0.31	3.34	0.54	0.77	22.00	3.88	Angiosperm	BT	1101	0.78
Oxydendrum arboreum	Ericaceae	0.08	0.42	2.96	0.46	1.34	25.00	3.49	Angiosperm	BT	1098	0.82
Picea abies	Pinaceae	0.53	0.85	2.55	0.45	1.30	70.00	3.97	Gymnosperm	CC	312	0.79
Picea glauca	Pinaceae	0.12	0.85	2.36	0.45	1.38	61.00	2.97	Gymnosperm	CC	2006	0.81
Picea mariana	Pinaceae	0.03	0.37	2.22	0.47	1.46	35.00	1.98	Gymnosperm	CC	6358	0.70
Picea rubens	Pinaceae	0.34	0.61	2.44	0.38	0.89	54.00	2.97	Gymnosperm	CC	6652	0.74
Pinus banksiana	Pinaceae	0.23	0.62	2.50	0.41	1.21	33.00	2.48	Gymnosperm	CC	1382	0.74
Pinus echinata	Pinaceae	0.19	0.60	2.37	0.49	1.05	42.00	3.33	Gymnosperm	CC	1131	0.70
Pinus ponderosa	Pinaceae	0.74	0.56	2.53	0.44	1.03	90.00	3.20	Gymnosperm	CC	607	0.62
Pinus resinosa	Pinaceae	0.12	0.80	2.45	0.40	1.08	46.00	3.27	Gymnosperm	CC	3371	0.82
Pinus rigida	Pinaceae	0.01	0.52	2.47	0.47	1.08	30.00	3.27	Gymnosperm	CC	715	0.72
Pinus strobus	Pinaceae	0.36	1.08	2.62	0.35	1.08	80.00	3.27	Gymnosperm	CC	5974	0.83
Pinus taeda	Pinaceae	0.16	1.31	2.34	0.47	1.08	54.00	3.76	Gymnosperm	CC	3915	0.67
Pinus virginiana	Pinaceae	0.21	0.71	2.38	0.45	1.40	40.00	3.27	Gymnosperm	CC	868	0.80
Platanus occidentalis	Platanaceae	0.04	1.13	2.70	0.43	0.47	51.00	NA	Angiosperm	BT	310	0.80
Populus balsamifera	Salicaceae	0.28	0.67	2.90	0.33	0.52	36.00	3.74	Angiosperm	BT	1097	0.77
Populus grandidentata	Salicaceae	0.46	0.93	3.14	0.36	0.60	30.00	3.39	Angiosperm	BT	1979	0.80
Populus tremuloides	Salicaceae	0.66	0.84	3.13	0.40	0.67	36.50	3.04	Angiosperm	BT	8544	0.75
Prunus pensylvanica	Rosaceae	0.53	0.74	3.18	0.54	1.52	30.00	NA	Angiosperm	BT	209	0.79
Prunus serotina	Rosaceae	0.38	0.84	3.20	0.54	1.52	40.00	NA	Angiosperm	BT	4344	0.81
Quercus alba	Fagaceae	0.18	0.60	3.08	0.54	0.31	46.00	3.42	Angiosperm	BT	8072	0.79
Quercus coccinea	Fagaceae	0.38	0.79	2.89	0.52	0.29	50.00	3.37	Angiosperm	BT	2057	0.76
Quercus ellipsoidalis	Fagaceae	0.57	0.86	3.06	0.58	0.29	21.30	3.37	Angiosperm	BT	272	0.69
Quercus falcata	Fagaceae	0.42	0.91	2.76	0.61	-0.08	40.00	3.77	Angiosperm	BT	488	0.62
Quercus macrocarpa	Fagaceae	0.06	0.55	3.15	0.58	0.29	52.00	3.37	Angiosperm	BT	1468	0.79
Quercus marilandica	Fagaceae	0.55	0.46	2.62	0.58	0.29	20.00	3.37	Angiosperm	BT	210	0.81
Quercus muehlenbergii	Fagaceae	0.59	0.52	2.89	0.58	0.29	30.48	3.37	Angiosperm	BT	491	0.83
Quercus nigra	Fagaceae	0.06	0.98	2.73	0.64	0.19	40.00	3.31	Angiosperm	BT	387	0.93
Quercus prinus	Fagaceae	0.18	0.58	2.89	0.58	0.29	40.00	3.37	Angiosperm	BT	6098	0.73
Quercus rubra	Fagaceae	0.32	0.86	3.10	0.51	0.81	50.00	3.24	Angiosperm	BT	7487	0.80
Quercus stellata	Fagaceae	0.12	0.44	2.73	0.66	0.27	30.50	3.91	Angiosperm	BT	1916	0.78
Quercus velutina	Fagaceae	0.54	0.82	3.00	0.56	0.93	46.00	2.36	Angiosperm	BT	3726	0.76
Robinia pseudoacacia	Leguminosae	0.32	0.64	3.59	0.67	-0.11	52.00	3.95	Angiosperm	BT	618	0.62
Sassafras albidum	Lauraceae	0.52	0.56	3.30	0.45	0.57	35.00	2.16	Angiosperm	BE	1274	0.74
Taxodium distichum	Cupressaceae	0.05	0.96	2.53	0.38	0.80	50.00	2.89	Gymnosperm	CC	359	0.89
Thuja occidentalis	Cupressaceae	0.28	0.41	2.49	0.30	1.26	35.00	3.51	Gymnosperm	CC	11464	0.71
Tilia americana	Malvaceae	0.10	0.66	3.23	0.32	NA	43.00	NA	Angiosperm	BT	2628	0.75
Tsuga canadensis	Pinaceae	0.08	0.71	2.51	0.38	1.12	53.30	4.20	Gymnosperm	CC	8270	0.75
Ulmus alata	Ulmaceae	0.10	0.56	2.90	0.43	-0.92	30.00	NA	Angiosperm	BT	404	0.65
Ulmus rubra	Ulmaceae	0.28	0.80	2.97	0.48	-0.92	41.10	NA	Angiosperm	BT	715	0.62

Appendix 4

Table 4: Results from the models considering traits as predictors of annual mortality probability at zero growth. estimate = slope values; std.error = standard error; statistic = models statistics; p.value = effect of the predictor on the response variable; r.squared = model R^2; adj.r.squared = adjusted R^2; model p.value = model p-value; logLik = model log-Likelihood; AIC = Akaike Information Criteria; df.residual = number of residual degrees of freedom; n.obs = total number of observations from the model fitted.

Terms	estimate	std.error	statistic	p.value	r.squared	adj.r.squared	model p.value	logLik	AIC	df.residual	n.obs
Intercept (group Angiosperms)	**0.21**	**0.03**	**6.71**	**0.00**	**0.10**	**0.08**	**0.03**	**18.59**	**-29.18**	**67**	**70**
LeafN	**0.10**	**0.04**	**2.77**	**0.01**							
group Gymnosperms	**0.18**	**0.08**	**2.26**	**0.03**							
Intercept (group Angiosperms)	0.25	0.03	9.14	0.00	0.03	0.00	0.36	16.10	-24.19	68	71
Hmax	0.04	0.03	1.40	0.17							
group Gymnosperms	-0.01	0.06	-0.23	0.82							
Intercept (group Angiosperms)	0.24	0.03	8.98	0.00	0.00	-0.01	0.76	15.09	-24.17	69	71
traitGymnosperm	0.02	0.05	0.30	0.76							
Intercept (group Angiosperms)	0.52	0.20	2.62	0.01	0.03	0.00	0.37	16.08	-24.16	68	71
deciduous (BT)	-0.28	0.20	-1.39	0.17							
deciduous (CC)	-0.25	0.20	-1.26	0.21							
Intercept (group Angiosperms)	0.25	0.03	8.79	0.00	0.02	-0.01	0.59	14.91	-21.81	67	70
WD	-0.03	0.03	-0.99	0.33							
group Gymnosperms	-0.01	0.06	-0.13	0.90							
Intercept (group Angiosperms)	0.25	0.03	8.40	0.00	0.00	-0.03	0.98	13.67	-19.33	65	68
p50	0.00	0.03	-0.02	0.98							
groupGymnosperm	0.01	0.06	0.18	0.86							
Intercept (group Angiosperms)	0.25	0.03	8.25	0.00	0.02	-0.01	0.55	12.33	-16.66	59	62
Slope	-0.03	0.03	-1.09	0.28							
group Gymnosperms	0.00	0.06	-0.04	0.97							

Appendix 5

Table 5: Results from the model considering (log) dbh, (transformed) growth, and time (between 2nd and 3rd census) as predictors of annual mortality across temperate species.

	Model coefficients			
Species	**Intercept**	**log(dbh)**	**growth (transformed)**	**time (between census 2 and 3)**
Abies balsamea	-4.66	1.73	-5.66	0.16
Acer negundo	-0.15	0.00	-3.90	0.11
Acer rubrum	-1.97	0.11	-5.23	0.10
Acer saccharinum	-4.85	-0.07	-4.06	0.86
Acer saccharum	-3.40	0.33	-5.19	0.18
Amelanchier indet	-6.20	1.68	-7.02	0.11
Betula alleghaniensis	-1.56	-0.34	-4.29	0.24
Betula lenta	-0.07	-0.74	-5.13	0.20
Betula papyrifera	-0.97	0.03	-5.23	0.11
Carya alba	-6.56	1.18	-4.25	0.20
Carya cordiformis	-0.18	-0.27	-4.06	0.12
Carya glabra	-2.05	-0.05	-4.22	0.10
Carya ovata	-2.02	-0.18	-4.99	0.21
Carya texana	-2.74	-0.24	-2.83	0.26
Celtis occidentalis	-3.81	1.16	-5.26	-0.07
Cornus florida	4.04	-2.28	-5.47	0.33
Fagus grandifolia	-2.07	0.39	-4.90	0.14
Fraxinus americana	-3.12	0.34	-4.38	0.42
Fraxinus nigra	-6.18	0.42	-4.04	0.73
Fraxinus pennsylvanica	-3.62	0.46	-2.46	0.29
Gleditsia triacanthos	2.64	-0.72	-3.56	0.01
Juglans nigra	0.80	-0.32	-4.74	-0.19
Juniperus virginiana	0.49	-0.96	-3.94	0.08
Larix laricina	-2.78	1.57	-2.02	-0.56
Liquidambar styraciflua	-1.69	-0.49	-2.62	0.20
Liriodendron tulipifera	3.28	-1.59	-3.41	0.18
Maclura pomifera	-5.21	0.88	-5.86	0.34
Magnolia acuminata	-2.82	0.55	-4.38	-0.18
Nyssa aquatica	-3.61	-0.23	-1.57	0.28
Nyssa biflora	-5.05	1.16	0.31	-0.42
Nyssa sylvatica	-2.32	-0.27	-3.91	0.12
Ostrya virginiana	-1.85	0.20	-5.20	0.03
Oxydendrum arboreum	-2.66	-0.03	-4.39	0.26
Picea abies	1.29	-0.39	-5.66	-0.16
Picea glauca	-2.72	0.15	-4.87	0.37
Picea mariana	-7.51	1.32	-4.18	0.54
Picea rubens	-1.18	0.25	-5.39	-0.11
Pinus banksiana	-1.30	-0.08	-4.96	0.28
Pinus echinata	1.23	-1.10	-2.91	0.10
Pinus ponderosa	0.53	0.32	-2.31	-0.29
Pinus resinosa	0.40	-1.00	-4.26	0.14
Pinus rigida	-5.39	-0.04	-1.95	0.62
Pinus strobus	0.83	-0.59	-4.62	0.07
Pinus taeda	0.64	-1.03	-3.51	0.33
Pinus virginiana	-3.35	0.76	-3.79	0.11
Platanus occidentalis	-3.33	-0.03	-2.52	0.34
Populus balsamifera	-2.18	0.29	-6.36	0.49
Populus grandidentata	-2.09	0.63	-7.19	0.34
Populus tremuloides	-1.20	0.69	-5.93	0.10
Prunus pensylvanica	0.19	-0.19	-4.69	0.43
Prunus serotina	1.46	-0.84	-5.14	0.20
Quercus alba	-2.88	0.48	-6.08	0.17
Quercus coccinea	-2.31	0.67	-4.72	0.13
Quercus ellipsoidalis	2.01	-0.73	-6.00	0.13
Quercus falcata	1.26	-0.70	-4.90	0.21
Quercus macrocarpa	-2.66	-0.13	-5.71	0.31
Quercus marilandica	-2.27	0.89	-7.15	0.23
Quercus muehlenbergii	1.21	-0.24	-5.20	-0.23
Quercus nigra	-5.65	0.85	-4.98	0.69
Quercus prinus	-1.26	-0.18	-4.36	0.19
Quercus rubra	-2.80	0.75	-7.12	0.16
Quercus stellata	-2.37	0.03	-5.74	0.27
Quercus velutina	-0.22	0.11	-5.26	0.09
Robinia pseudoacacia	0.74	-0.66	-2.72	0.21
Sassafras albidum	-1.26	0.48	-5.13	0.09
Taxodium distichum	2.94	-2.48	-2.90	0.38
Thuja occidentalis	-2.24	0.62	-4.65	-0.30
Tilia americana	-3.07	0.30	-4.78	0.16
Tsuga canadensis	-4.59	0.73	-4.75	0.24
Ulmus alata	-0.29	-0.77	-1.83	0.05
Ulmus rubra	-1.28	0.11	-0.90	0.07

Conclusão geral

Concluding remarks

Esta tese apresentou um panorama geral de estruturação e dinâmica de florestas de diferentes regiões no continente americano, indicando como variáveis bióticas e abióticas interagem para a estruturação de comunidades florestais ao longo do tempo. Uma vez que florestas correspondem à maior parte dos reservatórios e fluxos de carbono no planeta, compreender de que forma distintas variáveis bióticas e abióticas afetam processos de sobrevivência, mortalidade, recrutamento, e estocagem de carbono têm se tornado cada vez mais necessário e importante, especialmente considerando cenários de mudanças globais. Os resultados encontrados mostram o efeito de variáveis climáticas e da estrutura da floresta sobre a estocagem de biomassa em florestas subtropicais, de atributos funcionais de plantas sobre a probabilidade de morte de espécies de florestas temperadas e, de forma bastante surpreendente, a ausência de relação entre componentes da diversidade biológica sobre o estoque e sumidouro de carbono em florestas subtropicais. Ao longo de três capítulos cada uma dessas relações foi explorada, incluindo a discussão de como potencialmente serão alteradas diante de mudanças climáticas futuras. Além disso, todos os dados que compõem essa tese derivam de coletas realizadas em campo, por diversos grupos de pesquisa, reforçando a importância de parcerias e colaborações para o avanço científico.

No capítulo 1, foi realizada estimativa de estoque de biomassa em uma ampla região de florestas subtropicais maduras na América do Sul, incluindo 119 sítios na Mata Atlântica e no Pampa. Além disso, também foram avaliados os principais determinantes bióticos e abióticos desses estoques. As florestas subtropicais têm uma alta capacidade de armazenar biomassa, maior que em florestas subtropicais na China e similar a muitas florestas tropicais na Amazônia (Anexo 1). Esses estoques são influenciados positivamente pela proporção de árvores grandes, o que indica que manter áreas de floresta madura, com grandes árvores, é fundamental para a manutenção de estoques de biomassa nessas florestas. Por outro lado, o estudo também demonstrou que a amplitude anual de temperatura influencia negativamente os estoques de biomassa, o que provavelmente está ligado ao estresse causado pela alta amplitude térmica na região. Nesse sentido, os resultados alertam para o efeito negativo de mudanças no clima, as quais tendem a intensificar a ocorrência de eventos extremos como ondas de frio e calor, aumentando assim, a amplitude anual de temperatura.

No capítulo 2, dados temporais de 55 comunidades florestais subtropicais foram utilizados para calcular o balanço líquido de carbono nessas florestas (Anexo 1). O conjunto de dados é diferente do capítulo 1, pois inclui apenas florestas com informações temporais (i.e., dados de monitoramento em parcelas permanentes) e algumas florestas em diferentes estágios sucessionais, obtendo assim uma caracterização ampla da dinâmica de carbono nessa região (Anexo 1). Nesse capítulo, testamos a relação entre o balanço líquido de carbono (ganhos via produtividade menos as perdas devido à mortalidade) com métricas de diversidade (i.e., taxonômica, funcional e filogenética). Caso uma relação positiva fosse encontrada, poderia refletir em um co-benefício (diversidade e carbono) para estratégias de conservação. No entanto, o que observamos é que essas variáveis não são relacionadas, ou seja, áreas que possuem maior sumidouro de carbono (balanço líquido de carbono positivo) não são as mesmas áreas que possuem maior diversidade. Deste modo, conservar apenas carbono pode implicar em reduzir a proteção à biodiversidade, o que indica que ambos devem ser considerados como alvos separados em propostas de conservação.

No capítulo 3, passamos do nível de comunidade para espécies, onde obtivemos estimativas de probabilidade de morte em crescimento zero de espécies de florestas temperadas (angiospermas e gimnospermas) dos Estados Unidos, indicando suas tolerâncias à ausência de recursos. Relacionamos essas probabilidades ao crescimento máximo das espécies, a fim de entender as relações entre crescimento e mortalidade (*trade-offs*), assim como o efeito de atributos funcionais sobre a probabilidade de morte dessas espécies. O conjunto de dados utilizado nessas análises corresponde ao inventário florestal nacional dos Estados Unidos (*Forest Inventory and Analysis National Program, FIA*). A probabilidade de morte foi determinada para 71 espécies, as quais atenderam ao critério de seleção, através do resultado predito por um modelo que considerou o diâmetro, crescimento e tempo entre os censos, resultando assim em uma estimativa por espécie. Observamos que o *trade-off* entre crescimento e mortalidade é fraco entre as espécies, o que pode estar ligado ao fato de que essas relações de *trade-off* são mais fortes em plântulas e indivíduos jovens. Por outro lado, a relação foi mais forte para angiospermas que gimnospermas. Além disso, também observamos um efeito forte e positivo do nitrogênio foliar sobre a probabilidade de morte das espécies, o que corrobora a teoria de espécies aquisitivas estarem sujeitas a maior mortalidade, até mesmo em vista do crescimento mais rápido (*trade-off* crescimento-mortalidade).

Esta tese é a primeira avaliação da espacialização e dinâmica de carbono em florestas subtropicais que compreendeu um grande número de pontos amostrais, espacialmente distribuídos por toda a extensão dessas florestas. Também provemos a primeira estimativa da probabilidade de mortalidade de espécies de florestas temperadas em crescimento zero, refletindo suas tolerâncias à ausência de recursos. Estas avaliações só foram possíveis devido à avaliação temporal dos indivíduos que compõem essas comunidades. Deste modo, a manutenção de parcelas permanentes é crucial para que estudos de dinâmica de florestas sejam conduzidos. Além disso, este trabalho envolveu um grande número de pessoas, direta ou indiretamente, as quais devem ser valorizadas pelo trabalho de coleta e organização de dados. Assim, manter investimentos na manutenção de parcelas permanentes e cientistas vinculados é fundamental para a avaliação em longo prazo destas (e outras) importantes regiões, especialmente diante de mudanças no clima onde não sabemos como estas florestas irão reagir.

Anexo I

Tabela 1: Estado da arte de trabalhos que envolvem estrutura de dinâmica temporal de comunidades florestais na região tropical e subtropical do Brasil. São apresentados os resultados de trabalhos conduzidos em diferentes regiões do país, considerando a Floresta Amazônica e Mata Atlântica, principalmente, visando comparar como os ganhos, perdas, e estoques de carbono se apresentam dos trópicos aos subtrópicos.

Referência	Região de estudo	Critério de inclusão (diâmetro à altura do peito)	Variação líquida de biomassa, Mg ha^{-1} ano^{-1}	Ganho em biomassa (crescimento de sobreviventes, Mg ha^{-1} ano^{-1})	Ganho em biomassa (recrutamento, Mg ha^{-1} ano^{-1})	Perda de biomassa (mortalidade, Mg ha^{-1} ano^{-1})	Estoque de biomassa acima do solo, Mg ha^{-1}	Estoque de carbono acima do solo, Mg C ha^{-1}	Área basal, m^{2} ha^{-1}
Baker et al. 2004	Amazônia	≥ 10 cm	0.98				239		
Castilho et al. 2006	Amazônia	≥ 1 cm					327.8		
Lewis et al. 2004	Amazônia	≥ 10 cm							29.5
Sullivan et al. 2020	Amazônia	≥ 10 cm						130	
Finegan et al. 2015	Amazônia boliviana, brasileira e Costa Rica	≥ 10 cm		4.11	0.38		272.8		
Banin et al. 2014	Amazônia - Peru e Equador	≥ 10 cm							28.1
Baraloto et al. 2011	Amazônia - Peru e Guiana Francesa	≥ 10 cm					289.1		
van der Sande et al. 2017	Amazônia boliviana	≥ 10 cm	1.68	3.78	0.78	2.88			
Phillips et al. 2019	Amazônia colombiana	≥ 10 cm						241.3	
Vilanova et al. 2018	Amazônia venezuelana	-						159.4	28.6
Álvarez-Dávila et al. 2017	América Central e Amazônia peruana	-					194.4		23.1
Duque et al. 2021	Andes	≥ 10 cm						77.2	
Prado-Junior et al. 2016	Cerrado	≥ 5 cm	0.27	3.88	0.06	3.67	246.4		
Marimon et al. 2014	Cerrado e florestas de galeria	≥ 10 cm					210		
Pyles et al. 2018	Mata Atlântica, Espírito Santo	≥ 5 cm					276.5		
Rolim et al. 2005	Mata Atlântica, Espírito Santo	≥ 10 cm					334.5		
Bordin & Müller 2019	Mata Atlântica, floresta subtropical	≥ 9.5 cm	0.88	2.9	0.43	2.46			33.1
Capellesso et al. 2021	Mata Atlântica, floresta subtropical	≥ 5 cm					231		
Gross et al. 2018	Mata Atlântica, floresta subtropical	≥ 5 cm							35.8
Souza & Longhi 2019	Mata Atlântica, floresta subtropical	≥ 9.5 cm					366.7		
Alves et al. 2010	Mata Atlântica, São Paulo	≥ 4.8 cm					283.2		
Vibrans et al. 2022	Mata Atlântica, floresta subtropical	≥ 10 cm					117.7		23.8
Maia et al. 2020	Mata Atlântica, Minas Gerais	≥ 5 cm						89.3	
Oliveira-Filho et al. 2007	Mata Atlântica, Minas Gerais	≥ 5 cm							32.4
Bordin et al. 2021	Mata Atlântica, floresta subtropical	≥ 10 cm					246.5		
Bordin et al. under review	Mata Atlântica, floresta subtropical	≥ 10 cm	3.95	7.23		3.29	216	98.5	
Zhang et al. 2019	Florestas subtropicais na China	Mapa - sensoriamento remoto + dados de campo (≥ 2 cm)					123.2		

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