NATHÁLIA VIEIRA HISSA SAFAR

PRO-FOREST: DRIVERS OF STRUCTURE, DIVERSITY, FUNCTIONAL COMPOSITION AND VULNERABILITY OF BRAZILIAN ATLANTIC RAINFORESTS. A STUDY ON FUNCTIONING AND PROCESSES

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientador: Carlos Ernesto Gonçalves R. Schaefer

Coorientador: Luiz Fernando Silva Magnago

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Carlos Ernesto Gonçalves Reynaud Schaefer
Orientador

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RESUMO

SAFAR, Nathália Vieira Hissa, D.Sc. Universidade Federal de Viçosa, maio de 2023. **PRO-FLORESTA: Direcionadores da estrutura, diversidade, composição funcional e vulnerabilidade da floresta Atlântica brasileira. Um estudo sobre funcionamento e processos**. Orientador: Carlos Ernesto Gonçalves Reynaud Schaefer. Coorientador: Luiz Fernando Silva Magnago.

Florestas tropicais são um dos ecossistemas com maior biodiversidade e densidade de carbono do mundo, porém também um dos mais ameaçados. Portanto, promover sua conservação e garantir o sucesso do processo sucessional são etapas importantes para manter o funcionamento do ecossistema e mitigar efetivamente a perda de biodiversidade e as mudanças climáticas. Assim, o objetivo dessa tese foi determinar os principais direcionadores dos atributos florestais (e.g., estrutura, diversidade e composição funcional) que são informativos da montagem da comunidade e funcionamento do ecossistema, bem como entender e prever a vulnerabilidade funcional de florestas tropicais de alta diversidade situadas em solos pobres em nutrientes e em paisagens altamente fragmentadas e modificadas pelo homem. Para isso, foram desenvolvidos dois estudos independentes porém complementares: no primeiro (C1), foram utilizados dados de 1,9 ha de floresta madura e 1,6 ha de floresta secundária para determinar os efeitos da estrutura da paisagem (abertura da matriz, densidade de fragmentos) em nove atributos florestais relacionados à estrutura (área basal, altura máxima, heterogeneidade estrutural), diversidade (riqueza de espécies, diversidade de Simpson, riqueza funcional) e composição (proporção de espécies dispersadas por animais, tolerantes à sombra, tamanho das sementes) em quatro escalas espaciais (buffers de 400 a 3200 m) e três regiões diferentes (i.e. contextos de paisagem). A abertura da paisagem afetou negativamente a maioria dos atributos florestais, porém a magnitude desse efeito variou com i) atributo da paisagem, ii) atributo florestal e iii) região: o desmatamento teve um efeito negativo maior do que a fragmentação; a abertura da paisagem teve um efeito negativo maior na estrutura florestal e espécies dispersas por animais, efeitos contrastantes entre as regiões. Além disso, afetou os atributos estruturais em todas as escalas espaciais, as espécies dispersadas por animais em escalas maiores e o tamanho da semente em escalas menores. Esses resultados indicam que os efeitos da paisagem nos atributos florestais em paisagens modificadas pelo homem não podem ser generalizados, pois dependem do contexto da paisagem. No segundo estudo (C2), foram utilizados dados de 2,7 ha de floresta secundária para determinar como a idade da floresta, a estrutura da paisagem (abertura da matriz, densidade de fragmentos), a disponibilidade hídrica sazonal (déficit hídrico climático) e as propriedades do solo (soma de bases, nitrogênio, carbono orgânico e teor de argila) preveem o estoque de carbono acima do solo, a composição funcional (média ponderada do diâmetro máximo e altura máxima dos indivíduos arbóreos, e da densidade da madeira específica da espécie), e a redundância e vulnerabilidade funcionais das florestas secundárias. A idade da floresta e as propriedades do solo foram os principais impulsionadores do estoque de carbono acima do solo, da redundância funcional e da vulnerabilidade. Observou-se que a disponibilidade hídrica sazonal teve efeito no crescimento das espécies e a densidade da madeira; enquanto as propriedades do solo influenciam o crescimento das espécies, mas não a densidade da madeira, e que as áreas em paisagens altamente fragmentadas e desmatadas podem abrigar espécies dominantes em carbono. Esses resultados avançam o entendimento dos fatores que impulsionam o estoque de carbono e a vulnerabilidade nas florestas atlânticas secundárias e destacam a importância de considerar as condições locais nos esforços de restauração florestal e mitigação das mudanças climáticas.

Palavras-chave: Contexto da paisagem. Dispersão. Escala Espacial. Mudanças Climáticas. Mudança do uso do solo. Propriedades do Solo. Sucessão. Traços funcionais

ABSTRACT

SAFAR, Nathália Vieira Hissa, D.Sc. Universidade Federal de Viçosa, May, 2023. **PRO-FOREST: Drivers of structure, diversity, functional composition and vulnerability of Brazilian Atlantic rainforests. A study on functioning and processes.** Advisor: Carlos Ernesto Gonçalves Reynaud Schaefer. Co-advisor: Luiz Fernando Silva Magnago.

Tropical forests are one of the most biodiverse, carbon-dense, but also threatened ecosystems in the world. Hence, promoting their conservation and ensuring the success of the successional process are important steps to maintain ecosystem functioning and effectively mitigate biodiversity loss and climate change. Here we aimed to determine the main drivers of forests attributes (e.g., structure, diversity and functional composition) that are informative of community assembly and ecosystem functioning and understand the functional vulnerability of high-diversity tropical rainforests situated on nutrient-poor soils and within highly fragmented human-modified landscapes. For that, we developed two independent but complementary studies: in the first (C1), we used data from 1.9 ha old-growth and 1.6 ha second-growth forest plots to assess the effects of landscape structure (matrix openness, patch density) on nine forest attributes related to structure (basal area, maximum height, structural heterogeneity), diversity (species richness, Simpson diversity, functional richness), and composition (community weighted-mean animal-dispersal shade-tolerance and seed size) over four different spatial scales (400 to 3200 m buffer radius) in three different regions (i.e., landscape contexts). We found that landscape openness negatively affected most forest attributes, but the magnitude of effect varied with i) landscape attribute, ii) forest attribute, and iii) region (i.e. landscape context): deforestation had a negative stronger effect than fragmentation; landscape openness reduced most strongly forest structure and animal-dispersed species; landscape openness had different effects in different regions, and affected forest structural attributes at all spatial scales, animal dispersed species at larger spatial scales, and seed size at small spatial scales. These findings indicate that landscape effects on forest attributes in human-modified landscapes cannot be generalized as they depend on the landscape context. In the second study (C2), we used data from 2.7 ha second-growth forest plots to assess the how stand age, landscape structure (matrix openness, patch density), seasonal water availability (climatic water deficit), and soil properties (sum of base, nitrogen, organic carbon and clay contents) predict aboveground carbon stock and functional composition (community weighted-mean maximum stem diameter, maximum stem height and species-specific wood density), redundancy, and vulnerability of second-growth Atlantic forests. We found that forest age and soil properties were the main drivers of aboveground carbon stock, functional redundancy and vulnerability; that seasonal water availability predicted species growth and wood density; while soil properties predicted species growth, but not wood density; and finally, that stands in highly fragmented and deforested landscapes can harbor carbon-dominant species. These findings advance our understanding of the factors that drive carbon stock and vulnerability in second-growth Atlantic forests and highlight the importance of considering local site conditions in forest restoration and climate change mitigation efforts.

Keywords: Climate Change. Functional traits. Land use Change. Landscape context. Dispersal. Soil Properties. Spatial Scale. Succession

SUMÁRIO

I. Introdução Geral

As florestas tropicais são um dos ecossistemas com maior biodiversidade e densidade de carbono do mundo (Sullivan et al. 2017). No entanto, as mudanças no uso da terra induzidas pelo homem (e.g., extração de madeira, caça, incêndios florestais e fragmentação da paisagem) e as mudanças climáticas estão levando à perda de biodiversidade (Gibson et al. 2011; Newbold et al. 2015; Barlow et al. 2016) e liberação de grandes quantidades do gás de efeito estufa CO_2 (Magnago et al. 2015b; Baccini et al. 2017). Isso pode, consequentemente, afetar negativamente o funcionamento do ecossistema e vários serviços ecossistêmicos (e.g., controle da erosão do solo, dispersão de sementes, polinização, regulação do clima), que são cruciais para o bem-estar humano (Lewis et al. 2015; Walker et al. 2020). As florestas tropicais são, portanto, centrais para os esforços de mitigação da perda de biodiversidade e das mudanças climáticas (Brancalion et al. 2019; Edwards et al. 2019; Hansen et al. 2020).

Grande parte do debate sobre os esforços de conservação e mitigação (por exemplo, REDD+, Metas de Aichi e Objetivos de Desenvolvimento Sustentável) tende a se concentrar em florestas maduras porque são conhecidas por abrigar alta biodiversidade e armazenar grandes quantidades de carbono (Gibson et al. 2011; Anderson-Teixeira et al. 2016; Poulsen et al. 2020). No entanto, o papel crucial das florestas secundárias têm sido cada vez mais reconhecido nos trópicos (Chazdon et al. 2016; Poorter et al. 2016; Rozendaal et al. 2019; Matos et al. 2019; Safar et al. 2020), especialmente aquelas florestas capazes de manter e recuperar naturalmente sua estrutura, diversidade e função, apesar dos distúrbios ambientais (i.e. ecossistemas resilientes, Nimmo et al. 2015). No entanto, nem todos os ecossistemas florestais conseguem se recuperar naturalmente após o abandono do uso da terra ou quando cessam os distúrbios. Isso acontece porque o seu potencial de regeneração pode ser afetado, não só pelas restrições impostas pela disponibilidade de sementes e limitação da dispersão (e.g., composição e configuração da paisagem, como cobertura florestal, densidade de fragmentos, grau de isolamento, qualidade da matriz) e filtragem ambiental (e.g., solo e clima), mas também pelos traços/estratégias funcionais das espécies (Lebrija-Trejos et al. 2010; Boukili and Chazdon 2017; Le Bagousse-Pinguet et al. 2017; Toledo et al. 2018; Werden et al. 2018; Poorter et al. 2021a).

Os ecossistemas florestais fornecem sementes para a colonização de locais perturbados e são um habitat importante para os dispersores de sementes (Chazdon 2003). Portanto, a perda da cobertura florestal circundante (i.e., aumento da abertura da matriz) e a diminuição da conectividade entre os fragmentos florestais reduzem não apenas o conjunto de espécies florestais especialistas na paisagem (Pardini et al. 2010), mas também o número de árvores reprodutivas, a disponibilidade de propágulos e a dispersão de sementes (Traveset and Rodríguez-Pérez 2008). Portanto, como a regeneração florestal é influenciada por processos que operam em diferentes escalas espaciais, como a dispersão de sementes, a escala espacial em que ocorre a fragmentação da paisagem pode ser importante (Jackson and Fahrig 2015; Martin 2018; San-José et al. 2019). Por exemplo, como a maioria das sementes está dispersa em distâncias mais (Schurr et al. 2018), uma maior abertura da paisagem em escalas espaciais menores pode influenciar mais fortemente a dispersão de sementes a curta distância. Em contraste, a abertura da paisagem em escalas espaciais maiores pode influenciar a dispersão de sementes a longa distância por animais migratórios e de grande porte, devido à perda de habitat e limitação de movimento de dispersores de sementes de grande porte (Haddad et al. 2015; Schurr et al. 2018). Por esta razão, espera-se que diferentes atributos da floresta sejam afetados pela abertura da paisagem em diferentes escalas espaciais. Além disso, a perda e a fragmentação da floresta (ou seja, a abertura da paisagem) levam a uma área maior de bordas de floresta expostas e, portanto, aumentam os efeitos de borda, como maior perturbação do vento e temperaturas e menor umidade do ar e do solo (Magnago et al. 2015c; Arroyo-Rodríguez et al. 2017) que impactam o estabelecimento e o desempenho da planta.

A perda e a fragmentação da floresta levam a uma área maior de bordas de floresta expostas e, portanto, aumentam os efeitos da borda, como maior perturbação do vento e temperaturas e menor umidade do ar e do solo (Magnago et al. 2015c; Arroyo-Rodríguez et al. 2017) que afetam o estabelecimento e o desempenho das plantas. Além disso, a abundância de recursos, como água e nutrientes do solo, pode influenciar positivamente a diversidade de espécies (e.g., van der Sande et al., 2017a; Yang et al., 2019) e a recuperação de biomassa em florestas secundárias neotropicais (e.g., Poorter et al. 2016), principalmente porque a maior disponibilidade de recursos contribui para a coexistência das espécies e crescimento das árvores.

Os traços/estratégias funcionais das espécies determinam sua capacidade de retornar, estabelecer e crescer em locais que se recuperam de uma perturbação passada (Lebrija-Trejos et al. 2010; Boukili and Chazdon 2017; Poorter et al. 2021a). Espécies que investem em traços que aumentam a aquisição de recursos e eficiência no uso (e.g., baixa densidade de madeira; semente pequena) têm crescimento rápido e maior capacidade competitiva, enquanto espécies com traços que favorecem a conservação de recursos (e.g., alta densidade de madeira; semente grande) têm crescimento lento e alta sobrevivência (Westoby et al. 2002; Poorter and Bongers 2006; Poorter et al. 2008). Espécies com rápida aquisição de recursos são favorecidas quando recursos como luz, água e nutrientes são abundantes, enquanto espécies conservadoras de recursos tornam-se mais abundantes quando os recursos são limitados (Kitajima 1994; Westoby et al. 2002; Markesteijn et al. 2011; Werden et al. 2018). No geral, se as condições edáfico-climáticas pós-distúrbios não forem adequadas para a espécie e se a dispersão de seus propágulos for limitada, há uma baixa probabilidade de ocorrência da espécie. Portanto, entender como os fatores abióticos moldam as comunidades de árvores pode ajudar a prever as respostas das plantas às mudanças ambientais, mudanças no funcionamento do ecossistema e identificar ecossistemas vulneráveis. (Lohbeck et al. 2015; Poorter et al. 2016; Ouyang et al. 2019).

Uma abordagem baseada em traços funcionais pode quantificar e prever melhor os impactos causados pelo homem (Laliberté et al. 2010; Mouillot et al. 2013; Laughlin 2014), pois o grau em que a perda de uma espécie individual impacta o ecossistema depende se existem outras espécies dentro da comunidade que desempenham funções semelhantes (i.e., redundância funcional). A perda de qualquer grupo funcional (i.e., um conjunto de espécies de diferentes grupos taxonômicos que compartilham papéis semelhantes, se não idênticos, no ecossistema, Lavorel and Garnier, 2002) provavelmente resultará na perda de algumas funções do ecossistema e aumentará sua vulnerabilidade a perturbações futuras. Por outro lado, espera-se que um ecossistema seja menos vulnerável quando possui alta redundância funcional, porque a perda de qualquer espécie é protegida contra a perda de uma espécie individual (Fonseca and Ganade 2001). Assim, no contexto da mitigação das mudanças climáticas, o retorno de espécies que mais contribuem para o armazenamento de carbono, como espécies de árvores de grande porte (Slik et al. 2013) e espécies de madeira dura (Phillips et al. 2019), é essencial para restaurar a floresta funcionando e conservando o carbono terrestre.

Vários estudos mostraram que o status sucessional (Chazdon 2014), estrutura da paisagem (Collins et al. 2017; Matos et al. 2017; San-José et al. 2019; Safar et al. 2022), sazonalidade na disponibilidade de água (Becknell et al. 2012; Poorter et al. 2016, 2019), e propriedades do solo (Pinho et al. 2018; Toledo et al. 2018; Werden et al. 2018) são determinantes mais fortes da composição e funcionamento da comunidade florestal. Compreender as relações entre fatores abióticos e antropogênicos e os atributos florestais pode ajudar a prever mudanças no funcionamento do ecossistema, identificar ecossistemas vulneráveis (Lohbeck et al. 2015; Poorter et al. 2016; Ouyang et al. 2019) e projetar estratégias eficazes de restauração e mitigação da perda de biodiversidade e das mudanças climáticas destinadas a reverter a degradação florestal e alcançar metas ambientais locais e globais (como Aichi Targets, Bonn Challenge).

Neste contexto, essa tese busca determinar os principais direcionadores dos atributos florestais que são informativos da comunidade e funcionamento do ecossistema (estrutura, diversidade e composição funcional) e entender e prever a vulnerabilidade funcional de florestas tropicais de alta diversidade situadas em solos pobres em nutrientes e em paisagens altamente fragmentadas e modificadas pelo homem. Para isso, foram desenvolvidos dois estudos independentes, mas complementares (**Fig 1**).

(C1) No primeiro estudo, para aprimorar as estratégias de restauração, foi investigado como a estrutura da paisagem (abertura da matriz, densidade de fragmentos) afeta a estrutura, diversidade e composição funcional da floresta e em qual escala espacial os efeitos da paisagem são mais fortes. Até onde sabemos, a maioria dos estudos sobre os efeitos da paisagem nos ecossistemas florestais foi realizada em um único contexto de paisagem, em uma escala espacial e abordando poucos atributos florestais. Este estudo apresenta uma visão abrangente dos efeitos da estrutura da paisagem em nove atributos florestais em diferentes escalas espaciais (variando de 400 a 3200 metros) em três regiões distintas (ou seja, diferentes contextos de paisagem). Para isso, foram utilizados dados coletados de 19 parcelas de 0,1 ha de floresta madura e 16 parcelas de 0,1 ha de floresta secundária, focando em três atributos estruturais (área basal, altura máxima, heterogeneidade estrutural), três atributos de biodiversidade (riqueza de espécies, diversidade de Simpson, riqueza funcional) e três características regenerativas como atributos de composição (proporção de espécies dispersas por animais e tolerantes à sombra, tamanho da semente).

(C2) No segundo estudo, buscou-se compreender como as condições/contextos locais e regionais influenciam a função de estocagem de carbono em florestas secundária e sua vulnerabilidade. Para isso, investigou-se como a idade da floresta, a estrutura da paisagem, a disponibilidade hídrica sazonal e as propriedades do solo influenciam o estoque de carbono acima do solo, a composição funcional, a redundância funcional e a vulnerabilidade funcional das florestas secundárias da Mata Atlântica. A extensão na qual esses fatores afetam a vulnerabilidade do funcionamento de estocagem de carbono em florestas tropicais não é bem compreendida (mas veja Laliberté et al. 2010; Guo et al. 2020). Neste estudo foram utilizados dados de 27 parcelas de 0,1 ha de floresta secundária distribuídas em três regiões diferentes dentro de contextos de paisagens e condições edafoclimáticas distintos, com foco em atributos relacionadas ao carbono, incluindo o diâmetro e a altura máxima do tronco, e a densidade da madeira específica das espécies. Por fim, a tese é concluída com as implicações dos resultados para estratégias de conservação, restauração e mitigação de mudanças climáticas.

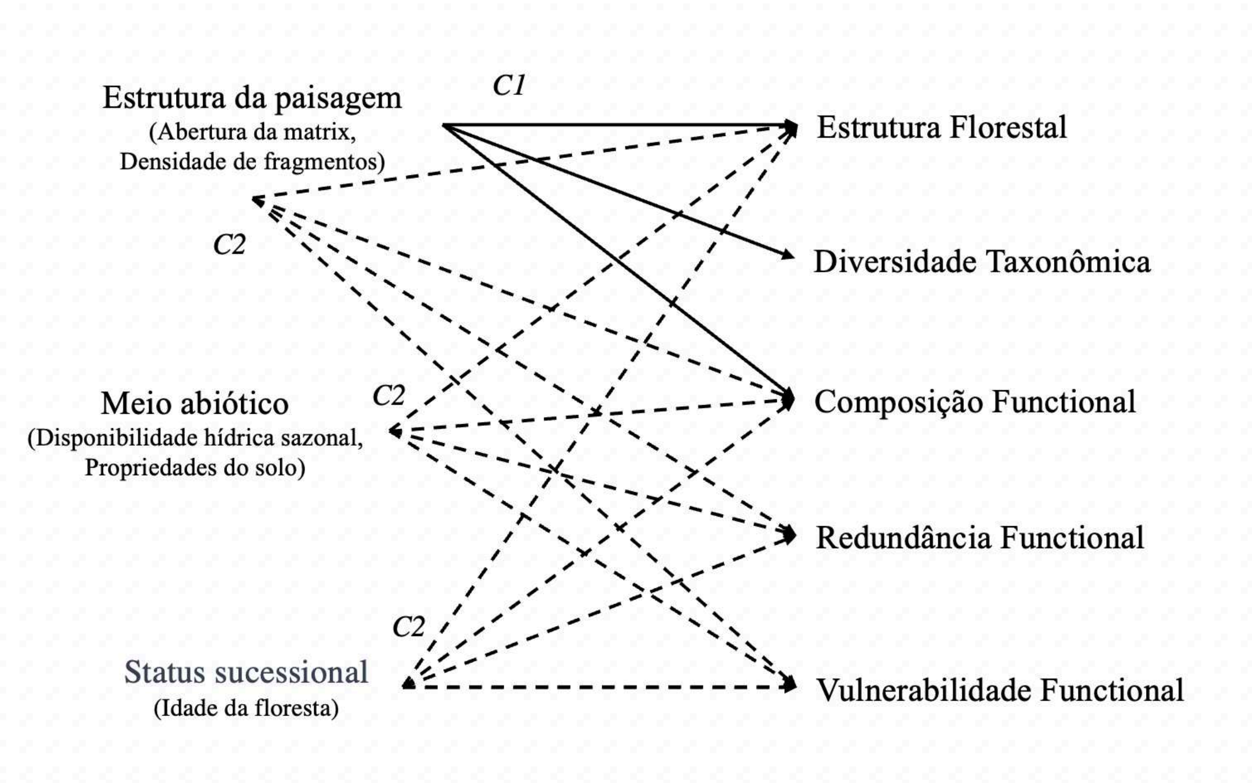

Fig 1. Estrutura conceitual mostrando as relações que serão testadas em cada capítulo (C1 e C2)

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II. General Introduction

Tropical forests are one of the most biodiverse and carbon-dense ecosystems on a global scale (Sullivan et al. 2017). However, human-induced land use change (e.g. logging, hunting, forest fire and landscape fragmentation) and climate change are driving the loss of biodiversity (Gibson et al. 2011; Newbold et al. 2015; Barlow et al. 2016) and the release of large amounts of greenhouse gas CO_2 (Magnago et al. 2015b; Baccini et al. 2017). This can, consequently, negatively affect ecosystem functions and multiple ecosystem services (e.g. soil erosion control, seed dispersal, pollination, climate regulation) that are crucial to human well-being (Lewis et al. 2015; Walker et al. 2020). Tropical forests are therefore central to biodiversity loss and climate change mitigation efforts (Brancalion et al. 2019; Edwards et al. 2019; Hansen et al. 2020).

Much of the debate on conservation and mitigation efforts (e.g. REDD+, Aichi Targets and Sustainable Development Goals) tend to focus on old-growth forests because they are known to harbor high biodiversity and store large amounts of carbon (Gibson et al. 2011; Anderson-Teixeira et al. 2016; Poulsen et al. 2020). However, the crucial role of second-growth forests is recently gaining increasing recognition in the tropics (Chazdon et al. 2016; Poorter et al. 2016; Rozendaal et al. 2019; Matos et al. 2019; Safar et al. 2020), especially those forests able to naturally maintain and recover their structure, diversity and function despite environmental disturbances (i.e. resilient ecosystems, Nimmo et al. 2015). Yet, not all forest ecosystems are able to recover naturally after land use abandonment or when disturbance ceases, because their regeneration potential can be affected, not only by the constraints imposed by seed availability and dispersal limitation (e.g., landscape composition and configuration, such as forest cover, density of patches, degree of forest isolation, matrix quality) and environmental filtering (e.g., soil and climate), but also by the species functional traits/strategies (Lebrija-Trejos et al. 2010; Boukili and Chazdon 2017; Le Bagousse-Pinguet et al. 2017; Toledo et al. 2018; Werden et al. 2018; Poorter et al. 2021a).

Forest ecosystems provide seeds for the colonization of disturbed sites and are an important habitat for seed dispersers (Chazdon 2003). Hence, the loss of surrounding forest cover (i.e., increased matrix openness) and decreased connectivity between forest patches reduce not only the pool of forest specialist species in the landscape (Pardini et al. 2010), but also the number of reproductive trees, propagule availability, and seed dispersal (Traveset and Rodríguez-Pérez 2008). Therefore, since forest regeneration is influenced by processes that operate at different spatial scales, such as seed dispersal, the spatial scale at which landscape fragmentation occurs may be important (Jackson and Fahrig 2015; Martin 2018; San-José et al. 2019). For example, as most seeds are dispersed over shorter distances (Schurr et al. 2018), greater landscape openness at smaller spatial scales could more strongly influence short-distance seed dispersal. In contrast, landscape openness at larger spatial scales may influence long-distance seed dispersal by migratory and large-sized animals, because of habitat loss and movement limitation of large-bodied seed dispersers (Haddad et al. 2015; Schurr et al. 2018). For this reason, different forest attributes are expected to be affected by landscape openness at different spatial scales.

Forest loss and fragmentation (i.e. landscape openness) also lead to a larger area of exposed forest edges thus increasing edge effects, such as higher temperature and wind disturbance, and lower air and soil humidity (Magnago et al. 2015c; Arroyo-Rodríguez et al. 2017), that impact plant establishment and performance. Furthermore, the abundance of resources such as water and soil nutrients can positively influence species diversity (e.g., van der Sande et al., 2017a; Yang et al., 2019) and structure in Neotropical secondary forests (e.g., Poorter et al. 2016), mainly because greater resources availability contributes to species coexistence and trees growth.

The functional traits/strategies of species determine their capacity to return, establish and grow in sites recovering from a past disturbance (Lebrija-Trejos et al. 2010; Boukili and Chazdon 2017; Poorter et al. 2021a). Species that invest in traits that enhance resource acquisition and use efficiency (e.g. softwood density; small seed) have fast growth and higher competitive ability, while species with resource conservation traits (e.g. hardwood density; large seed) have slow growth and high survival (Westoby et al. 2002; Poorter and Bongers 2006; Poorter et al. 2008). Fast-resource acquisitive species are favored when resources such as light, water and nutrients are abundant, whilst resource-conservative species become more abundant when resources are limited (Kitajima 1994; Westoby et al. 2002; Markesteijn et al. 2011; Werden et al. 2018). Overall, if the post-disturbance edaphic-climatic conditions are not suitable for the species and if its propagules dispersal is limited, there is a low probability of species occurrence. Hence, understanding how abiotic factors shape tree communities can help predict plant responses to environmental changes, changes in ecosystem functioning, and identify vulnerable ecosystems (Lohbeck et al. 2015; Poorter et al. 2016; Ouyang et al. 2019).

A trait-based approach can better quantify and predict human-driven impacts (Laliberté et al. 2010; Mouillot et al. 2013; Laughlin 2014), as the degree to which the loss of an individual species impacts the ecosystem depends on whether there are other species within the community that perform similar functions (i.e. functional redundancy). The loss of any functional group (i.e. a collection of species from different taxonomic groups that share similar, if not identical, roles in the ecosystem, Lavorel and Garnier, 2002) will likely result in the loss of some ecosystem functions and increase its vulnerability to future disturbances. On the other hand, an ecosystem is expected to be less vulnerable when having high functional redundancy, because the loss of any species is buffered against the loss of an individual species (Fonseca and Ganade 2001). So, in the context of climate change mitigation, the return of species that contribute the most to carbon storage, such as large tree species (Slik et al. 2013) and hardwood species (Phillips et al. 2019), is essential for restoring forest functioning and conserving terrestrial carbon.

Several studies have shown that successional status (Chazdon 2014), landscape structure (Collins et al. 2017; Matos et al. 2017; San-José et al. 2019; Safar et al. 2022), seasonality in water availability (Becknell et al. 2012; Poorter et al. 2016, 2019), and soil properties (Pinho et al. 2018; Toledo et al. 2018; Werden et al. 2018) are stronger determinants of forest community composition and functioning. Understanding the relationships between abiotic and anthropogenic drivers and forest attributes can help predict changes in ecosystem functioning, identify vulnerable ecosystems (Lohbeck et al. 2015; Poorter et al. 2016; Ouyang et al. 2019) and design effective restoration, and climate change and biodiversity loss mitigation projects aimed at reversing forest degradation and achieving local and large-scale environmental targets (such as Aichi Targets, Bonn Challenge).

Here we aimed to determine the main drivers of forests attributes that are informative of community assembly and ecosystem functioning (structure, diversity and functional composition), and understand the functional vulnerability of high-diversity tropical rainforests situated on nutrient-poor soils and within highly fragmented human-modified landscapes. To achieve this, we conducted two distinct yet complementary studies (**Fig. 2**):

(C1) In the first study, to help improve restoration strategies, we investigated how landscape structure (matrix openness, patch density) affects forest structure, diversity and functional composition and at which spatial scale the landscape effects are strongest. To our knowledge, most studies on the effects of landscape on forest ecosystems have been carried out in one landscape context, at one single spatial scale, addressing few forest attributes. Here we provide a comprehensive picture of the effects of landscape structure on nine forest attributes over different spatial scales (ranging from 400 to 3200 meters) in three different regions (i.e., landscape contexts). For that, we used data collected from 19 0.1 ha old-growth and 16 0.1 ha second-growth forest plots and focused on three structural attributes (basal area, maximum height, structural heterogeneity), three biodiversity attributes (species richness, Simpson diversity, functional richness) and three regenerative traits as compositional attributes (proportion of animal-dispersed and shade-tolerant species, seed size).

(C2) In the second study, we sought to understand how local and regional conditions/contexts influence the carbon storage function of second-growth forests and its vulnerability. To do this, we investigated how stand age, landscape structure, seasonal water availability, and soil properties drive aboveground carbon stock, functional composition, functional redundancy, and functional vulnerability of second-growth Atlantic forests. The extent to which these drivers affect the vulnerability of carbon storage functioning in tropical forests is not well understood (but see Laliberté et al. 2010; Guo et al. 2020). For this chapter, we used data from 27 0.1 ha second-growth forest plots distributed in three different regions within different landscape and edaphoclimatic contexts, and focused on carbon-related traits, including maximum stem diameter, maximum stem height, and species-specific wood density. Finally, we conclude the thesis with the implications of our findings for forest conservation, restoration and climate change mitigation strategies.

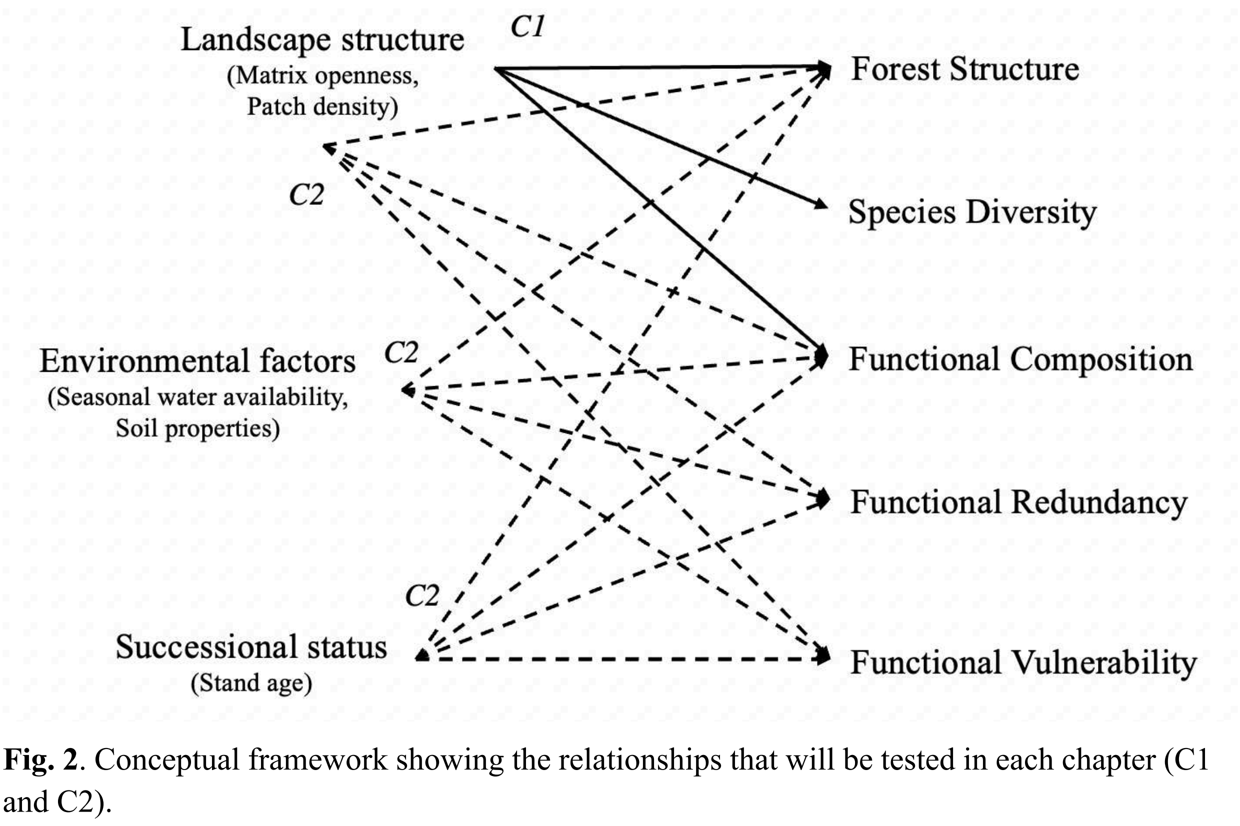

Fig. 2. Conceptual framework showing the relationships that will be tested in each chapter (C1 and C2).

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III. CAPÍTULO I

LANDSCAPE OPENNESS HAS DIFFERENT EFFECTS ON THE STRUCTURE, DIVERSITY AND FUNCTIONAL COMPOSITION OF BRAZILIAN RAINFORESTS

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Abstract

Landscape openness leads to harsher environmental conditions and reduced propagule dispersal, but how it affects different forest attributes and over what spatial scale remains unclear. We evaluate the effects of landscape openness (i.e., increased forest loss and fragmentation) on nine forest attributes related to structure, diversity, and composition for four different spatial scales, and three regions in Brazilian Atlantic forest. For 35 0.1 ha forest plots we calculated nine forest attributes related to structure (basal area, maximum height, structural heterogeneity), tree biodiversity (species richness, Simpson diversity, functional richness) and functional composition (proportion of animal-dispersed and shade-tolerant species, seed size). To assess at what spatial scales landscape characteristics play a role, we calculated for each plot local matrix openness and forest patch density using four concentric circles of 400 to 3200 m radius. Landscape openness negatively affected most forest attributes, but the magnitude of effect varied with 1) landscape attribute, 2) forest attribute, and 3) region. First, matrix openness had a negative stronger effect than patch density, indicating that landscape forest loss is more detrimental than forest fragmentation. Second, landscape openness reduced most strongly forest structure and animal-dispersed species, probably because open landscapes increase edge effects which especially affect large-sized trees, and reduce the abundance and activity of zoochorous seed dispersers, while landscape openness had opposite effects on diversity in different regions. Third, landscape openness had different effects in different regions, probably because of regional differences in tree species composition, landscape configuration and composition. Finally, landscape openness affected forest structural attributes at all spatial scales, animal-dispersed species at larger spatial scales (> 1600 m), and seed size at small spatial scales (< 400 m). In sum, landscape openness reduced most forest attributes, although the strength varied with the landscape attribute, forest attribute, and landscape context. Conservation and restoration projects should therefore restore landscape forest cover to improve forest structure, diversity and composition, and take into account the landscape context.

Keywords: Dispersal; Fragmentation; Landscape context; Matrix openness; Patch density; Spatial scale

1 Introduction

Habitat loss and fragmentation are among the greatest threats to global biodiversity and ecosystem functioning (Haddad et al. 2015) because they alter the type and amount of habitats and the degree of fragmentation and isolation. Fragmentation shapes forest maintenance and recovery as it has a strong negative effect on seed availability and dispersal (Traveset and Rodríguez-Pérez 2008) and microclimatic conditions (Magnago et al. 2015c; Arroyo-Rodríguez et al. 2017). Changes in landscape structure can lead therefore to reductions in forest structure (Magnago et al. 2017) and diversity (Laurance et al. 2002) and strongly modify community composition (Collins et al. 2017). Although there are many studies on the effects of landscape structure on forest attributes (e.g., Arroyo-Rodríguez et al., 2017; Laurance et al., 2000; Magnago et al., 2017; Villard and Metzger, 2014), few have evaluated at which spatial scale this effect is stronger (but see Crouzeilles and Curran, 2016; Melito et al., 2017; San-José et al., 2019). Understanding this would allow us to preliminary recommend the optimal landscape extent at which conservation and restoration projects should be carried out to improve forest landscape restoration success. This study aims therefore to understand how landscape structure affects different forest attributes (structure, diversity and functional composition) in fragmented and highly diverse tropical rainforest landscapes.

Forest ecosystems provide seeds for the colonization of disturbed sites and are an important habitat for seed dispersers (Chazdon 2003). Hence, loss of surrounding forest cover (i.e., increased matrix openness) and decreased connectivity between forest patches reduce not only the pool of forest specialist species in the landscape (Pardini et al. 2010), but also the number of reproductive trees, propagule availability, and seed dispersal (Traveset and Rodríguez-Pérez 2008). Additionally, forest loss and fragmentation lead to a larger area of exposed forest edges and, hence, increased forest edge effects, such as higher wind disturbance and temperatures, and lower air and soil humidity (Magnago et al. 2015c; Arroyo-Rodríguez et al. 2017) that impact plant establishment and performance. If there are few seed sources left (i.e., source limitation), if seeds are unable to reach a site (i.e., dispersal limitation), and establish and survive (i.e., recruitment limitation) then in mature forests the species richness, composition and structure will change, whereas in disturbed areas the recovery of these forest attributes will be hampered (Melo et al. 2010; Thier and Wesenberg 2016; Magnago et al. 2017). Hence, in general forests in deforested and fragmented landscapes are more fragile and have a lower potential for recovery.

The capacity of species to recolonize disturbed sites or arrive at a focal old-growth is not only determined by landscape constraints, but also by their functional characteristics (Lebrija-Trejos et al. 2010; Boukili and Chazdon 2017; Poorter et al. 2021a). Hence, fragmentation is likely to affect the functional composition (i.e., the distribution of trait values) of the forest. For example, in fragmented tropical landscapes the recruitment of animal dispersed, shade-tolerant and large-seeded trees is likely to be reduced (Melo et al. 2010; Thier and Wesenberg 2016; Rocha-Santos et al. 2017). This is because they are generally dispersed by large animals that usually travel greater distances (Nathan et al. 2008). The presence and movement of these animals depend on landscape connectedness, which typically decreases with reduced forest cover. Hence, the abundance and composition of vertebrate animal dispersers is crucial for the recovery of old-growth forest tree species and plays a critical role in forest regeneration (Gardner et al. 2019). Also, large and shade tolerant species (Laurance et al. 2000) are particularly sensitive to changes in environmental conditions and increased disturbances due to edge effects (Arroyo-Rodríguez et al. 2017). In contrast, open landscapes are more windy and favor long-distance dispersals of small, wind-dispersed seeds (Naylor 2003; Traveset and Rodríguez-Pérez 2008), whereas the more open canopy in forest edges favors the establishment of light-demanding, heat and drought tolerant species (Tabarelli et al. 2008, 2010; Thier and Wesenberg 2016). Hence forest fragmentation is expected to strongly change the functional composition of the forest.

Because forest regeneration is influenced by processes that operate at different spatial scales, the spatial scale at which landscape fragmentation occurs may be important (Jackson and Fahrig 2015; Martin 2018; San-José et al. 2019). For example, as most seeds are dispersed over shorter distances (Schurr et al. 2018), greater landscape openness at smaller spatial scales (e.g., <1600m radius) could more strongly influence short-distance seed dispersal. This is likely because most community assembly processes are determined by the availability of trees and seeds in nearby forest areas (see Martin 2018; San-José et al. 2019). Landscape openness at larger spatial scales may influence long-distance seed dispersal by migratory and large-sized animals, because of habitat loss and movement limitation of large-bodied seed dispersers (Haddad et al. 2015; Schurr et al. 2018). For this reason, different forest attributes are expected to be affected by landscape openness at different spatial scales. For example, qualitative forest attributes such as species richness and functional composition, would be particularly vulnerable to landscape openness at larger spatial scales because they are influenced by forces acting at larger spatial scales (e.g., long-distance dispersal) (Trakhtenbrot et al. 2005), while quantitative forest attributes (e.g., structure) would be more affected by landscape openness at small spatial scales as similar structure can be achieved regardless of species identity so it would depend more on colonization from nearby forests.

Several studies have shown that landscape structure can strongly influence forest structure and composition in human-modified tropical forests (Collins et al. 2017; Matos et al. 2017; San-José et al. 2019). Yet, the spatial scale at which the effect of different landscape drivers on different forest attributes is strongest is still not well understood (but see Crouzeilles and Curran, 2016; Melito et al., 2017; San-José et al., 2019). To our knowledge, most studies on the effects of landscape on forest ecosystem have been carried out in one landscape context, at one single spatial scale, addressing few forest attributes. Here we provide a comprehensive picture of landscape effects by assessing how different landscape drivers (matrix openness and patch density) affect forest attributes over different spatial scales (ranging from 400 to 3200 meters). We assess multiple forests attributes that are informative of community assembly and ecosystem functioning (structure, diversity and functional composition). To obtain a wider generalization we did so for three different regions (one consisting of old-growth forests, the others of old- and second-growth forests) representing three landscape contexts.

We ask how landscape openness (measured as matrix openness and patch density) affect forest structure, diversity and functional composition in tropical rainforests landscapes and how these landscape effects differ between the landscape driver, forest attribute, and spatial scale (**Fig. 3**). We expect that:

(H1) Landscape openness will reduce forest structure, diversity and functional composition because of increased edge effects, affecting the establishment and growth of trees (Magnago et al. 2015c) and because of a lower availability of seed sources and dispersal agents and a lower abundance of old-growth species in the surrounding environment, affecting richness and late-successional species (Tabarelli et al. 2008).

(H2) Landscape openness will have the strongest effect on functional composition and species diversity because they depend more on the old-growth species pool in the landscape and long-distance dispersal (Trakhtenbrot et al. 2005), which are reduced in open landscapes (Pardini et al. 2010). Landscape openness will have weaker effects on forest structure because recovery of structure can be done by any species able to reach, establish and survive in the community.

(H3) Landscape openness will affect species diversity and functional composition across larger spatial scales because in fragmented landscapes long-distance dispersal is important for the diversity and presence of late-successional species (i.e., animal dispersed, shade-tolerant, large seeded species) (Clark et al. 2005). In contrast, landscape openness will affect forest structure most strongly at smaller spatial scales because the recovery of structure can be done by any species so it is more dependent on short-distance seed dispersal from nearby forests (see Martin 2018; San-José et al. 2019).

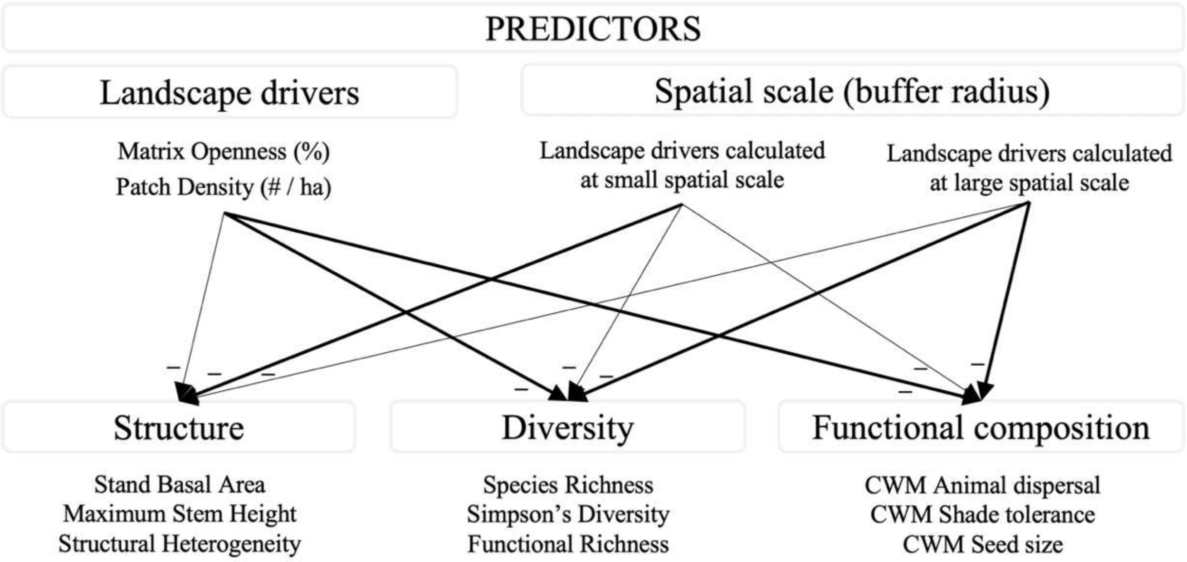
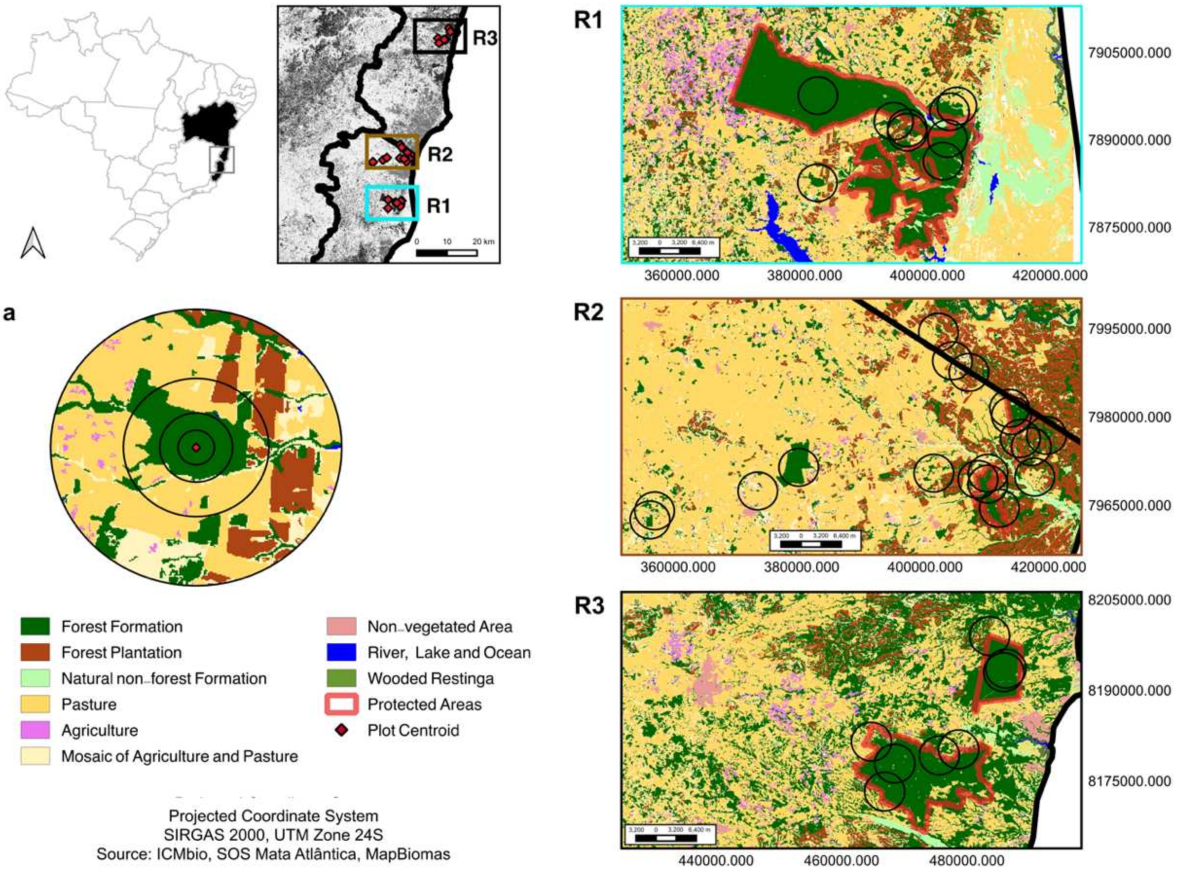


Fig. 3 Conceptual framework showing the magnitude of the expected negative effect size of landscape drivers and spatial scales on forest attributes related to structure, diversity, and functional composition. A larger arrow thickness indicates strong negative landscape effect size, while thin arrow thickness indicates a weak effect size. Structural heterogeneity here was measured using the Gini coefficient of stem basal area. CWM = community weighted mean.

2 Material and methods

2.1 Research regions

To check for the wider validity of landscape effects on forest attributes, research was conducted in three different Atlantic forest regions (R1, R2, R3), where R1 and part of R2 are located in northern Espírito Santo State (ES) and R3 and part of R2 in southern Bahia State (BA), Brazil (**Fig. 4**). Plots were established within and nearby seven Protected Areas (see also Appendix Fig. S1): Reserva Natural da Vale (RNV, 21,787 ha) and Reserva Biológica de Sooretama (RBS, 27,860 ha) located in R1, Reserva Biológica do Córrego Grande (RBCG, 1,504 ha), Floresta Nacional do Rio Preto (FNRP, 2,817 ha) and Reserva Biológica do Córrego do Veado (RBCV, 4,436 ha) located in R2; and the Parque Nacional do Pau Brasil (PNPB, 19,027 ha) and the Reserva Particular do Patrimônio Natural Estação Veracel (RPPNEV, 6,069 ha) located in R3.



Projected Coordinate System
SIRGAS 2000, UTM Zone 24S
Source: ICMbio, SOS Mata Atlântica, MapBiomas

Fig. 4 Location of the three study regions in the Atlantic rainforest of Brazil: Region 1 (R1, $n = 9$), Region 2 (R2, $n = 18$), Region 3 (R3, $n = 8$). The circles represent the maximum spatial extent for each of the 35 plots (3,215 ha; 3200 m radius) selected in each region and the red polygons represent the limits of the Protected Areas. (a) An example of a landscape sample with the four buffer sizes (400–3200 m radius) where landscape drivers were measured. Forest formations include both wet and dry, old- and secondary tropical forests. Land use and cover are derived from MapBiomas (https://mapbiomas.org/)

The three regions are similar in terms of soil and vegetation types but slightly different in terms of climate. The vegetation is classified as Lowland forest or Coastal Tableland forest (IBGE 2012), as it is geologically developed on sedimentary plateaus of the Tertiary Barreiras Group (Embrapa 2014). The predominant soil type is generally deep, acid, kaolinitic, highly weathered and nutrient-poor soil, ranging from Yellow Argisols (Ultisols) and Yellow Latosols (Oxisols) (Garay et al. 2003; Embrapa 2006). The climate in the northern ES varies between tropical rainforest (“Af”) and tropical wet (“Am”) according to Köppen system, with a mean annual temperature and rainfall of 23°C and ~ 1,227 (± 273) mm, and a dry season from April to September (Rolim et al. 2016). In southern BA, the climate is predominantly hot and humid tropical rainforest (“Af”), with mean annual temperature and rainfall of 23°C and ~1,635 mm, without a defined dry season (ICMBIO 2011; RPPN 2016).

The three regions differ in native forest cover (respectively 23, 12 and 32%) and matrix quality (Fig. S1 and Table S1), and differ slightly in their structure, species diversity and composition (Fig. S6). Region 1 has a significantly higher stand basal area, maximal tree height and structural heterogeneity, but a lower proportion of animal-dispersed species compared to the other two regions (Fig. S6a-c,g). Region 2 has a significantly lower species richness and Simpson diversity compared to the other two regions whereas functional richness (3.9 ± 0.6) and seed size (10.7 ± 2.7 mm) are statistically similar across the three regions (Fig. S5d-f,i).

The long history of exploitation and expansion of agriculture and urban areas in the Atlantic Forest has resulted in the loss of about 88% of its original cover and in highly fragmented Atlantic forest landscapes (Fundação SOS Mata Atlântica and INPE 2022). The remaining old-growth forest patches are embedded in a heterogeneous matrix of second-growth forests at different successional stages, small scale agriculture, pastures, and plantations of *Eucalyptus*, coffee, and papaya (Rolim et al. 2005). A recent report shows that deforestation rate increased with 66% between 2020 and 2021 (Fundação SOS Mata Atlântica and INPE 2022). Yet, the study regions are part of one of the best preserved sub-regions of the Atlantic Forest (Silva & Casteleti (2003), holding 18% of its original vegetation (Ribeiro et al. 2009). So these regions can provide important insights into how landscape structure may affect natural regeneration and old-growth forest remnants in highly fragmented and highly diverse tropical rainforests.

2.2 Study design and permanent sample plots

We used data from 35 0.1 ha permanent sample plots of Atlantic rain forests distributed across three different Atlantic forest regions, of which 19 are old-growth forest plots (R1, n = 9; R2, n = 7; R3, n = 3) and 16 forests recovering from different past disturbances or land use (R1, n = 0; R2, n = 11; R3, n = 5), such as fire, clear-cut and pasture. We acknowledge that the type of disturbance can influence forest regeneration, however, disturbances are very variable in highly fragmented and human-modified landscapes, and difficult to quantify accurately (see also Safar et al., 2020). Disturbance is defined as any natural or anthropogenic event that causes the loss of forest coverage, affecting the structure, diversity and functional composition of ecosystem. Henceforth these plots are referred to as second-growth, which varied in age from 14 to 29 years after disturbance or abandonment. Forest age was defined as the approximate time since the last disturbance (i.e., when disturbance ceased and succession started) or abandonment (i.e., when a land used for traditional agricultural activities was abandoned and left to regenerate naturally), and was determined based on Landsat images from Google Earth complemented with information from landowners and Protected Areas staff. We consider old-growth forest plots those forests with no indication of disturbance by human activities or fire in the last 50 years and that are at a late and relatively stable stage of succession, but not static, in terms of forest dynamics (Chazdon, 2014). Old-growth forests may include undisturbed forests, old secondary forests and forests that have been disturbed in years before the start of the Landsat archive (1970s). Plots were established in different periods (2011, 2017, and 2020) and the detailed information on each plot is available in Appendix Table S2.

To capture local-scale variation, forest inventories were performed using a nested plot design. Each 35 permanent sample plot consisted of ten 10x10 m plots established with a nearest distance between two neighboring plots of 20 m. Following the recommendations by de Lima et al. (2015), for each plot all living trees with a stem diameter at breast height (DBH, stem diameter at 1.3 m height) $\geq$ 4.8 cm were measured for their stem diameter and identified to species. The nomenclature of the specimens was checked using the database Flora do Brazil (Reflora), following the Angiosperm Phylogeny Group IV guidelines (APG IV 2016). We recorded a total of 5030 trees belonging to 550 species ($R1_{(0.9ha)} = 324$, $R2_{(1.8ha)} = 328$, $R3_{(0.8ha)} = 237$) and 70 families.

To describe how the surrounding landscape affects the type of species that are able to arrive and establish in the plots, we classified all species for three regenerative traits related to dispersal syndrome (abiotic/self-dispersed species = 0, animal-dispersed species = 1), regeneration strategy (pioneer = 0, shade-tolerant species = 1) and seed size (seed diameter in mm). Data on species traits were compiled from various bibliographic sources (e.g., Matozinhos and Konno 2011; Magnago et al. 2014; Freitas et al. 2016) and virtual inspection of herbarium specimens collection with preserved seeds, in the online database *SpeciesLink* (https://specieslink.net/) (Table S3). The regeneration strategy of tree species has been reported in the literature in different ways. For this study we classified all 'pioneer' and 'early-successional' species as pioneers, and all 'late-successional' and 'climax' species as shade-tolerant. For those 59 out of 540 identified species (11%) for which no information was found, we imputed missing trait values using the function *mice*() from the R package ‘mice’ (van Buuren et al. 2021). This imputation was based on the trait values of the species for which we already had data, together with phylogenetic information that we included in the form of eigenvectors to improve the estimation of missing traits values (Penone et al. 2014). Many traits tend to show high degrees of phylogenetic signal, that is, closely related species tend to have more similar values for a particular trait than expected by chance, as they are likely to perform ecologically similar roles and respond similarly to environmental selection pressures (Harvey and Pagel 1991; Martínez-Blancas et al. 2018).

2.4 Landscape openness

We described the landscape openness using two metrics; the matrix openness and patch density. Matrix openness (MO) is the percentage of open area in the surrounding landscape covered by all land use and cover classes (e.g. grassland, agriculture, pasture, urban area, and water bodies) that are not natural forest formations or forest plantations (mainly *Eucalyptus* plantations). Matrix openness indicates the extent of forest conversion towards other types of land use (i.e. forest loss) and high values indicates a more deforested landscape. Forest patch density (PD) is the number of natural forest formation patches per ha (#/ha), without considering planted forests, as we are focusing only on seed sources. High values indicate a more fragmented landscape, however, this is not only a metric of forest fragmentation, but also indicates the amount of stepping stones in the landscape for forest-dependent animal and plant species. We refer to these metrics as “openness” as both refer to a more open, converted, and fragmented forest landscape. These landscape drivers were calculated using land use and cover maps freely available from the multi-disciplinary network MapBiomas (https://mapbiomas.org/), whose classification was based on Landsat images with a resolution of 30 m by 30 m (see Souza et al. 2020). We selected the maps referring to the year in which the plots were sampled (see Table S2 for details).

To assess how landscape drivers over different spatial scales may affect forest attributes, we established four circular landscape buffers (400, 800, 1600, 3200 m radius, i.e., landscapes of 50.24 - 3,215 ha) from the center of each plot (see Crouzeilles & Curran 2016) (**Fig. 4**a). The buffer range of 400-3200 m encompasses the potential dispersal distances and home ranges of the Atlantic Forest fauna, including birds, bats and small/large-sized mammals (Hatfield et al. 2018; de la Sancha et al. 2021). We decided to not use spatial scales larger than 3200 because we observed a large buffer overlap at a larger scale (average 74.4% across all region-scale combinations, Fig. S2) since some of our plots are relatively close (Fig. S1). For each plot and buffer, we obtained matrix openness and forest patch density, which were moderately to strongly correlated (Table S4), using the R package ‘landscapemetrics’ (v. 1.5.2) (Hesselbarth et al. 2021). At an intermediate radius of 1600 m, matrix openness varied from 0-96% and patch density varied from 0.12-3.35 n/ha across plots (Fig. S3). The three regions had similar average patch density across all buffer sizes (Fig. S3f-j), indicating a similar degree of natural forest fragmentation; while, regarding matrix openness, region 2 showed an overall higher percentage on most scales compared to the other regions (Fig. S3a-e). Matrix openness was higher at larger spatial scales in region 1 and similar across all buffer sizes in the other regions, while patch density varied slightly with buffer size, depending on the region (Fig. S4).

2.5 Forest Attributes

To understand how different forest attributes respond to landscape drivers, we combined per plot the data collected from the ten subplots and calculated for each plot nine forest attributes related to forest structure, biodiversity and functional composition. We focused on structural attributes (i.e., stand basal area, maximal stem height, and Gini coefficient of stem basal area) as they are important for aboveground biomass and ecosystem processes (van der Sande et al. 2017b), on diversity attributes (i.e., species richness, Simpson diversity, and functional richness) because they are important for species conservation (i.e., what alpha diversity can be conserved) while functional richness indicates the response diversity to environmental change. We focus on functional composition using regenerative traits (i.e., dispersal syndrome, regeneration strategy and seed diameter) as they inform about community assembly (Violle et al. 2007) and may be strongly influenced by the surrounding landscape. Although attributes related to forest structure are highly correlated with each other (average Pearson's r = 0.83) and to diversity attributes (average r = 0.8) (Table S5), they are not fully exchangeable as they reflect different aspects of community assembly and functioning (Table *1*). By including three attributes per category we can generalize to what extent structural, diversity, and functional composition attributes show really different responses to landscape drivers.

As structural attributes we used the stand basal area (BA, m^2/ha), maximal stem height (H_{MAX}, m) and structural heterogeneity (SH, dimensionless). The stand basal area was calculated as the sum of the basal area (m^2) of the ten plots divided by total sampled plot area (0.1 ha) and is an indicator of forest biomass and leaf area index. The maximal stem height is the height of the tallest tree found at the ten plots, and indicates potential canopy development. The structural heterogeneity indicates the variation in tree size in the plot and was calculated as the Gini coefficient index of tree basal area. The index ranges from 0 (all the trees are of equal size) to 1 (all the trees are of unequal size), and it was calculated using the function *gini.wtd*() from the R package 'dineq' (Schulenberg 2018).

Table 1 The nine forest attributes with abbreviation, description, units, and an explanation of what they indicate

Abbreviation	Description	Units	Indicator of
STRUCTURE			
BA	Stand basal area	m^2/ha	forest biomass and leaf area index
H_{MAX}	Maximal stem height in the plot	m	potential canopy development
SH	Structural heterogeneity	index (0-1)	variation in tree basal area in the stand
DIVERSITY			
SR	Species richness	#/plot	species richness
SD	Simpson diversity	#/plot	richness of the dominant species
FR	Functional richness	#/plot	effective number of functional groups
FUNCTIONAL COMPOSITION			
AD_{CWM}	Community-weighted mean animal dispersal	index (0-1)	high values indicate a high proportion of animal-dispersed species
ST_{CWM}	Community-weighted mean shade tolerance	index (0-1)	high values indicate a high proportion of shade-tolerant species
SS_{CWM}	Community-weighted mean Seed size (in diameter)	mm	small seed size indicates a high abundance, and hence, high dispersal capacity in space or time (in the seedbank)

As diversity attributes we used species richness (SR), Simpson diversity (SD), and functional richness (FR). SR is the effective number of species, SD is the effective number of highly abundant species (i.e., dominant), and FR is the total effective number of functional groups (functional-group richness) or functional "species" (Chao et al. 2021) and was calculated based on species regenerative traits (AD, ST and SS). To control for the effect of stem density on the diversity metrics, we calculated species richness (q = 0, i.e., the total number of species expected to be present), Simpson diversity (inverse of the Simpson concentration index, q = 2, in which species are weighted more than proportional to their abundance, this reflects the number of common species) and functional richness (q = 0, which indicates the number of distinct functional groups) based on Hill-Chao numbers and sample standardization via coverage-based rarefaction and extrapolation using the R package 'iNEXT.3D' (Chao et al.

2021). q is the scale parameter of the Hill-Chao number that defined sensitivity of the diversity measure to the relative abundance of rare ($q = 0$) and dominant species ($q = 2$). Coverage-based standardization (a measure of sample completeness, proportion of individuals that belong to the observed species) provides robust results as it takes into account not only the sample size but also the true relative abundance of species present in the sample (i.e., true diversity of the community) (Chao and Jost 2012; Roswell et al. 2021). To avoid excluding data from the estimation, we rarefied or extrapolated (depending on the plot) species and functional richness to 71% of coverage as a reference, which is the minimum coverage value obtained from the samples extrapolated to double the reference sample size, and we obtained the Simpson diversity from the estimated asymptote (Chao et al. 2021).

As functional composition attributes, we used community-weighted mean (CWM) animal dispersal syndrome (AD_{CWM}), shade tolerance (ST_{CWM}) and seed size (SS_{CWM}). The CWM describes the average trait values across all individuals in the community by weighing the trait value of a species by its proportional basal area in the plot. We weighed by basal area rather than by stem number because it is more robust as it takes into account both stem size and abundance. The AD_{CWM} indicates the proportion of species dispersed by animals, and varies between 0 (all species dispersed abiotically, e.g., by wind, explosive, or ballistic) and 1 (all species dispersed by animals). The ST_{CWM} indicates the proportion of species that are shade-tolerant and mainly regenerate in the shade, and varies between 0 (only pioneer species) and 1 (only shade-tolerant species). SS_{CWM} indicates the seed diameter (millimeters, mm). CWM trait values were calculated using the R package ‘FD’ (Laliberté et al. 2015). Ten individuals were completely unidentified and not included in the estimate of functional richness and functional composition attributes.

2.6 Statistical Analyses

For the sole purpose of understanding the structure of the data that underly our main question analysis, we performed explanatory analysis to verify how the nine forest attributes related to structure, diversity and functional composition respond to landscape drivers at the intermediate buffer size (1600-m of radius) in each region. Forest attributes were used as response variables and landscape drivers and regions as predictors. For index variables (SH, AD_{CWM}, ST_{CWM}) we performed beta regressions using the R package ‘betareg’ (Zeileis et al. 2020), for parametric variables (SR, SD, SS_{CWM}) we performed linear regression and for the non-parametric variables (BA, Hmax, FR) we performed linear regression with logarithmic transformations.

To answer our research question, we adopted a two-step approach. In the first step, we quantified the effects of landscape drivers (matrix openness and patch density) on forest attributes (forest structure, diversity and functional composition) using regression analyses. We included the percentage of buffer overlap as one of the levels of landscape attributes to control for the effect that overlap might have on our results. We ran 216 regression models, each including one landscape predictor variable: for each of the forest attributes (nine levels), we predicted the effect of each of the two landscape drivers calculated at each of the four buffer sizes and for each of the three regions. Hence, this resulted in the combinations of landscape drivers (two levels), forest attributes (nine levels), spatial scales (four levels) and regions (three levels) (i.e., N = 216 combinations). Plots were used as the unit of replication. Region 2 and 3 had secondary and old-growth forest plots, and we therefore additionally included plot age as predictor. The potential differences in disturbance types amongst the landscapes were statistically captured by the site effect. We extracted the standardized regression coefficient (i.e., the standardized effect size) of the landscape effect to use in the second step.

In the second step, we assessed how the effect sizes depend on the landscape driver, forest attribute, spatial scale and region considered, by performing an analysis of variance (ANOVA type II) with four predictors and all six combinations of two-way interactions. The region was included as the main factor because it appeared to have a strong influence on the effect of landscape drivers on forest attributes. If the effect of a predictor was significant, then this indicated that the levels of that predictor (e.g., the different spatial scales) had different landscape effects on forest attributes. To assess how the levels of the significant predictors differed in their effect and verify whether the effects sizes were significantly different from zero, we performed multiple-comparison post-hoc tests using the R package 'emmeans' (Lenth et al. 2021). Significant effect sizes were determined by the non-overlap between 95% confidence intervals and the zero effect. All statistical analyses were performed using R 4.0.3 (R Core Team 2022).

3 Results

To illustrate how the landscape drivers affects forest attributes in different regions, we show the bivariate relationships for an intermediate buffer size of 1600 m for the three regions (**Fig. 5**, Appendix Fig. S5 for patch density). In general, an increasing matrix openness tends to reduce stand structural attributes (**Fig. 5**a-c), species richness and Simpson diversity (**Fig. 5** d,e), and the proportion of animal-dispersed species (g), but the magnitude and significance varied substantially across regions.

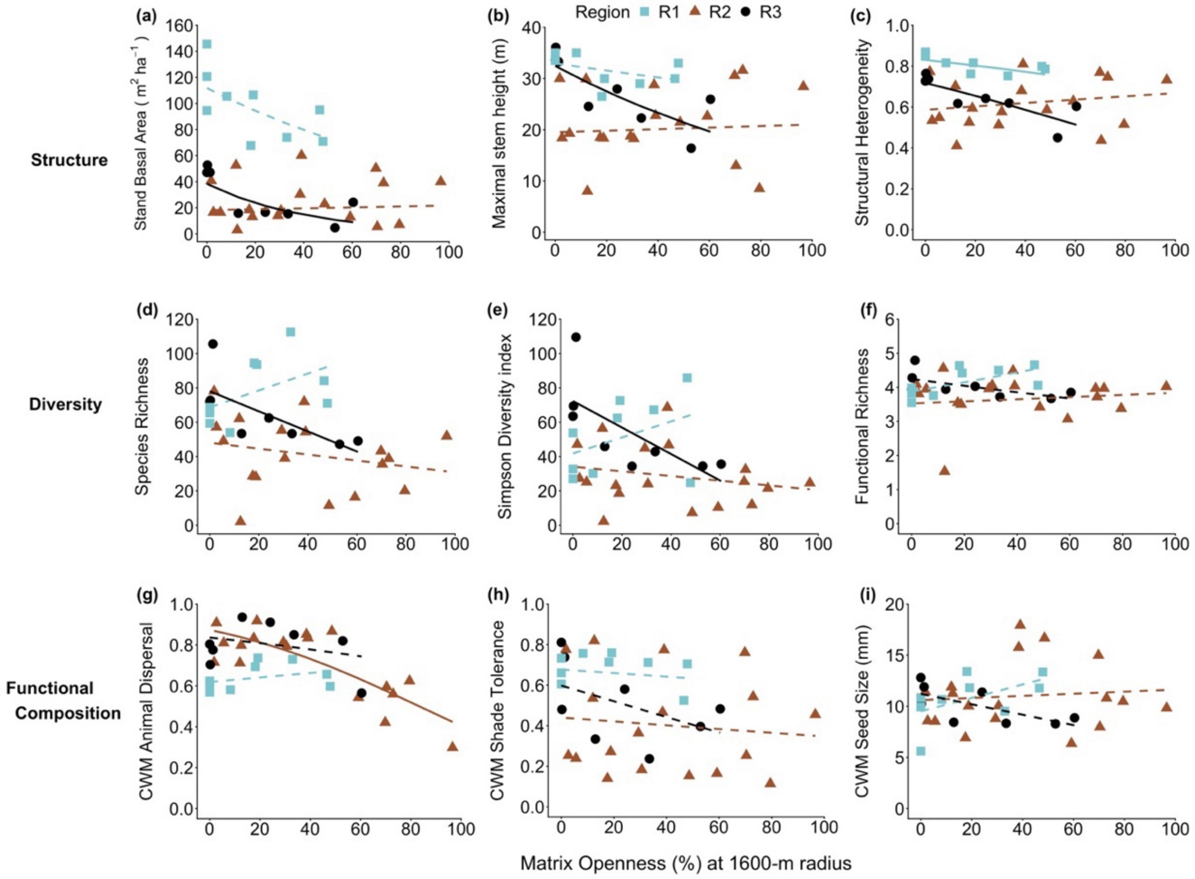


Fig. 5 Relationships between structural (a-c), diversity (d-f), functional composition (g-i) attributes and Matrix Openness in three different regions (as indicated by different symbols and colors) at the intermediate buffer size of 1600 m radius. Data points represent the forest attribute values found in the forest plots (R1, *n* = 9; R2, *n* = 18; R3, *n* = 8). Continuous regression lines indicate significant effects of matrix openness on the forest attributes and dashed lines indicate non-significant effects at $p < 0.05$. The lines are based on simple regressions and meant for illustration purposes only. For index variables (SH, AD_{cwm}, ST_{cwm}) we performed beta regressions using R package 'betareg' (Zeileis et al. 2020), for parametric variables (SR, SD, SS_{cwm}) we performed linear regression and for the non-parametric variables (BA, H_{max}, FR) we performed linear regression with logarithmic transformations. We found similar patterns for patch density and they can be found in Appendix Fig. S3.

We then assessed how landscape effects on forest attributes (i.e., the standardized effect size) differed between 1) landscape drivers, 2) forest attributes, 3) spatial scales, and 4) regions using an ANOVA. The ANOVA results indicated that matrix openness has a stronger negative effect on forest attributes than patch density (F=6.72, Table 2), indicating that deforestation affects forest attributes more than fragmentation (**Fig. 6**a). The effect size of the landscape on forest attributes varied slightly with forest attribute (F=17.08, Table 2); in general, a higher landscape openness (i.e., matrix openness and patch density) led to a significant and strong reduction in maximal height, structural heterogeneity and the proportion of animal-dispersed species, a moderate reduction in basal area and a significant and weaker increase in seed size (**Fig. 6**b). However, landscape drivers had no significant effects on the three diversity attributes and the proportion of shade-tolerant species (**Fig. 6**b). The effect of landscape openness was similar across all buffer sizes, but it was only significant at larger scales (> 800 m radius) (**Fig. 6**d). Also, we found that the effect size of the landscape on forest attributes varied most strongly among regions (F=69.09, Table 2); in general, landscape openness had the strongest negative effect on forest attributes in Region 3, a moderate negative effect in Region 2, and a moderate positive significant effect in Region 1 (**Fig. 6**c).

Table 2 ANOVA results showing the effect of four predictors (landscape driver, forest attribute, spatial scale and region) and their interactions (**Fig. 6**) on the effect size obtained from the relationship between each landscape driver (MO, PD) and each forest attribute (BA, H_{max}, SH, SR, SD, FR, AD_{CWM}, ST_{CWM}, SS_{CWM}) at each spatial scale (400-3200 m) within each region (R1, R2, R3). Hence, the total number of observations (i.e., standardized effect sizes) used was 2 drivers x 9 attributes x 4 scales x 3 regions = 216.

Response variable	**Predictor**	**Df**	**F value**	***p*-value**
Effect size	**Region**	2	69.09	**<.001**
	Forest Attribute * Region	16	28.53	**<.001**
	Forest attribute	8	17.08	**<.001**
	Landscape driver	1	6.72	**<.005**
	Buffer size	3	2.46	0.066
	Forest attribute * Buffer size	24	1.3	0.175
	Landscape driver * Region	2	0.96	0.386
	Forest attribute * Landscape driver	8	0.89	0.521
	Buffer size * Landscape driver	3	0.78	0.510
	Buffer size * Region	6	0.72	0.634

We found a significant interaction between forest attribute and region (Table 2). This means that landscape openness affect forest attributes in considerably different ways between regions (F=28.58) as indicated by the significant two-way interactions (Table 2, **Fig. 6**e). In R1, landscape openness significantly reduced structure but increased the three diversity attributes, the proportion of animal-dispersed species and seed size. In contrast, in R2 and R3 landscape openness showed no or opposite effects (**Fig. 6**e).

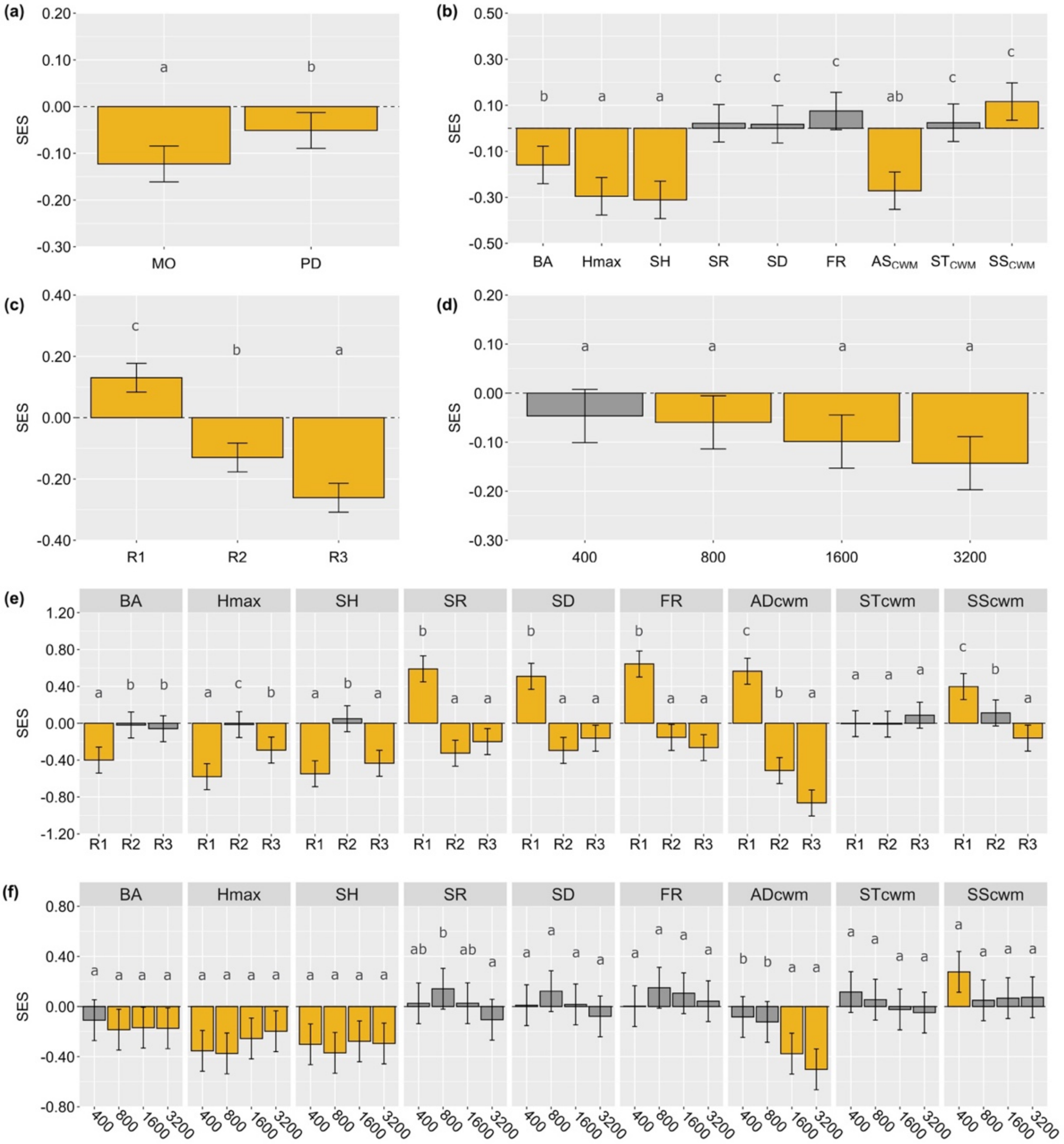


Fig. 6 Variation in the standardized effect size (SES) among (a) landscape drivers, (b) forest attributes, (c) forest regions, (d) spatial scales, (e) forest attributes interacting with regions, (f) forest attributes interacting with spatial scales (see Table 2 or ANOVA results). The vertical bar indicates the mean standardized effect size of landscape drivers on forest attributes and the whiskers represent the 95% confidence intervals. The yellow bar indicates that the effect size is significantly different from zero (non-overlap between confidence intervals and zero effect) and the gray bar indicates non-significant effects (overlap between confidence intervals and zero effect). Different lower case letters indicate significant differences between levels at $p < 0.05$. MO = matrix openness, PD = patch density, R1 = region 1, R2 = region 2, R3 = region 3, BA = basal area, SH = structural heterogeneity, Hmax = stem maximal height; S = species richness, SD = Simpson diversity index, FR = functional richness; ADcwm = community weighted-mean animal dispersal, $\mathrm{ST}_{\mathrm{cwm}}$ = community weighted-mean shade tolerance, $\mathrm{SS}_{\mathrm{cwm}}$ = community weighted-mean seed size.

There were no significant interactions between buffer size and forest attributes (Table 2), indicating that the effects of landscape openness on forest attributes were similar across all spatial scales (**Fig. 6**f). Yet, we found that landscape openness had a significant effect on structure at most spatial scales, on the proportion of animal-dispersed species at larger spatial scales (> 1600 m), whereas seed size only showed a significant response at smaller spatial scale (400 m) (**Fig. 6**f).

4 Discussion

We assessed the effects of landscape openness on nine forest attributes related to structure, diversity and functional composition at four different spatial scales in three different Atlantic forest regions. We found that landscape openness (i.e., matrix openness and patch density) generally had negative effects on forest attributes, but that this varied with the landscape drivers, forest attributes, spatial scales and regions considered (We then assessed how landscape effects on forest attributes (i.e., the standardized effect size) differed between 1) landscape drivers, 2) forest attributes, 3) spatial scales, and 4) regions using an ANOVA. The ANOVA results indicated that matrix openness has a stronger negative effect on forest attributes than patch density (F=6.72, **Table 2), indicating that deforestation affects** forest attributes more than fragmentation (Fig. 6a). The effect **size of** the landscape on forest attributes varied slightly with forest attribute (F=17.08, Table 2); in general, **a higher landscape openness (i.e**., matrix openness and patch density) led to a significant and strong reduction in maximal height, structural heterogeneity and the proportion of animal-dispersed species, a moderate reduction in basal area and a significant and weaker increase in seed size (Fig. 6b). However, landscape drivers had no significant **effects on** the three diversity attributes and the proportion of shade-tolerant species (Fig. 6b). The effect of landscape openness was similar **across all** buffer sizes, but it was only significant at larger scales (> 800 m radius) (Fig. 6d). Also, we found that the effect **size of** the landscape on forest attributes varied most strongly among regions (F=69.09, Table 2); in general, landscape openness had the strongest **negative effect on forest attributes in** Region 3, a moderate negative effect in Region 2, and a moderate positive significant effect in Region 1 (Fig. 6c).

Table 2, **Fig. 6**). Here, we will discuss the landscape openness effects and end with the implications for forest regeneration and conservation.

4.1 Matrix openness has stronger effects on forest attributes

We focused on two indices of landscape structure, matrix openness (i.e., a measure of landscape composition) and forest patch density (i.e., a measure of landscape configuration) that reflect deforestation and fragmentation in the landscape. Our results indicate that, in general, the effects of forest loss are much stronger than the effects of fragmentation (Table 2, **Fig. 6**a), supporting the findings of several other studies (see Fahrig, 2003). These drivers describe landscape structure (i.e., the different types of land use and their cover spatial arrangement Melito et al., 2017; San-José et al., 2019), rather than landscape quality (i.e., the abundance and composition of seed trees and animal dispersers in those landscapes, Collins et al. 2017). Future studies could also assess landscape quality metrics such as the abundance and guilds of animal dispersers (birds, rodents, large mammals) in the landscape. Because the two landscape drivers have negative effects on forest attributes and are mostly highly correlated (r = 0.6 ± 0.09 across all region-scale combinations), we refer to them in the rest of the discussion as 'landscape openness'.

4.2 Landscape openness reduces mainly forest structure and animal-dispersed species

We hypothesized that landscape openness (i.e., matrix openness and patch density) would negatively affect all forest attributes (H1) and that this effect would be stronger for diversity and functional composition than on structural attributes (H2) because of less seed sources and dispersal agent and a harsher environment. We found that landscape openness reduced forest structure and animal-dispersed species and increased seed size. Contrary to our expectations, landscape openness had the strongest effects on forest structure and no significant effects on diversity and shade-tolerant species (**Fig. 6**b).

Structure. We hypothesized and found that landscape openness had negative effects on forest structure (see also Melito et al. 2021), however, these effects were of relatively greater magnitudes than those on functional composition and diversity (**Fig. 6**b) rather than weaker as expected. This may be because larger trees are especially affected by the edge effects (Laurance et al., 2000; Oliveira et al., 2008), which is expected to increase with habitat loss and fragmentation (Magnago et al. 2015; Arroyo-Rodríguez et al. 2017). Another possible explanation is that the recovery of forest structure can be closely related to species composition. For example, the tallest forest trees tend to belong to animal-dispersed species (Bello et al., 2015) and to large-seeded species (in R2 and R3, Table S5). Landscape openness is expected to limit the population of large-bodied dispersers, limiting the dispersal and recruitment of animal-dispersed and large-seeded species (Clark et al., 2005). Therefore, the loss of these species is being accompanied by a parallel decline of forest structure (Rocha-Santos et al., 2016).

Diversity. We hypothesized that an increased landscape openness would lead to a strong reduction in species diversity, because few tree sources and associated specialized dispersal agents would lead to a slower arrival of species. Although we found no significant overall effects on any diversity attribute (see also Magnago et al. 2014) (**Fig. 6**b), our results show that landscape openness did affect negatively diversity in regions 2 and 3 and positively in region 1 (**Fig. 6**e). Hence, the lack of a main effect of landscape openness on diversity is probably due to the counterbalance of these opposite effects that landscape openness had across regions. This contrasting result is further discussed in item 4.3 and it suggests that diversity responses to landscape openness is context-dependent.

Functional composition. Landscape openness had a strong negative effect on the proportion of animal-dispersed (Rocha-Santos et al., 2017), a positive effect on seed size, but no effects on the proportion of shade-tolerant species (**Fig. 6**b). Animal-dispersed species require the presence of highly coevolved mutualists (Rogers et al., 2021), which may have limited movement specially with increasing open-area matrices (Boesing et al., 2018) and become less abundant or disappeared (i.e., defaunation) from the landscape because of hunting and habitat loss (Tucker et al., 2018) leading to less dispersal and recruitment (Caughlin et al., 2014; Fricke et al., 2022). The positive effect of landscape openness on seed size was detected only in region 1 (**Fig. 6**e), possibly because small fragments, when associated with large forest blocks such as those of this region (Table S1), may especially act as stepping stones contributing to the displacement of large seed dispersers in these areas (Arroyo-Rodríguez et al., 2020; Hernández-Ruedas et al., 2014). Finally, shade-tolerant species were not significantly affected by any of the landscape drivers, which is quite surprising as we had expected more pioneer species and, hence, less shade tolerant species in more open landscapes.

4.3 The landscape context matters

The magnitude of the landscape openness on forest attributes varied considerably among regions (**Fig. 6**c, cf. Pardini et al. 2010; Villard and Metzger 2014). The landscape context matters for community assembly probably because of regional differences in landscape composition and configuration (Boesing et al., 2018; Melito et al., 2017; Pardini et al., 2010; Villard and Metzger, 2014), land use history (Martínez-Ramos et al., 2016), environmental conditions (Robinson et al., 2015; van Breugel et al., 2019), and composition of the plant community (Collins et al. 2017).

Surprisingly, the strongest negative landscape effects (e.g., in animal-dispersed species and seed size, **Fig. 6**e) were observed in region 3, which had the highest forest cover among regions (32%, Table S1). Stronger biological responses to changes in landscape structure in regions with moderate levels of forest cover (30% to 50%) have also been reported in other studies (Melito et al., 2021, 2017; Pardini et al., 2010; Villard and Metzger, 2014). We speculate that, even in a context of moderate forest cover, relatively minor increases in matrix openness and patch density would strongly affect this plant community (**Fig. 6**c) because they are mainly composed by animal-dispersed species (Fig. S6). Their animal dispersers might be restricted to the larger fragments and be specially sensible to deforestation (Jorge et al., 2013), limiting the dispersal and recruitment of zoochoric species. It would be insightful to further unpack the animal dispersal guild and quantify the mutualistic dispersal network by assessing what part of their animal-dispersed seeds is dispersed by small-, medium- or large-bodied animals, as landscape structure would affect them differently due to different habitat requirements (Galetti et al., 2017; Villard and Metzger, 2014).

In region 1 the landscape openness increased all diversity attributes, the proportion of animal-dispersed species and seed size, which contrasts with other regions and our expectations. Significant positive responses of forests to increased fragmentation have been described in many other studies (see Fahrig, 2017). We believe that the increasing amount of different-sized habitat patches (i.e. habitat diversity) in the landscape combined with very large blocks of continuous forests (ca. 50,000ha, Table S1) with a more developed structure and local diversity (Fig. S6), allowed these forests to sustain their tree diversity and the population of animal dispersers (Galetti et al., 2009). This reasoning highlights the conservation value of both large and small patches (Magnago et al., 2014). Nonetheless, our results suggests that landscape effects on forest structure, diversity and functional composition depend not only on the quantity of forest cover but also on the configuration and quality of the remaining patches and the non-forest area matrix (see also Pardini et al. 2010; Villard and Metzger 2014).

4.4 Spatial scale

We hypothesized and found that the effects of landscape openness on forest attributes tended to vary with spatial scale (H3, **Fig. 6**f). Although we found that landscape openness had a similar effect on forest attributes at all spatial scales (p=0.175, Table 2), the spatial at which the effect was significantly different from zero varied among forest attributes (**Fig. 6**f). Our results show that forest structure was affected by landscape openness at most spatial scales, while animal-dispersed species mainly at larger scales (> 1600 m) and seed size at small scales (< 400 m) (see also Crouzeilles and Curran 2016; San-José et al. 2019). Furthermore, we found that the effects of landscape openness on forest attributes tended to increase with spatial scale (p=0.066, Table 2), showing significant overall effects above 800 m radius (**Fig. 6**d). These findings highlight the importance of local and landscape forest cover for seed dispersal, recruitment, and build-up of forest structure. The presence of forest cover at larger spatial scales is crucial for the dispersal of zoochoric species, as the expansion of forest cover increases the chance of having seeds of a specialist tree species and its associated mutualist disperser. A more intact and large forest matrix also guarantees a higher abundance of seed-dispersing animals in the landscape. In our Atlantic forests, animal-dispersed species have on average greater seeds (Fig. S7), which are generally dispersed by large-bodied animals (Fricke et al., 2022), which in turn require certain levels of forest cover and connectivity in the landscape for their displacement (Nathan et al., 2008).

4.5 Implication for forest restoration and conservation

Our study shows that bigger trees and animal-dispersed species can be particularly vulnerable to natural forest loss. An increased landscape openness leads to a reduced structure (BA, H_{max}, SH) and less food sources for seed-dispersing animals (AD), and hence, a reduced mitigation and conservation value. We plea therefore to conserve the remaining forests in the surrounding landscape and implement natural or assisted restoration projects to increase landscape forest cover. Increasing forest cover in sufficient large landscapes patches (with a 3200 m radius buffer) may help to recover forest structure through natural regeneration and bring back dispersers. In addition to restoring forest cover, increasing connectivity between forest patches could maximize restoration success, as natural regeneration has been found to work best if there is contiguous forest up to 10 km around a disturbed site (Crouzeilles and Curran, 2016), probably because this facilitates the movement of seed dispersers and increases the immigration rates, thus contributing to the maintenance of plant communities (Craven et al., 2016; Uroy et al., 2019). Moreover, small forest patches surrounding large forest blocks and embedded in a heterogeneous matrix may specially act as stepping stones for forest-dependent animal and plant species (Arroyo-Rodríguez et al., 2020; Hernández-Ruedas et al., 2014) that facilitate the movement of animal dispersers in the landscape (Boesing et al., 2018; Fahrig, 2007). Hence, when designing management plans and setting targets for ecological conservation and restoration in human-modified tropical landscape, policymakers and restoration practitioners should adopt an integrated planning strategy accounting for the landscape context.

5 Conclusions

We evaluated how two landscape drivers (matrix openness and patch density) affect forest structure, diversity and functional composition at different spatial scales and in three different human-modified regions. The landscape drivers had negative effects on most forest attributes, but with different strengths. The effects of matrix openness were much stronger than those of patch density, and landscape openness, overall, affected negatively and more strongly forest structure and animal-dispersed species, whereas it had opposite effects on diversity and seed size in different regions. Forest structure was affected at most spatial scales, animal-dispersed species at larger scales and seed size at small scales. Surprisingly, we found that these effects varied strongly among the regions, showing that the landscape effects on forest attributes are context-dependent. Future research could focus on the role of matrix quality (e.g., different types of land uses) in shaping forest attributes in human-modified landscape. These findings highlight the importance of properly assessing the landscape context surrounding areas targeted for conservation and reforestation, in order to guide the management of fragmented landscapes to safeguard forest structure, diversity and functioning.

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Supplementary material (Appendix) for Safar et al.; 2022. Landscape effects on structure, diversity and functional composition in Brazilian rainforests

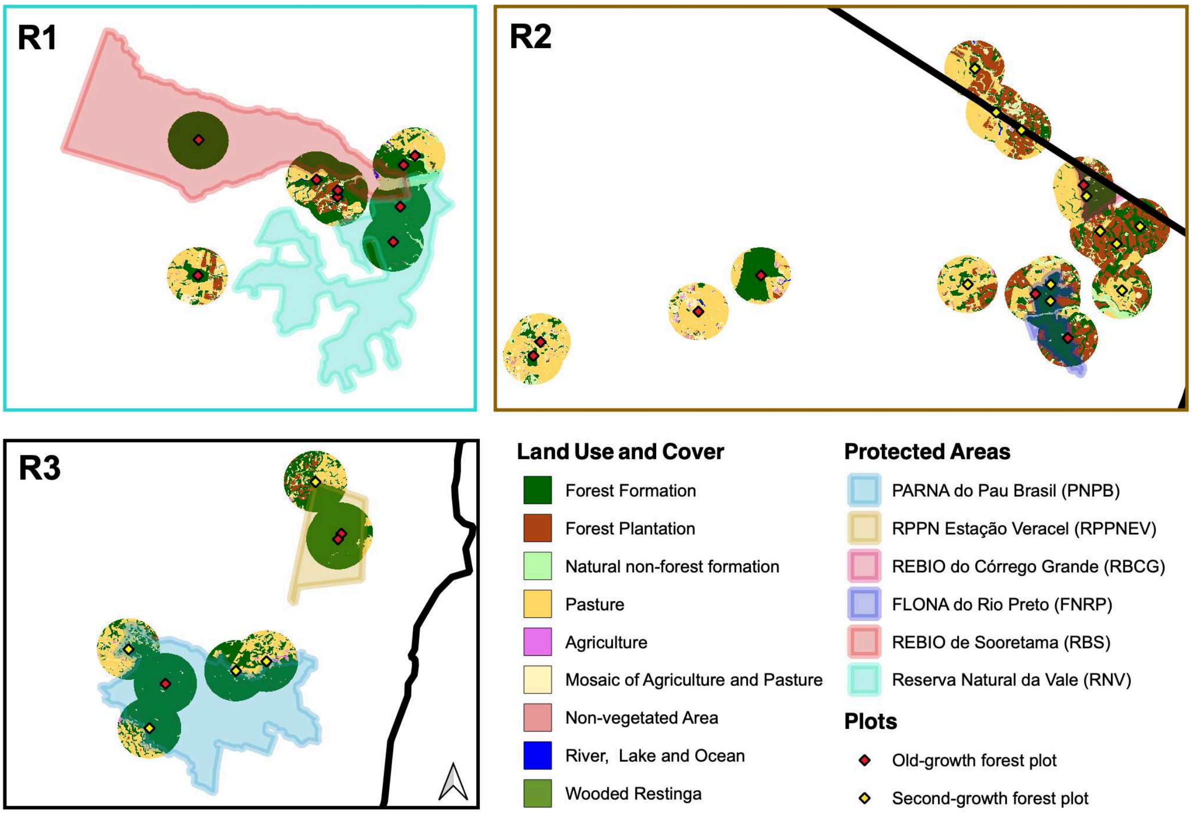

Fig. S1 Land use and cover in the 3200-m radius around each plot in three Atlantic forest regions: Region 1 (R1, *n* = 9), Region 2 (R2, *n* = 18) and Region 3 (R3, *n* = 8). Old-growth and second-growth sampled plots are indicated with red and yellow dots respectively. Protected Areas RBS and RNV are located in R1, RBCG and FNRP in R2; and RPPNEV and PNPB in R3. Land use and cover provided by MapBiomas (Collection 6, https://mapbiomas.org/)

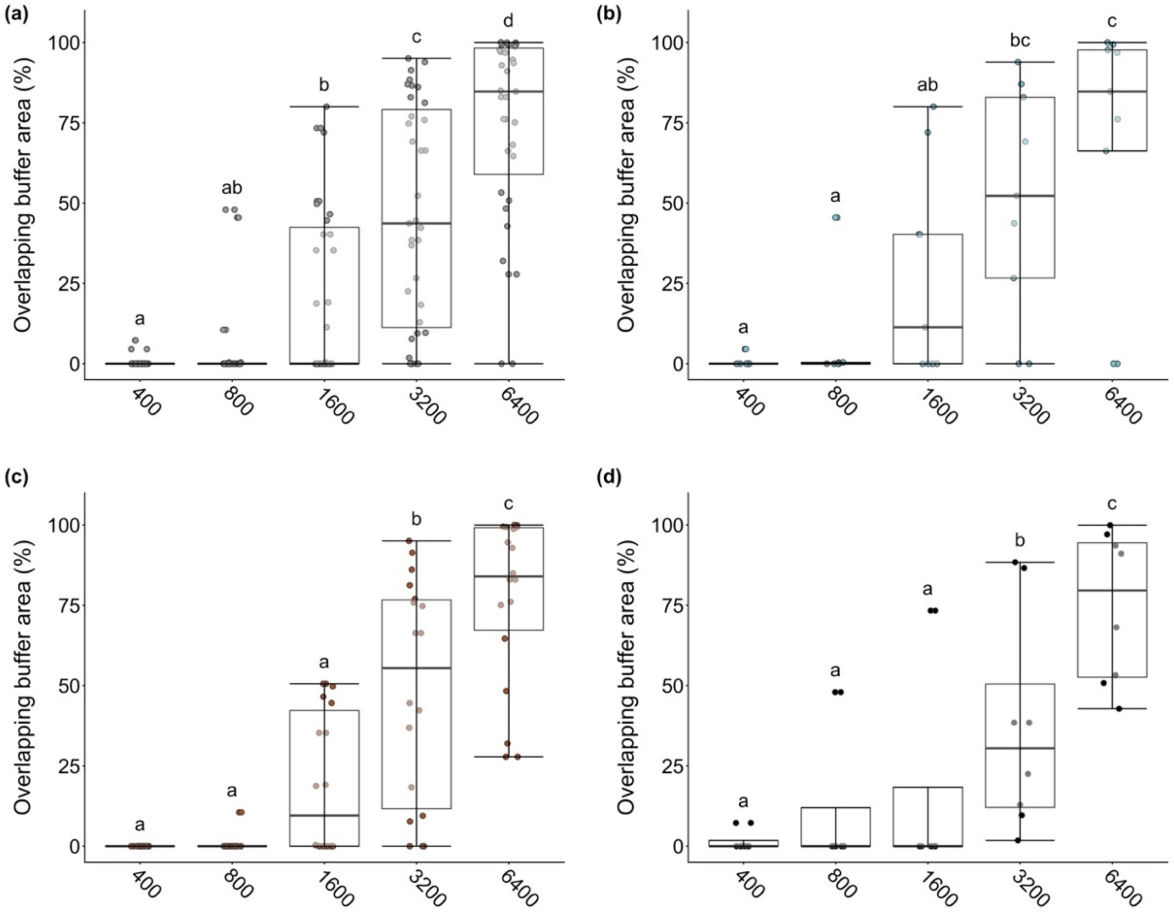

Fig. S2 Variation in buffer overlap at each spatial scale for (a) all regions combined, (b) region 1, (c) region 2, (d) region 3. Data points represent the percentage of buffer overlap around each plot (replication unit) at each buffer size (a, *n* = 35; b, *n* = 9; c, *n* = 18; d, *n* = 8). Solid horizontal line indicates the median, vertical box represents the interquartile range (25th and 75th percentiles) and the whiskers indicate the minimum and maximum data values (the 5 and 95% percentiles). Differences in average percentage overlap between buffer sizes were tested using betareg models (Zeileis et al. 2020), indicated for proportion data, and the package ‘emmeans’ (Lenth et al. 2021). Different lower case letters indicate significant differences between buffer levels at $p < 0.05$

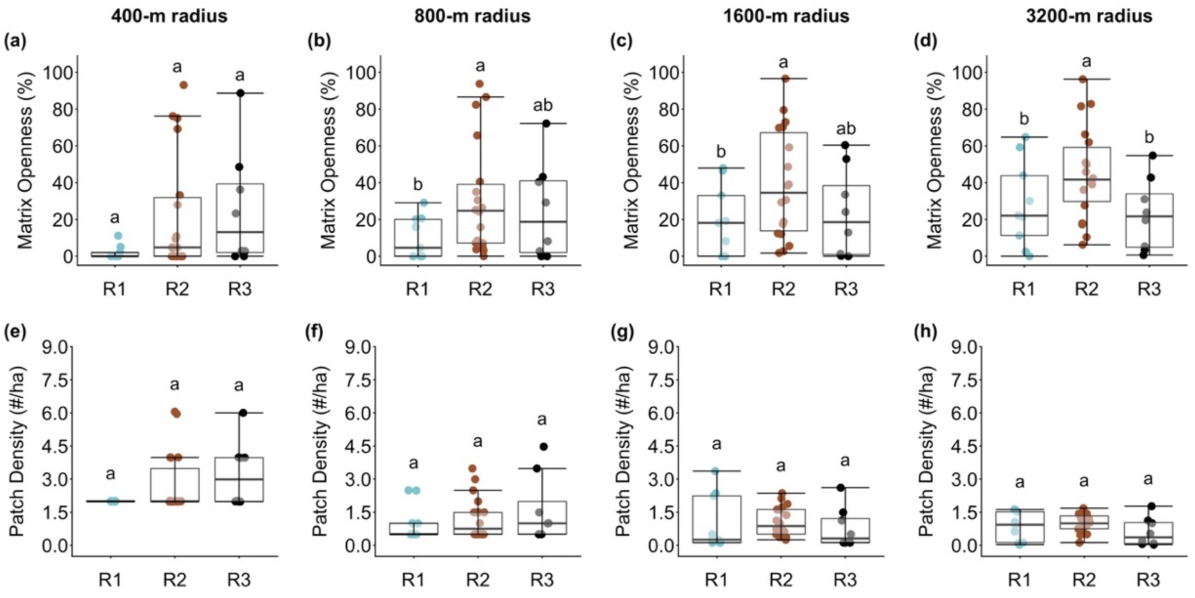

Fig. S3 Variation in Matrix Openness (a-d) and Patch Density (e-h) within four buffer sizes (400-3200 m radius) in three different Atlantic forest regions. Data points represent the landscape attribute values found within the buffer around each plot (replication unit) (R1, *n* = 9; R2, *n* = 18; R3, *n* = 8). Solid horizontal line indicates the median, vertical box represents the interquartile range (25th and 75th percentiles) and the whiskers indicate the minimum and maximum data values (the 5 and 95% percentiles). Differences in matrix openness across buffer sizes were tested using betareg models (Zeileis et al. 2020), indicated for percentage data and the package 'emmeans' (Lenth et al. 2021). Differences in patch density means were tested using Kruskal–Wallis test and post-hoc pairwise comparisons were applied using Dunn's test (Dinno 2017) indicated for nonparametric data. Different lower case letters indicate significant differences between region levels at $p < 0.05$

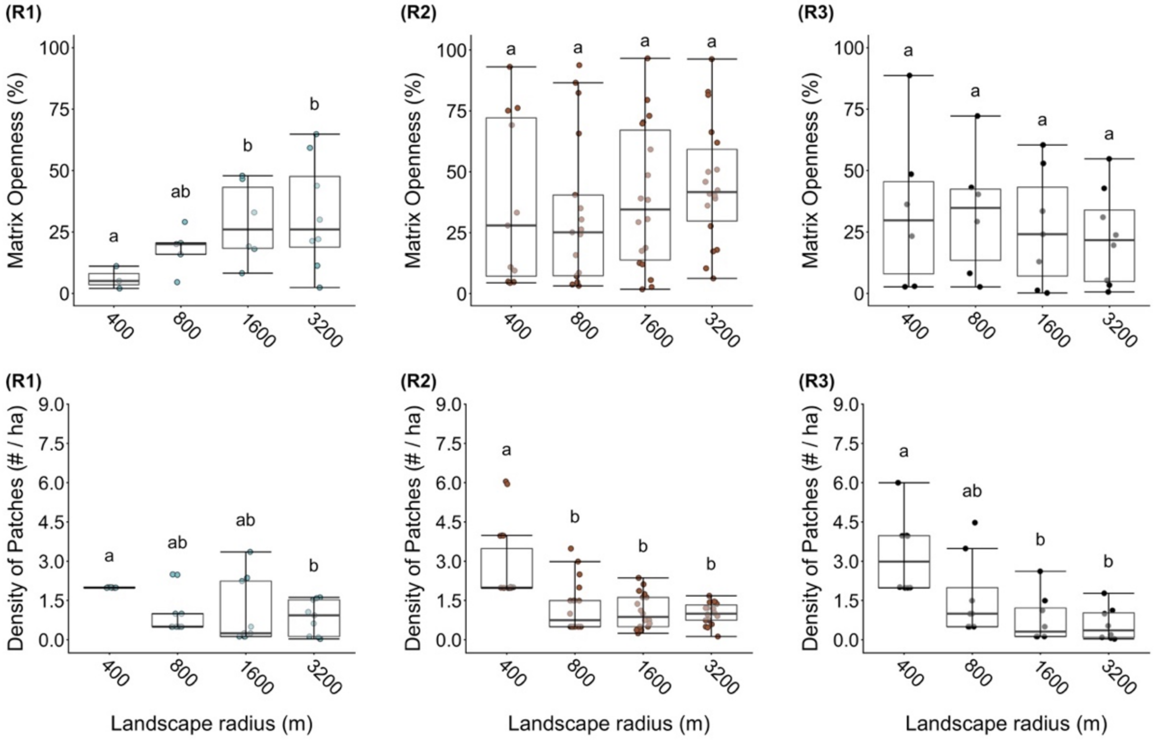

Fig. S4 Variation in Matrix Openness and Patch Density across four buffer sizes (400-3200 m radius) in three different Atlantic forest regions (R1, R2, R3). Data points represent the landscape attribute values found in each buffer within each region (R1, *n* = 9; R2, *n* = 18; R3, *n* = 8). Solid horizontal line indicates the median, vertical box represents the interquartile range (25th and 75th percentiles) and the whiskers indicate the minimum and maximum data values (the 5 and 95% percentiles). Differences in matrix openness across buffer sizes were tested using betareg models (Zeileis et al. 2020), indicated for percentage data and the package 'emmeans' (Lenth et al. 2021). Differences in patch density means were tested using Kruskal–Wallis test and post-hoc pairwise comparisons were applied using Dunn's test (Dinno 2017) indicated for nonparametric data. Different lower case letters indicate significant differences between region levels at $p < 0.05$

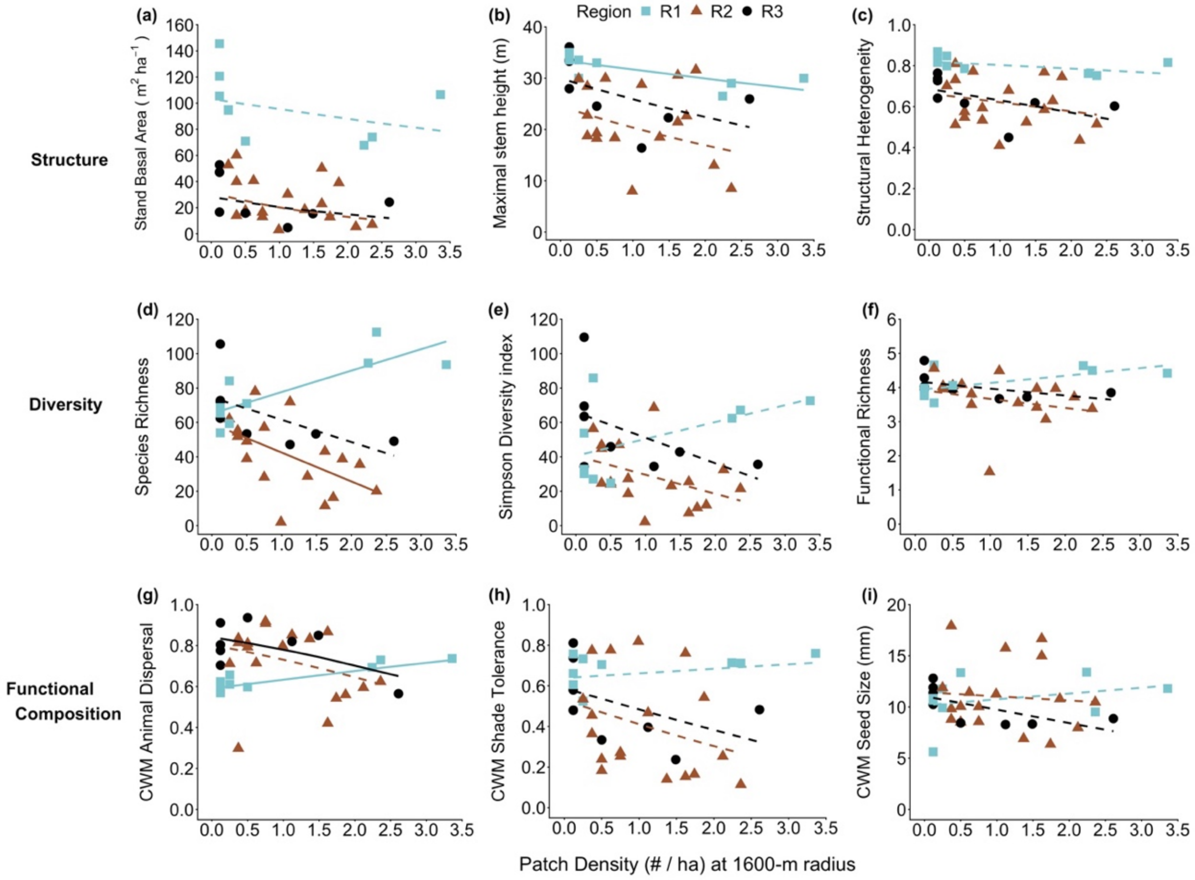

Fig. S5 Relationship between structural (a-c), diversity (d-f), functional composition (g-i) attributes and Patch Density in three different regions (as indicated by different symbols and colors) at the intermediate buffer size of 1600-m radius. Data points represent the forest attribute values found within each forest plot (*n* = 35). Continuous regression lines indicate significant effects of Patch Density on the forest attributes and dashed lines indicate non-significant effects at $p < 0.05$. The lines are based on simple regressions and meant for illustration purposes only. For index variables (SH, $\mathrm{AD}_{\mathrm{cwm}}$, $\mathrm{ST}_{\mathrm{cwm}}$) we performed beta regressions using R package ‘betareg’ (Zeileis et al. 2020), for parametric variables (SR, SD, $\mathrm{SS}_{\mathrm{cwm}}$) we performed linear regression and for the non-parametric variables ($\mathrm{H}_{\mathrm{max}}$, BA, FR) we performed linear regression with logarithmic transformations.

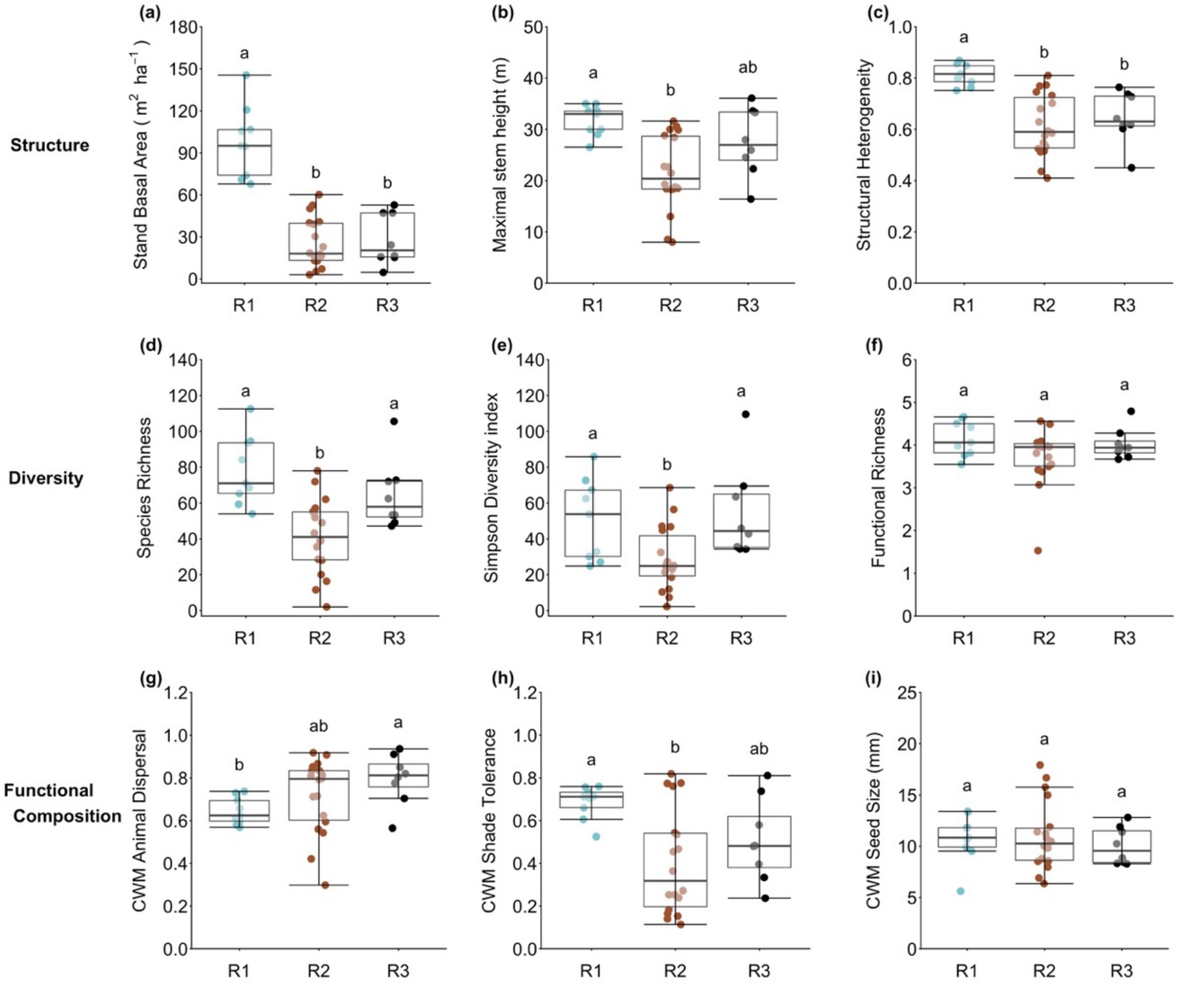

Fig. S6 Variation in structure (a-c), diversity (d-f) and functional composition (g-i) attributes across three different Atlantic forest regions. Data points represent the forest attribute values found in each study plot (R1, *n* = 9; R2, *n* = 18; R3, *n* = 8). Solid horizontal line indicates the median, vertical box represents the interquartile range (25th and 75th percentiles) and the whiskers indicate the minimum and maximum data values (the 5 and 95% percentiles). Differences in forest attributes means between regions were tested using the package ‘emmeans’ (Lenth et al. 2021) and beta regression models for the index variables (SH, AD_{cwm}, ST_{cwm}), linear regression models for the parametric variables (SR, SD, SS_{cwm}) and log-transformed models for the non-parametric variables (BA, H_{max}, FR). Different lower case letters indicate significant differences between region levels at $p < 0.05$

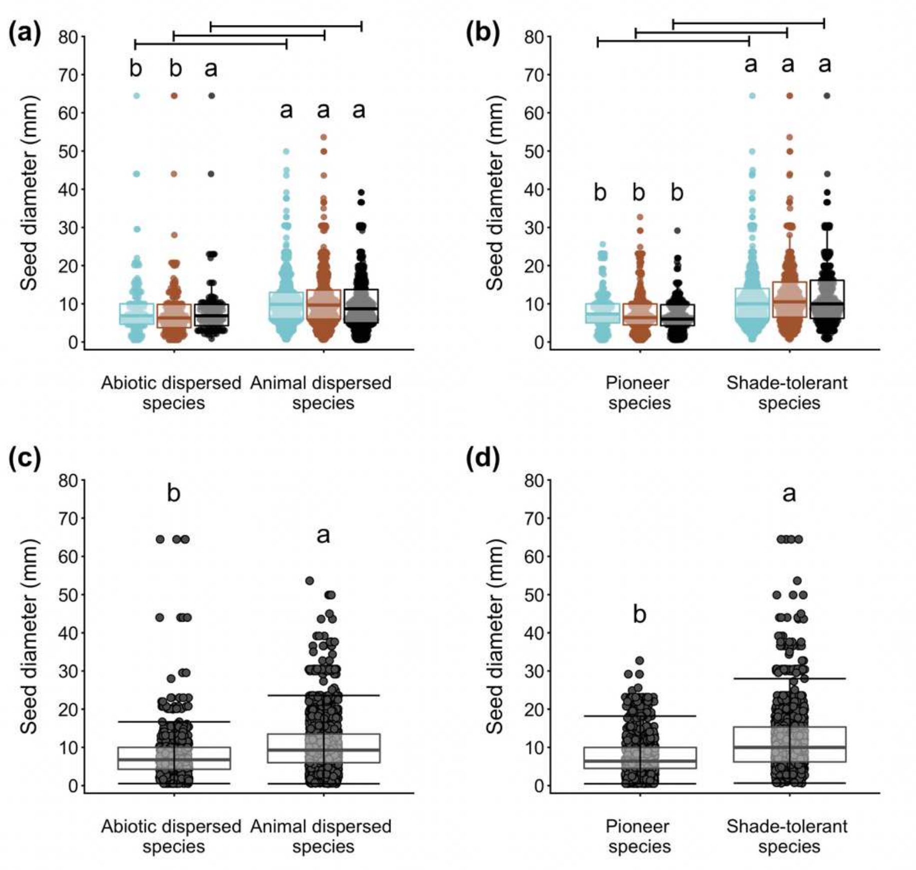

Fig. S7 Variation in seed size across the levels of dispersal syndrome (a,c) and regeneration strategy (b,d) in three different Atlantic forest regions. (a,b) Data points represent the tree species found in all 35 plots (R1, *n* = 324; R2, *n* = 324; R3, *n* = 231; total, *n* = 540), not including unidentified individuals. Region 1 is represented by light blue, Region 2 by light brown and Region 3 by black. (c,d) Data points represent the tree species found in all 35 plots without distinguishing the regions. Solid horizontal line indicates the median, vertical box represents the interquartile range (25th and 75th percentiles) and the whiskers indicate the minimum and maximum data values (the 5 and 95% percentiles). Differences in seed size means between species dispersal syndrome and regenerative traits were tested using o Kruskal–Wallis test for nonparametric data, followed by post-hoc pairwise comparisons performed with Dunn's test (Dinno 2017). Different lower case letters indicate significant differences between region levels at p < 0.05

References

Dinno A (2017) Package ‘dunn.test’: Dunn’s Test of Multiple Comparisons Using Rank Sums. CRAN Repos.

Lenth R V., Buerkner P, Herve M, et al (2021) Package ‘ emmeans ’: Estimated Marginal Means, aka Least-Squares Means. CRAN Repos.

Zeileis A, Cribari-neto F, Gruen B, et al (2020) Package ‘ betareg ’: Beta regression. CRAN Repos. 1–32

Table S1 General characteristics of the three studied Atlantic forest regions of Brazil. The landscape metrics were measured in 500,000 hectares square landscapes encompassing all sampled plots

Parameters	**R1**	**R2**	**R3**
Land use and cover map (year-base)	2011	2017	2020
Altitude (m a.s.l.) [a]	20-200	20 - 220	40 - 140
Precipitation (mm/year) [a]	1171	1285	1463
Natural forest formation cover (%)	23.17	11.78	31.68
Natural non-forest formation cover (%) [b]	4.83	0.96	1.03
Forest plantation cover (%)	4.99	17.08	4.88
Pasture cover (%)	44.30	53.99	41.36
Agriculture cover (%)	3.57	0.51	1.50
Mosaic of agriculture and pasture cover (%)	13.99	9.77	10.55
Non-vegetated area cover (%) [c]	0.62	0.50	1.36
Water bodies (%) [d]	1.70	0.42	0.20
Open areas in the matrix (%) [e]	69.88	66.19	56.17
Matrix composition	Heterogeneous but dominated by cattle pasture	Mainly cattle pasture and forest plantation	Heterogeneous but dominated by cattle pasture
Density of natural forest patches (#/ha)	1.46	0.93	1.34
Mean natural forest patch area (ha) [f]	15.92 ± 599.07	12.70 ± 125.35	23.70 ± 585.65
Maximal forest patch area (ha) [g]	51208	6156	35655
Mean planted forest patch area (ha)	11.80	47.90	10.20
Mean pasture patch area (ha)	47.10	122.00	49.30
Mean distance to nearest forest patch (m)	131.43	184.69	121.26

[a] All forest plots in both regions were located in lowland areas (< 600 m asl)

[b] All land cover classes that are natural formations but not forests, such as wetlands, grassland, salt flat, rocky outcrop. It does not include forest plantation

[c] Includes urban areas, mining, beach, dune and sand spot, and other non-vegetated areas

[d] Includes rivers, lakes, ocean, and aquaculture

[e] All land use and cover classes that are not natural forests or forest plantations

[f] Mean natural forest patch area and standard deviation.

[g] The minimum and maximum area of natural forest patches in hectares.

Table S2 Details of the 35 permanent sample plots located in three different Atlantic forest regions. R1 = Region 1 (*n* = 9); R2 = Region 2 (*n* = 18); R3 = Region 3 (*n* = 8); ES = Espírito Santo State; BA = Bahia State; RBS = Reserva Biológica de Sooretama; RNV = Reserva Natural da Vale; RBCG = Reserva Biológica do Córrego Grande; FNRP = Floresta Nacional do Rio Preto; RBCV = Reserva Biológica do Córrego do Veado; PNPB = Parque Nacional do Pau Brasil; RPPNEV = Reserva Particular do Patrimônio Natural Estação Veracel

Region	**Plot**	**Successional Stage**	**Stand Age (yr)**	**Disturbance type**	**Coordinates**	**State**	**Location**	**Sampling period**
R1	A69	old-growth	uneven-age	natural disturbance	-14.5011, -39.0852	ES	close to RBS	2011
R1	A70	old-growth	uneven-age	natural disturbance	-14.479, -39.1047	ES	close to RNV	2011
R1	A74	old-growth	uneven-age	natural disturbance	-14.4944, -39.0894	ES	close to RBS	2011
R1	A75	old-growth	uneven-age	natural disturbance	-14.5002, -39.1382	ES	RBS	2011
R1	A76	old-growth	uneven-age	natural disturbance	-14.4999, -39.0706	ES	RNV	2011
R1	A77	old-growth	uneven-age	natural disturbance	-14.4988, -39.0647	ES	RBS	2011
R1	A79	old-growth	uneven-age	natural disturbance	-14.4802, -39.1035	ES	RNV	2011
R1	A80	old-growth	uneven-age	natural disturbance	-14.484, -39.1179	ES	close to RNV	2011
R1	A81	old-growth	uneven-age	natural disturbance	-14.4965, -39.0807	ES	close to RNV	2011
R2	A1	old-growth	uneven-age	natural disturbance	-18.2551, -39.8178	ES	RBCG	2017
R2	A3	second-growth	28	fire	-18.3015, -39.8017	ES	Close to RBCG	2017
R2	A4	second-growth	14	pasture	-18.3141, -39.7846	ES	Close to RBCG	2017
R2	A6	second-growth	26	clearcut	-18.2001, -39.8802	ES	Close to RBCG	2017
R2	A7	second-growth	29	fire	-18.2967, -39.7612	ES	Close to RBCG	2017
R2	A8	second-growth	28	fire	-18.266, -39.8149	ES	RBCG	2017

R2	A9	second-growth	14	pasture	-18.3608, -39.7793	ES	Close to RBCG	2017
R2	A11	second-growth	28	fire	-18.3715, -39.8510	ES	FNRP	2017
R2	A12	second-growth	28	fire	-18.3549, -39.8509	ES	FNRP	2017
R2	A13	second-growth	20	clearcut	-18.3548, -39.9340	ES	Close to FNRP	2017
R2	A14	old-growth	uneven-age	natural disturbance	-18.4087, -39.8336	ES	FNRP	2017
R2	A15	second-growth	20	pasture	-18.1383, -39.9268	BA	Close to RBCG	2017
R2	A16	old-growth	uneven-age	natural disturbance	-18.3644, -39.8662	ES	FNRP	2017
R2	A17	second-growth	27	clearcut	-18.1822, -39.9055	BA	Close to RBCG	2017
R2	A71	old-growth	uneven-age	natural disturbance	-14.4924, -39.132	ES	close to RBCV	2011
R2	A72	old-growth	uneven-age	natural disturbance	-14.4911, -39.1323	ES	close to RBCV	2011
R2	A73	old-growth	uneven-age	natural disturbance	-14.4851, -39.1205	ES	close to RBCV	2011
R2	A78	old-growth	uneven-age	natural disturbance	-14.4924, -39.1207	ES	RBCV	2011
R3	A18	old-growth	uneven-age	natural disturbance	-16.4801, -39.2959	BA	PNPB	2020
R3	A19	second-growth	22	fire	-16.4478, -39.3319	BA	PNPB	2020
R3	A20	second-growth	18	fire	-16.4599, -39.1998	BA	PNPB	2020
R3	A21	second-growth	26	fire	-16.2895, -39.1537	BA	RPPNEV	2020
R3	A22	old-growth	uneven-age	natural disturbance	-16.3391, -39.1290	BA	RPPNEV	2020
R3	A23	old-growth	uneven-age	natural disturbance	-16.3444, -39.1324	BA	RPPNEV	2020
R3	A24	second-growth	24	fire	-16.4687, -39.2285	BA	PNPB	2020

R3	A25	second-growth	17	fire	-16.5222, -39.3108	BA	PNPB	2020

Table S3 List of tree species found in the 35 permanent sample plots located in northern Espírito Santo State and southern Bahia State, Brazil, and the traits that were used in this study. NZOO = abiotic/self-dispersed, ZOO = animal dispersed; P = pioneer; SDT = shade-tolerant; NA = information not available

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Achariaceae	Carpotroche brasiliensis (Raddi) A Gray	ZOO	SDT	13.00
Anacardiaceae	Anacardium sp1	ZOO	P	2.50
Anacardiaceae	Astronium concinnum Schott	NZOO	P	0.54
Anacardiaceae	Astronium graveolens Jacq.	NZOO	P	1.88
Anacardiaceae	Schinus terebinthifolia Raddi	ZOO	P	3.50
Anacardiaceae	Spondias macrocarpa Engl.	ZOO	P	17.70
Anacardiaceae	Spondias venulosa (Mart. ex Engl.) Engl.	ZOO	P	19.52
Anacardiaceae	Tapirira guianensis Aubl.	ZOO	P	7.01
Anacardiaceae	Thyrsodium spruceanum Benth.	ZOO	P	12.67
Annonaceae	Anaxagorea silvatica R.E.Fr.	NZOO	SDT	6.00
Annonaceae	Annona acutiflora Mart.	ZOO	SDT	5.10
Annonaceae	Annona cacans Warm.	ZOO	P	6.30
Annonaceae	Annona dolabripetala Raddi	ZOO	P	4.50
Annonaceae	Annona sp1	ZOO	P	4.80
Annonaceae	Annona sp2	ZOO	P	4.80
Annonaceae	Annonaceae sp1	ZOO	P	9.00
Annonaceae	Duguetia chrysocarpa Maas	ZOO	P	6.00
Annonaceae	Ephedranthus sp. nov.	ZOO	SDT	22.00
Annonaceae	Ephedranthus sp. nov.2	ZOO	SDT	22.00
Annonaceae	Guatteria australis A.St.-Hil.	ZOO	P	6.20
Annonaceae	Guatteria ferruginea A.St.-Hil.	ZOO	SDT	9.50
Annonaceae	Guatteria sellowiana Schltdl.	ZOO	P	6.50
Annonaceae	Guatteria sp1	ZOO	P	4.00
Annonaceae	Oxandra espintana (Spruce ex Benth.) Baill.	ZOO	SDT	8.33
Annonaceae	Oxandra martiana (Schltdl.) R.E.Fr.	ZOO	SDT	5.00

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Annonaceae	Oxandra sp1	ZOO	SDT	5.75
Annonaceae	Oxandra unibracteata J.C.Lopes, Junikka & Mello-Silva	ZOO	SDT	11.00
Annonaceae	Pseudoxandra spiritus-sancti Maas	ZOO	SDT	5.00
Annonaceae	Xylopia decorticans D.M.Johnson & Lobão	ZOO	P	6.00
Annonaceae	Xylopia frutescens Aubl.	ZOO	P	5.00
Annonaceae	Xylopia ochrantha Mart.	ZOO	SDT	4.70
Annonaceae	Xylopia sericea A.St.-Hil.	ZOO	P	5.00
Apocynaceae	Aspidosperma cylindrocarpon Müll. Arg.	NZOO	SDT	16.70
Apocynaceae	Aspidosperma desmanthum Benth. ex Müll. Arg.	NZOO	SDT	20.78
Apocynaceae	Aspidosperma discolor A.DC.	NZOO	SDT	44.00
Apocynaceae	Aspidosperma illustre (Vell.) Kuhlm. & Pirajá	NZOO	SDT	64.46
Apocynaceae	Aspidosperma parvifolium A.DC.	NZOO	SDT	29.53
Apocynaceae	Aspidosperma pyricollum Müll. Arg.	NZOO	SDT	28.00
Apocynaceae	Geissospermum laeve (Vell.) Miers	ZOO	SDT	11.00
Apocynaceae	Himatanthus bracteatus (A. DC.) Woodson	NZOO	SDT	9.86
Apocynaceae	Macoubea guianensis Aubl.	ZOO	SDT	5.70
Apocynaceae	Malouetia cestroides (Nees ex Mart.) Müll.Arg.	NZOO	P	3.75
Apocynaceae	Rauvolfia capixabae I.Koch & Kin.-Gouv.	ZOO	SDT	10.43
Apocynaceae	Tabernaemontana salzmannii A.DC.	ZOO	P	6.14
Araliaceae	Dendropanax brasiliensis (Seem.) Frodin	ZOO	SDT	5.60
Araliaceae	Didymopanax morototoni (Aubl.) Decne. & Planch.	ZOO	P	3.00
Arecaceae	Allagoptera caudescens (Mart.) Kuntze	ZOO	P	18.19

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Arecaceae	Astrocaryum aculeatissimum (Schott) Burret	ZOO	SDT	30.44
Arecaceae	Attalea burretiana Bondar	ZOO	P	9.67
Arecaceae	Bactris ferruginea Burret	ZOO	P	10.00
Arecaceae	Elaeis guineensis Jacq.	ZOO	P	12.80
Arecaceae	Euterpe edulis Mart.	ZOO	SDT	11.08
Arecaceae	Syagrus botryophora (Mart.) Mart.	ZOO	P	19.17
Asteraceae	Baccharis reticularia DC.	NZOO	P	0.86
Bignoniaceae	Handroanthus chrysotrichus (Mart. ex DC.) Mattos	NZOO	P	20.00
Bignoniaceae	Handroanthus cristatus (A.H.Gentry) S.Grose	NZOO	P	6.98
Bignoniaceae	Handroanthus heptaphyllus (Vell.) Mattos	NZOO	P	6.53
Bignoniaceae	Handroanthus riodocensis (A.H.Gentry) S.Grose	NZOO	P	7.65
Bignoniaceae	Handroanthus serratifolius (Vahl) S.Grose	NZOO	P	8.20
Bignoniaceae	Handroanthus sp.	NZOO	P	12.00
Bignoniaceae	Jacaranda puberula Cham.	NZOO	P	6.77
Bignoniaceae	Paratecoma peroba (Record) Kuhlm.	NZOO	SDT	4.00
Bignoniaceae	Sparattosperma leucanthum (Vell.) K.Schum.	NZOO	P	1.31
Bignoniaceae	Tabebuia elliptica (DC.) Sandwith	NZOO	P	6.00
Bignoniaceae	Tabebuia obtusifolia (Cham.) Bureau	NZOO	P	9.60
Bignoniaceae	Tabebuia roseoalba (Ridl.) Sandwith	NZOO	P	5.10
Bignoniaceae	Tabebuia sp.	NZOO	P	8.26
Boraginaceae	Cordia acutifolia Fresen.	ZOO	P	9.39
Boraginaceae	Cordia ecalyculata Vell.	ZOO	P	9.69
Boraginaceae	Cordia magnoliifolia Cham.	ZOO	P	6.60
Boraginaceae	Cordia sellowiana Cham.	ZOO	P	13.31

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Boraginaceae	Cordia sp3	ZOO	P	25.60
Boraginaceae	Cordia trichoclada DC.	ZOO	P	11.00
Burseraceae	Protium aracouchini (Aubl.) Marchand	ZOO	P	7.00
Burseraceae	Protium atlanticum (Daly) Byng & Christenh.	ZOO	SDT	7.30
Burseraceae	Protium heptaphyllum (Aubl.) Marchand	ZOO	P	7.50
Burseraceae	Protium heptaphyllum (Aubl.) Marchand subsp. heptaphyllum	ZOO	P	7.50
Burseraceae	Protium warmingianum Marchand	ZOO	P	9.00
Cardiopteridaceae	Citronella paniculata (Mart.) R.A.Howard	ZOO	SDT	11.53
Caricaceae	Jacaratia heptaphylla (Vell.) A.DC.	ZOO	P	3.07
Caryocaraceae	Caryocar edule Casar.	ZOO	SDT	30.00
Celastraceae	Cheiloclinium cognatum (Miers) A.C.Sm.	ZOO	P	16.57
Celastraceae	Monteverdia cestrifolia (Reissek) Biral	ZOO	P	8.31
Celastraceae	Monteverdia obtusifolia (Mart.) Biral	ZOO	SDT	5.00
Celastraceae	Monteverdia samydiformis (Reissek) Biral	ZOO	SDT	7.30
Chrysobalanaceae	Chrysobalanaceae sp1	ZOO	P	6.50
Chrysobalanaceae	Chrysobalanaceae sp2	ZOO	P	6.50
Chrysobalanaceae	Couepia schottii Fritsch	ZOO	SDT	22.00
Chrysobalanaceae	Exellodendron gracile (Kuhlm.) Prance	ZOO	SDT	10.15
Chrysobalanaceae	Hirtella hebeclada Moric. ex DC.	ZOO	SDT	9.00
Chrysobalanaceae	Hirtella insignis Briq. ex Prance	ZOO	SDT	8.00
Chrysobalanaceae	Hirtella sprucei Benth. ex Hook.f.	ZOO	SDT	7.00
Chrysobalanaceae	Licania belemii Prance	ZOO	SDT	13.89
Chrysobalanaceae	Licania kunthiana Hook.f.	ZOO	SDT	19.86
Chrysobalanaceae	Licania sp1	ZOO	SDT	22.00

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Chrysobalanaceae	Licania sp2	ZOO	SDT	22.00
Chrysobalanaceae	Moquilea salzmannii Hook.f.	ZOO	SDT	53.61
Chrysobalanaceae	Parinari parvifolia Sandwith	ZOO	SDT	15.65
Clusiaceae	Garcinia brasiliensis Mart.	ZOO	SDT	22.49
Clusiaceae	Garcinia gardneriana (Planch. & Triana) Zappi	ZOO	SDT	14.80
Clusiaceae	Tovomita guianensis Aubl.	ZOO	SDT	10.00
Combretaceae	Terminalia glabrescens Mart.	NZOO	P	3.02
Combretaceae	Terminalia hoehneana (N.F.Mattos) Gere & Boatwr.	NZOO	SDT	3.30
Combretaceae	Terminalia mameluco Pickel	NZOO	P	1.63
Connaraceae	Connarus detersus Planch.	ZOO	P	6.00
Dichapetalaceae	Stephanopodium blanchetianum Baill.	ZOO	SDT	16.00
Ebenaceae	Diospyros brasiliensis Mart. ex Miq.	ZOO	P	12.00
Ebenaceae	Diospyros lasiocalyx (Mart.) B.Walln	ZOO	P	10.00
Elaeocarpaceae	Sloanea garckeana K.Schum.	ZOO	SDT	6.34
Elaeocarpaceae	Sloanea granulosa Ducke	ZOO	SDT	10.00
Elaeocarpaceae	Sloanea sinemariensis Aubl.	ZOO	SDT	4.81
Elaeocarpaceae	Sloanea sp1	ZOO	SDT	6.28
Erythropalaceae	Heisteria ovata Benth.	ZOO	SDT	4.58
Erythropalaceae	Heisteria sp.	ZOO	SDT	6.00
Erythroxylaceae	Erythroxylum columbinum Mart.	ZOO	SDT	2.78
Erythroxylaceae	Erythroxylum pulchrum A.St.-Hil.	ZOO	SDT	6.54
Euphorbiaceae	Actinostemon concolor (Spreng.) Müll. Arg.	NZOO	SDT	4.58
Euphorbiaceae	Actinostemon klotzschii (Didr.) Pax	NZOO	SDT	4.58
Euphorbiaceae	Alchornea glandulosa Poepp. & Endl.	ZOO	P	4.45
Euphorbiaceae	Aparisthmium cordatum (A.Juss.) Baill.	NZOO	P	3.30

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Euphorbiaceae	Brasiliocroton mamoninha P.E.Berry & Cordeiro	NZOO	P	6.31
Euphorbiaceae	Caryodendron grandifolium (Müll.Arg.) Pax	ZOO	P	22.00
Euphorbiaceae	Croton floribundus Spreng.	NZOO	P	3.30
Euphorbiaceae	Euphorbiaceae sp1	ZOO	P	32.71
Euphorbiaceae	Glycydendron espiritosantense Kuhlm.	ZOO	SDT	32.71
Euphorbiaceae	Joannesia princeps Vell.	ZOO	P	23.15
Euphorbiaceae	Micrandra sp.	ZOO	P	10.08
Euphorbiaceae	Pachystroma longifolium (Nees) I.M.Johnst.	NZOO	SDT	12.00
Euphorbiaceae	Pausandra morisiana (Casar.) Radlk.	ZOO	SDT	5.60
Euphorbiaceae	Sapium glandulosum (L.) Morong	ZOO	P	6.00
Euphorbiaceae	Senefeldera verticillata (Vell.) Croizat	NZOO	SDT	10.00
Fabaceae	Acosmium lentiscifolium Schott	NZOO	SDT	6.90
Fabaceae	Albizia pedicellaris (DC.) L.Rico	NZOO	P	9.17
Fabaceae	Albizia polycephala (Benth.) Killip ex Record	NZOO	P	6.89
Fabaceae	Anadenanthera colubrina (Vell.) Brenan	NZOO	P	10.00
Fabaceae	Andira anthelmia (Vell.) Benth.	ZOO	SDT	22.00
Fabaceae	Andira fraxinifolia Benth.	ZOO	P	29.16
Fabaceae	Andira legalis (Vell.) Toledo	ZOO	SDT	45.00
Fabaceae	Andira ormosioides Benth.	ZOO	SDT	30.00
Fabaceae	Apuleia leiocarpa (Vogel) J.F.Macbr.	NZOO	SDT	6.21
Fabaceae	Arapatiella psilophylla (Harms) R.S.Cowan	NZOO	SDT	23.00
Fabaceae	Barnebydendron riedelii (Tul.) J.H.Kirkbr.	NZOO	SDT	16.11
Fabaceae	Bauhinia forficata Link	NZOO	P	9.23
Fabaceae	Bauhinia rufa (Bong.) Steud.	NZOO	P	9.25

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Fabaceae	Centrolobium sclerophyllum H.C.Lima	NZOO	SDT	4.62
Fabaceae	Centrolobium tomentosum Guillem. ex Benth.	NZOO	SDT	9.60
Fabaceae	Chamaecrista aspleniifolia (H.S.Irwin & Barneby) H.S.Irwin & Barneby	NZOO	P	6.00
Fabaceae	Chamaecrista ensiformis (Vell.) H.S.Irwin & Barneby	NZOO	P	7.58
Fabaceae	Chamaecrista sp.	NZOO	P	11.70
Fabaceae	Copaifera duckei Dwyer	ZOO	P	8.62
Fabaceae	Copaifera langsdorffii Desf.	ZOO	P	11.87
Fabaceae	Copaifera lucens Dwyer	ZOO	P	12.41
Fabaceae	Dalbergia nigra (Vell.) AllemÃ£o ex Benth.	NZOO	P	4.89
Fabaceae	Deguelia longeracemosa (Benth.) A.M.G. Azevedo	NZOO	P	3.87
Fabaceae	Dialium guianense (Aubl.) Sandwith	NZOO	SDT	5.65
Fabaceae	Dimorphandra jorgei M.F.Silva	NZOO	P	22.00
Fabaceae	Diplotropis incexis Rizzini & A.Mattos	NZOO	P	10.32
Fabaceae	Exostyles venusta Schott	ZOO	SDT	9.75
Fabaceae	Fabaceae sp1	NZOO	P	11.80
Fabaceae	Goniorrhachis marginata Taub.	NZOO	SDT	20.73
Fabaceae	Hymenaea altissima Ducke	ZOO	SDT	22.00
Fabaceae	Hymenaea aurea Y.T.Lee & Langenh.	ZOO	SDT	16.55
Fabaceae	Hymenaea courbaril L.	ZOO	SDT	19.10
Fabaceae	Hymenolobium janeirense Kuhlm.	NZOO	SDT	9.00
Fabaceae	Inga cabelo T.D.Penn.	ZOO	P	6.61
Fabaceae	Inga capitata Desv.	ZOO	P	7.30
Fabaceae	Inga cylindrica (Vell.) Mart.	ZOO	P	9.98
Fabaceae	Inga exfoliata T.D.Penn. & F.C.P.GarcÃa	ZOO	SDT	6.78

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Fabaceae	Inga flagelliformis (Vell.) Mart.	ZOO	SDT	8.42
Fabaceae	Inga hispida Schott ex Benth.	ZOO	SDT	7.10
Fabaceae	Inga sp.	ZOO	P	6.61
Fabaceae	Inga striata Benth.	ZOO	P	7.91
Fabaceae	Inga subnuda Salzm. ex Benth. subsp. subnuda	ZOO	P	10.00
Fabaceae	Inga thibaudiana DC. subsp. thibaudiana	ZOO	P	4.00
Fabaceae	Inga unica Barneby & J.W.Grimes	ZOO	P	8.50
Fabaceae	Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	NZOO	P	5.72
Fabaceae	Machaerium brasiliense Vogel	NZOO	P	1.93
Fabaceae	Machaerium fulvovenosum H.C.Lima	NZOO	SDT	13.14
Fabaceae	Machaerium ovalifolium Glaz. ex Rudd	NZOO	SDT	8.41
Fabaceae	Machaerium sp1	NZOO	P	6.30
Fabaceae	Macrolobium latifolium Vogel	ZOO	SDT	36.56
Fabaceae	Melanoxylon brauna Schott	NZOO	SDT	4.14
Fabaceae	Moldenhawera papillanthera L.P.Queiroz et al.	NZOO	SDT	13.08
Fabaceae	Moldenhawera sp1	NZOO	P	7.82
Fabaceae	Myrocarpus frondosus Allemao	NZOO	SDT	5.13
Fabaceae	Ormosia arborea (Vell.) Harms	ZOO	P	12.32
Fabaceae	Ormosia nitida Vogel	ZOO	P	10.35
Fabaceae	Parapiptadenia pterosperma (Benth.) Brenan	NZOO	P	14.09
Fabaceae	Peltogyne angustiflora Ducke	NZOO	SDT	15.28
Fabaceae	Piptadenia paniculata Benth.	NZOO	P	11.58
Fabaceae	Platymiscium floribundum Vogel	NZOO	P	9.35
Fabaceae	Poeppigia procera C.Presl	NZOO	P	6.00
Fabaceae	Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima	NZOO	P	7.90

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Fabaceae	Pseudopiptadenia psilostachya (DC.) G.P.Lewis & M.P.Lima	NZOO	P	22.00
Fabaceae	Pterocarpus rohrii Vahl	NZOO	P	4.55
Fabaceae	Senegalia polyphylla (DC.) Britton & Rose	NZOO	P	6.66
Fabaceae	Swartzia acutifolia Vogel	ZOO	SDT	30.41
Fabaceae	Swartzia alternifoliolata Mansano	ZOO	SDT	30.00
Fabaceae	Swartzia apetala Raddi var. apetala	ZOO	SDT	15.71
Fabaceae	Swartzia apetala var. glabra (Vogel) R.S.Cowan	ZOO	SDT	15.71
Fabaceae	Swartzia euxylophora Rizzini & A.Mattos	ZOO	SDT	19.10
Fabaceae	Swartzia flaemingii Raddi	ZOO	SDT	35.00
Fabaceae	Swartzia linharensis Mansano	ZOO	SDT	17.06
Fabaceae	Swartzia myrtifolia var. elegans (Schott) R.S.Cowan	ZOO	SDT	8.62
Fabaceae	Swartzia simplex var. continentalis Urb.	ZOO	SDT	9.29
Fabaceae	Swartzia sp1	ZOO	SDT	16.29
Fabaceae	Sweetia fruticosa Spreng.	NZOO	SDT	7.01
Fabaceae	Tachigali pilgeriana (Harms) Oliveira-Filho	NZOO	P	15.50
Fabaceae	Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	NZOO	P	10.40
Fabaceae	Vatairea heteroptera (Allemão) Ducke	ZOO	P	22.00
Fabaceae	Vataireopsis araroba (Aguiar) Ducke	NZOO	P	9.74
Fabaceae	Zollernia glabra (Spreng.) Yakovlev	ZOO	SDT	11.45
Fabaceae	Zollernia ilicifolia (Brongn.) Vogel	ZOO	SDT	17.01
Fabaceae	Zollernia modesta A.M.Carvalho & Barneby	ZOO	SDT	18.00

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Humiriaceae	Humiriastrum dentatum (Casar.) Cuatrec.	ZOO	SDT	3.00
Humiriaceae	Humiriastrum spiritu-sancti Cuatrec.	ZOO	SDT	20.10
Hypericacaeae	Vismia guianensis (Aubl.) Choisy	ZOO	P	1.10
Hypericacaeae	Vismia martiana Reichardt	ZOO	P	1.40
Lacistemataceae	Lacistema aggregatum (P.J.Bergius) Rusby	ZOO	SDT	3.00
Lamiaceae	Vitex megapotamica (Spreng.) Moldenke	ZOO	P	8.90
Lamiaceae	Vitex orinocensis Kunth	ZOO	P	6.00
Lauraceae	Aniba canelilla (Kunth) Mez	ZOO	SDT	6.00
Lauraceae	Aniba firmula (Nees & Mart.) Mez	ZOO	SDT	15.40
Lauraceae	Aniba sp1	ZOO	SDT	20.00
Lauraceae	Beilschmiedia linharensis Sa. Nishida & van der Werff	ZOO	SDT	37.62
Lauraceae	Cryptocarya saligna Mez	ZOO	P	24.87
Lauraceae	Endlicheria glomerata Mez	ZOO	SDT	12.50
Lauraceae	Lauraceae sp1	ZOO	P	20.96
Lauraceae	Lauraceae sp2	ZOO	P	20.96
Lauraceae	Lauraceae sp3	ZOO	P	20.96
Lauraceae	Licaria bahiana Kurz	ZOO	SDT	14.28
Lauraceae	Licaria guianensis Aubl.	ZOO	SDT	2.00
Lauraceae	Ocotea argentea Mez	ZOO	SDT	9.00
Lauraceae	Ocotea beulahiae J.B. Baitello	ZOO	SDT	20.00
Lauraceae	Ocotea confertiflora (Meisn.) Mez	ZOO	SDT	9.18
Lauraceae	Ocotea divaricata (Nees) Mez	ZOO	SDT	30.00
Lauraceae	Ocotea indecora (Schott) Mez	ZOO	SDT	9.88
Lauraceae	Ocotea lancifolia (Schott) Mez	ZOO	SDT	10.00
Lauraceae	Ocotea longifolia Kunth	ZOO	P	15.00
Lauraceae	Ocotea marcescens L.C.S.Assis & Mello-Silva	ZOO	SDT	5.50

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Lauraceae	Ocotea mosenii Mez	ZOO	SDT	5.00
Lauraceae	Ocotea neesiana (Miq.) Kosterm.	ZOO	SDT	4.00
Lauraceae	Ocotea nitida (Meisn.) Rohwer	ZOO	SDT	11.00
Lauraceae	Ocotea nutans (Nees) Mez	ZOO	SDT	7.00
Lauraceae	Ocotea pluridomatiata A.Quinet	ZOO	SDT	6.00
Lauraceae	Ocotea prolifera (Nees & Mart.) Mez	ZOO	SDT	15.00
Lauraceae	Ocotea sp1	ZOO	SDT	11.24
Lauraceae	Ocotea sp2	ZOO	SDT	11.24
Lauraceae	Ocotea sp3	ZOO	SDT	11.24
Lauraceae	Ocotea sp4	ZOO	SDT	11.24
Lauraceae	Ocotea spectabilis (Meisn.) Mez	ZOO	SDT	20.00
Lauraceae	Ocotea velutina (Nees) Rohwer	ZOO	SDT	6.50
Lecythidaceae	Cariniana estrellensis (Raddi) Kuntze	NZOO	SDT	7.23
Lecythidaceae	Cariniana legalis (Mart.) Kuntze	NZOO	SDT	8.20
Lecythidaceae	Cariniana parvifolia S.A.Mori, Prance & Menandro	NZOO	SDT	13.49
Lecythidaceae	Couratari asterotricha Prance	NZOO	SDT	20.12
Lecythidaceae	Couratari macrosperma A.C.Sm.	NZOO	SDT	15.41
Lecythidaceae	Eschweilera ovata (Cambess.) Mart. ex Miers	ZOO	SDT	17.78
Lecythidaceae	Lecythis lanceolata Poir.	ZOO	SDT	10.52
Lecythidaceae	Lecythis lurida (Miers) S.A.Mori	ZOO	SDT	23.59
Lecythidaceae	Lecythis pisonis Cambess.	ZOO	SDT	14.01
Lecythidaceae	Lecythis sp.	ZOO	SDT	14.01
Malpighiaceae	Byrsonima cacaophila W.R.Anderson	ZOO	P	13.13
Malpighiaceae	Byrsonima crispa A.Juss.	ZOO	P	7.80
Malpighiaceae	Byrsonima sericea DC.	ZOO	P	5.00
Malpighiaceae	Byrsonima stipulacea A.Juss.	ZOO	P	10.29
Malvaceae	Cavanillesia umbellata Ruiz & Pav.	NZOO	SDT	15.00

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Malvaceae	Ceiba pubiflora (A.St.-Hil.) K.Schum.	NZOO	SDT	6.00
Malvaceae	Eriotheca candolleana (K.Schum.) A.Robyns	NZOO	P	7.34
Malvaceae	Eriotheca macrophylla (K.Schum.) A.Robyns	NZOO	P	5.77
Malvaceae	Guazuma crinita Mart.	NZOO	P	0.89
Malvaceae	Hydrogaster trinervis Kuhlm.	NZOO	P	9.78
Malvaceae	Luehea mediterranea (Vell.) Angely	NZOO	P	1.43
Malvaceae	Pachira endecaphylla (Vell.) Carv.-Sobr.	NZOO	P	9.12
Malvaceae	Pavonia calyculosa A.St.-Hil. & Naudin	NZOO	P	6.00
Malvaceae	Pavonia crassipedicellata Krapov.	NZOO	P	6.00
Malvaceae	Pseudobombax majus (A.Robyns) Carv.-Sobr.	NZOO	P	11.80
Malvaceae	Pterygota brasiliensis Allemão	NZOO	SDT	13.02
Malvaceae	Quararibea penduliflora (A.St.-Hil.) K.Schum.	ZOO	SDT	11.99
Malvaceae	Sterculia apetala (Jacq.) H.Karst.	ZOO	SDT	20.96
Malvaceae	Sterculia excelsa Mart.	ZOO	SDT	14.25
Melastomataceae	Henriettea succosa (Aubl.) DC.	ZOO	P	1.20
Melastomataceae	Miconia cinnamomifolia (DC.) Naudin	ZOO	P	6.00
Melastomataceae	Miconia prasina (Sw.) DC.	ZOO	P	0.63
Melastomataceae	Miconia rimalis Naudin Naud.	ZOO	P	2.00
Melastomataceae	Miconia splendens (Sw.) Griseb.	ZOO	P	0.59
Melastomataceae	Mouriri arborea Gardner	ZOO	SDT	23.47
Melastomataceae	Mouriri glazioviana Cogn.	ZOO	SDT	12.00
Meliaceae	Guarea pendula R.S.Ramalho, A.L. Pinheiro & T.D.Penn. A.L.Pinheiro	ZOO	SDT	8.55
Meliaceae	Trichilia casaretti C.DC.	ZOO	SDT	8.01

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Meliaceae	Trichilia elegans A.Juss. subsp. elegans	ZOO	SDT	4.87
Meliaceae	Trichilia lepidota subsp. schumanniana (Harms) T.D. Penn.	ZOO	SDT	10.00
Meliaceae	Trichilia pallens C.DC.	ZOO	SDT	6.18
Meliaceae	Trichilia pseudostipularis (A.Juss.) C.DC.	ZOO	SDT	8.00
Meliaceae	Trichilia quadrijuga Kunth subsp. quadrijuga	ZOO	SDT	5.73
Meliaceae	Trichilia silvatica C.DC.	ZOO	SDT	3.00
Meliaceae	Trichilia sp1	ZOO	SDT	10.00
Meliaceae	Trichilia surumuensis C.DC.	ZOO	SDT	11.37
Metteniusaceae	Emmotum nitens (Benth.) Miers	ZOO	SDT	22.46
Monimiaceae	Mollinedia lamprophylla Perkins	ZOO	SDT	9.10
Monimiaceae	Mollinedia ovata Ruiz & Pav.	ZOO	SDT	4.00
Moraceace	Naucleopsis oblongifolia (Kuhlm.) Carauta	ZOO	SDT	15.58
Moraceae	Brosimum glaucum Taub.	ZOO	SDT	10.64
Moraceae	Brosimum glaziovii Taub.	ZOO	P	10.00
Moraceae	Brosimum guianense (Aubl.) Huber	ZOO	SDT	10.00
Moraceae	Brosimum lactescens (S.Moore) C.C.Berg	ZOO	P	12.00
Moraceae	Brosimum rubescens Taub.	ZOO	SDT	12.50
Moraceae	Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	ZOO	SDT	10.90
Moraceae	Clarisia racemosa Ruiz & Pav.	ZOO	SDT	12.71
Moraceae	Ficus cyclophylla (Miq.) Miq.	ZOO	SDT	1.00
Moraceae	Ficus enormis Mart. ex Miq.	ZOO	SDT	1.00
Moraceae	Ficus gomelleira Kunth	ZOO	P	0.70
Moraceae	Ficus mariae C.C.Berg, Emygdio & Carauta	ZOO	SDT	0.74
Moraceae	Ficus nymphaeifolia Mill.	ZOO	SDT	1.18
Moraceae	Ficus pulchella Schott	ZOO	SDT	0.64

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Moraceae	Ficus sp1	ZOO	SDT	0.88
Moraceae	Helicostylis pedunculata Benoist	ZOO	SDT	7.70
Moraceae	Helicostylis tomentosa (Poepp. & Endl.) Rusby	ZOO	SDT	5.39
Moraceae	Sorocea bonplandii (Baill.) W.C.Burger et al.	ZOO	SDT	7.00
Moraceae	Sorocea guilleminiana Gaudich.	ZOO	SDT	8.84
Myristicaceae	Virola gardneri (A.DC.) Warb.	ZOO	SDT	19.53
Myristicaceae	Virola officinalis Warb.	ZOO	SDT	7.00
Myrtaceae	Campomanesia espiritosantensis Landrum	ZOO	SDT	3.84
Myrtaceae	Campomanesia guazumifolia (Cambess.) O.Berg	ZOO	SDT	6.08
Myrtaceae	Campomanesia lineatifolia Ruiz & Pav.	ZOO	SDT	6.94
Myrtaceae	Eugenia badia O.Berg	ZOO	SDT	10.00
Myrtaceae	Eugenia bahiensis DC.	ZOO	SDT	8.25
Myrtaceae	Eugenia batingabranca Sobral	ZOO	SDT	6.88
Myrtaceae	Eugenia beaurepairiana (Kiaersk.) D.Legrand	ZOO	SDT	18.89
Myrtaceae	Eugenia brasiliensis Lam.	ZOO	SDT	12.00
Myrtaceae	Eugenia cataphyllea M.Souza & Sobral	ZOO	SDT	34.35
Myrtaceae	Eugenia excelsa O.Berg	ZOO	SDT	5.44
Myrtaceae	Eugenia fluminensis O.Berg	ZOO	SDT	12.07
Myrtaceae	Eugenia fusca O.Berg	ZOO	SDT	6.50
Myrtaceae	Eugenia gemmiflora O.Berg	ZOO	SDT	25.09
Myrtaceae	Eugenia guanabarina (Mattos & D.Legrand) Giaretta & M.C.Souza	ZOO	SDT	12.95
Myrtaceae	Eugenia handroi (Mattos) Mattos	ZOO	SDT	8.18
Myrtaceae	Eugenia involucrata DC.	ZOO	SDT	7.00
Myrtaceae	Eugenia itapemirimensis Cambess.	ZOO	SDT	17.56
Myrtaceae	Eugenia ligustrina (Sw.) Willd.	ZOO	P	5.92
Myrtaceae	Eugenia macrosperma DC.	ZOO	SDT	14.10

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Myrtaceae	Eugenia melanogyna (D.Legrand) Sobral	ZOO	SDT	15.00
Myrtaceae	Eugenia moonioides O.Berg	ZOO	SDT	11.50
Myrtaceae	Eugenia pisiformis Cambess.	ZOO	SDT	7.00
Myrtaceae	Eugenia platyphylla O.Berg	ZOO	SDT	7.59
Myrtaceae	Eugenia platysema O.Berg	ZOO	SDT	7.59
Myrtaceae	Eugenia prasina O.Berg	ZOO	SDT	14.90
Myrtaceae	Eugenia sp1	ZOO	SDT	18.19
Myrtaceae	Eugenia sp2	ZOO	SDT	18.19
Myrtaceae	Eugenia sp3	ZOO	SDT	18.19
Myrtaceae	Eugenia sp6	ZOO	SDT	18.19
Myrtaceae	Eugenia sp7	ZOO	SDT	18.19
Myrtaceae	Eugenia sp8	ZOO	SDT	18.19
Myrtaceae	Eugenia sp9	ZOO	SDT	18.19
Myrtaceae	Eugenia sp10	ZOO	SDT	18.19
Myrtaceae	Eugenia sp11	ZOO	SDT	18.19
Myrtaceae	Eugenia subterminalis DC.	ZOO	SDT	6.00
Myrtaceae	Myrcia amazonica DC.	ZOO	SDT	1.00
Myrtaceae	Myrcia eumecephylla (O.Berg) Nied.	ZOO	SDT	12.00
Myrtaceae	Myrcia excoriata (Mart.) E.Lucas & C.E.Wilson Mart.	ZOO	SDT	8.29
Myrtaceae	Myrcia grandifolia Cambess.	ZOO	P	15.50
Myrtaceae	Myrcia isaiana G.M.Barroso & Peixoto	ZOO	SDT	8.00
Myrtaceae	Myrcia lineata (O.Berg) Nied.	ZOO	SDT	9.00
Myrtaceae	Myrcia multiflora (Lam.) DC.	ZOO	SDT	5.58
Myrtaceae	Myrcia multipunctata Mazine (O.Berg) Kiaersk.	ZOO	SDT	4.00
Myrtaceae	Myrcia neoestrellensis E.Lucas & C.E.Wilson	ZOO	SDT	6.00
Myrtaceae	Myrcia neoglabra E.Lucas & C.E.Wilson	ZOO	SDT	10.00

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Myrtaceae	Myrcia neolucida A.R.Lourenço & E.Lucas	ZOO	SDT	2.91
Myrtaceae	Myrcia obversa (D.Legrand) E.Lucas & C.E.Wilson D.Legrand	ZOO	SDT	11.10
Myrtaceae	Myrcia plusiantha Kiaersk.	ZOO	SDT	10.32
Myrtaceae	Myrcia pubipetala Miq.	ZOO	P	4.80
Myrtaceae	Myrcia riodocensis G.M.Barroso & Peixoto	ZOO	P	8.00
Myrtaceae	Myrcia sp1	ZOO	P	20.78
Myrtaceae	Myrcia sp9	ZOO	P	20.78
Myrtaceae	Myrcia splendens (Sw.) DC.	ZOO	P	4.60
Myrtaceae	Myrcia strigipes Mart.	ZOO	P	8.70
Myrtaceae	Myrcia sucrei (G.M.Barroso & Peixoto) E.Lucas & C.E.Wilson	ZOO	P	6.40
Myrtaceae	Myrcia vittoriana Kiaersk.	ZOO	SDT	3.50
Myrtaceae	Myrciaria floribunda (H.West ex Willd.) O.Berg	ZOO	SDT	3.51
Myrtaceae	Myrtaceae sp1	ZOO	P	4.89
Myrtaceae	Myrtaceae sp2	ZOO	P	4.89
Myrtaceae	Myrtaceae sp3	ZOO	P	4.89
Myrtaceae	Myrtaceae sp4	ZOO	P	4.89
Myrtaceae	Myrtaceae sp5	ZOO	P	4.89
Myrtaceae	Neomitranthes sctictophylla (G.M.Barroso & Peixoto) M.Souza	ZOO	SDT	7.81
Myrtaceae	Plinia grandifolia (Mattos) Sobral	ZOO	SDT	9.85
Myrtaceae	Plinia involucrata (O.Berg) McVaugh	ZOO	SDT	12.10
Myrtaceae	Plinia phitrantha (Kiaersk.) Sobral	ZOO	SDT	4.97
Myrtaceae	Plinia renatiana G.M.Barroso & Peixoto	ZOO	SDT	27.30
Myrtaceae	Plinia rivularis (Cambess.) Rotman	ZOO	SDT	14.81
Myrtaceae	Psidium cauliflorum Landrum & Sobral	ZOO	SDT	4.00

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Myrtaceae	Psidium guineense Sw.	ZOO	SDT	2.00
Myrtaceae	Psidium oblongatum O.Berg	ZOO	SDT	5.70
Myrtaceae	Psidium sartorianum (O.Berg) Nied.	ZOO	SDT	5.50
Nyctaginaceae	Guapira noxia (Netto) Lundell	ZOO	P	2.00
Nyctaginaceae	Guapira opposita (Vell.) Reitz	ZOO	P	6.30
Nyctaginaceae	Guapira venosa (Choisy) Lundell	ZOO	P	3.00
Nyctaginaceae	Neea floribunda Poepp. & Endl.	ZOO	P	4.00
Nyctaginaceae	Pisonia ambigua Heimerl	ZOO	P	3.30
Ochnaceae	Elvasia sp.1	ZOO	SDT	5.00
Ochnaceae	Elvasia sp.2	ZOO	SDT	5.00
Ochnaceae	Ouratea cuspidata (A.St.-Hil.) Engl.	ZOO	P	5.48
Ochnaceae	Ouratea sp1	ZOO	P	10.00
Olacaceae	Dulacia sp.	ZOO	P	10.00
Peraceae	Pera glabrata (Schott) Baill.	ZOO	P	2.00
Peraceae	Pera heteranthera (Schrank) I.M.Johnst.	NZOO	SDT	2.89
Peraceae	Pera sp1	ZOO	P	6.00
Peraceae	Pogonophora schomburgkiana Miers ex Benth.	NZOO	P	3.04
Phyllanthaceae	Hyeronima oblonga (Tul.) Müll.Arg.	ZOO	P	8.00
Phyllanthaceae	Margaritaria nobilis L.f.	ZOO	P	1.75
Picramniaceae	Picramnia ramiflora Planch.	ZOO	SDT	2.00
Picramniaceae	Picramnia sellowii Planch.	ZOO	SDT	10.00
Polygalaceae	Acanthocladus pulcherrimus (Kuhlm.) J.F.B.Pastore & D.B.O.S.Cardoso	ZOO	P	9.00
Polygonaceae	Coccoloba densifrons Mart. ex Meisn.	ZOO	P	6.00
Primulaceae	Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	ZOO	P	2.40

Family	Species	Dispersal Syndrome	Regeneration Strategy	Seed Diameter (mm)
Primulaceae	Myrsine guianensis (Aubl.) Kuntze	ZOO	P	2.60
Proteaceae	Roupala montana Aubl.	NZOO	P	11.00
Putranjivaceae	Drypetes sp.	ZOO	P	8.78
Quiinaceae	Lacunaria crenata subsp. decastyla (Radlk.) J.V.Schneid. & Zizka	NZOO	SDT	2.10
Rhamnaceae	Rhamnidium glabrum Reissek	ZOO	P	4.24
Rhamnaceae	Sarcomphalus glaziovii (Warm.) Hauenschild	ZOO	SDT	11.45
Rubiaceae	Alseis floribunda Schott	NZOO	P	1.00
Rubiaceae	Alseis involuta K.Schum.	NZOO	SDT	10.32
Rubiaceae	Amaioua intermedia var. brasiliana (DC.) Steyerm.	ZOO	P	9.61
Rubiaceae	Bathysa sp1	NZOO	P	5.77
Rubiaceae	Calycophyllum papillosum J.H.Kirkbr.	NZOO	SDT	2.22
Rubiaceae	Coussarea contracta (Walp.) Müll.Arg.	ZOO	P	22.43
Rubiaceae	Coutarea hexandra (Jacq.) K.Schum.	NZOO	P	5.00
Rubiaceae	Duroia valesca C.H.Perss. & Delprete	ZOO	SDT	2.24
Rubiaceae	Faramea corymbosa Aubl.	ZOO	SDT	2.00
Rubiaceae	Ferdinandusa guainiae Spruce ex K.Schum.	NZOO	P	5.00
Rubiaceae	Guettarda angelica Mart. ex Müll.Arg.	ZOO	P	6.40
Rubiaceae	Guettarda viburnoides Cham. & Schltdl.	ZOO	P	13.30
Rubiaceae	Ixora brevifolia Benth.	ZOO	P	4.74
Rubiaceae	Melanopsidium nigrum Colla	ZOO	P	6.00
Rubiaceae	Molopanthera paniculata Turcz.	ZOO	P	1.73
Rubiaceae	Posoqueria latifolia (Rudge) Schult.	ZOO	P	9.39
Rubiaceae	Psychotria carthagenensis Jacq.	ZOO	P	4.30

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Rubiaceae	Psychotria sp1	ZOO	P	6.00
Rubiaceae	Psychotria sp2	ZOO	P	6.00
Rubiaceae	Randia armata (Sw.) DC.	ZOO	P	5.91
Rubiaceae	Ravenia infelix Vell.	NZOO	SDT	1.80
Rubiaceae	Rubiaceae sp1	NZOO	P	1.00
Rubiaceae	Simira alba (Mart.) Delprete, Margalho & Groppo	NZOO	SDT	4.28
Rubiaceae	Simira grazielae Peixoto	NZOO	SDT	9.23
Rubiaceae	Simira sampaioana (Standl.) Steyerm.	NZOO	SDT	9.45
Rubiaceae	Tocoyena brasiliensis Mart.	ZOO	SDT	2.10
Rutaceae	Almeidea rubra A.St.-Hil.	NZOO	P	6.00
Rutaceae	Dictyoloma vandellianum A.Juss.	NZOO	P	2.14
Rutaceae	Esenbeckia grandiflora Mart. subsp. grandiflora	NZOO	P	14.81
Rutaceae	Galipea laxiflora Engl.	NZOO	SDT	2.70
Rutaceae	Metrodorea maracasana Kaastra	NZOO	SDT	4.38
Rutaceae	Neoraputia alba (Nees & Mart.) Emmerich ex Kallunki	NZOO	SDT	7.10
Rutaceae	Neoraputia magnifica (Engl.) Emmerich ex Kallunki	NZOO	SDT	5.00
Rutaceae	Rauia nodosa (Engl.) Kallunki	NZOO	SDT	2.00
Rutaceae	Zanthoxylum rhoifolium Lam.	ZOO	P	3.00
Salicaceae	Banara brasiliensis (Schott) Benth.	ZOO	P	1.20
Salicaceae	Casearia commersoniana Cambess.	ZOO	SDT	6.00
Salicaceae	Casearia oblongifolia Cambess.	ZOO	P	2.78
Salicaceae	Casearia sp. nov.1	ZOO	P	10.00
Salicaceae	Casearia sp. nov.2	ZOO	P	10.00
Salicaceae	Casearia sp1	ZOO	P	6.00
Salicaceae	Casearia sp2	ZOO	P	6.00
Salicaceae	Casearia ulmifolia Vahl ex Vent.	ZOO	P	1.50

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Salicaceae	Macrothumia kuhlmannii (Sleumer) M.H.Alford	ZOO	SDT	4.43
Salicaceae	Xylosma prockia (Turcz.) Turcz.	ZOO	P	2.60
Salicaceae	Xylosma sp1	ZOO	P	5.21
Sapindaceae	Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	ZOO	P	5.74
Sapindaceae	Allophylus petiolulatus Radlk.	ZOO	SDT	6.28
Sapindaceae	Cupania bracteosa Radlk.	ZOO	P	20.00
Sapindaceae	Cupania emarginata Cambess.	ZOO	P	6.38
Sapindaceae	Cupania oblongifolia Mart.	ZOO	P	9.70
Sapindaceae	Cupania rugosa Radlk.	ZOO	P	9.78
Sapindaceae	Cupania scrobiculata Rich.	ZOO	P	11.03
Sapindaceae	Dilodendron elegans (Radlk.) Gentry & Steyerm.	ZOO	SDT	7.53
Sapindaceae	Matayba guianensis Aubl.	ZOO	P	8.26
Sapindaceae	Melicoccus espiritosantensis Acev.-Rodr.	ZOO	P	9.30
Sapindaceae	Melicoccus oliviformis subsp. intermedius (Radlk.) Acev.-Rodr.	ZOO	P	12.00
Sapindaceae	Melicoccus sp1	ZOO	P	9.93
Sapindaceae	Pseudima frutescens (Aubl.) Radlk.	ZOO	SDT	30.53
Sapindaceae	Toulicia patentinervis Radlk.	NZOO	SDT	5.10
Sapotaceae	Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	ZOO	SDT	9.92
Sapotaceae	Chrysophyllum januariense Eichler	ZOO	SDT	20.00
Sapotaceae	Chrysophyllum lucentifolium Cronquist	ZOO	SDT	11.00
Sapotaceae	Chrysophyllum lucentifolium Cronquist subsp. lucentifolium	ZOO	SDT	11.00
Sapotaceae	Chrysophyllum sp	ZOO	SDT	22.00
Sapotaceae	Chrysophyllum splendens Spreng.	ZOO	SDT	8.71
Sapotaceae	Ecclinusa ramiflora Mart.	ZOO	SDT	11.34

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Sapotaceae	Manilkara bella Monach	ZOO	SDT	13.62
Sapotaceae	Manilkara salzmannii (A.DC.) H.J.Lam	ZOO	SDT	10.20
Sapotaceae	Micropholis crassipedicellata (Mart. & Eichler) Pierre	ZOO	SDT	8.05
Sapotaceae	Micropholis gardneriana (A.DC.) Pierre	ZOO	SDT	5.27
Sapotaceae	Micropholis gnaphaloclados (Mart.) Pierre	ZOO	SDT	8.00
Sapotaceae	Pouteria bangii (Rusby) T.D.Penn.	ZOO	SDT	17.00
Sapotaceae	Pouteria bapeba T.D.Penn.	ZOO	SDT	15.00
Sapotaceae	Pouteria bullata (S.Moore) Baehni	ZOO	SDT	10.00
Sapotaceae	Pouteria butyrocarpa (Kuhlm.) T.D.Penn.	ZOO	SDT	12.71
Sapotaceae	Pouteria coelomatica Rizzini	ZOO	SDT	8.09
Sapotaceae	Pouteria cuspidata (A.DC.) Baehni	ZOO	SDT	10.00
Sapotaceae	Pouteria durlandii (Standl.) Baehni	ZOO	SDT	9.00
Sapotaceae	Pouteria filipes Eyma	ZOO	SDT	12.59
Sapotaceae	Pouteria gardneriana (A.DC.) Radlk.	ZOO	SDT	9.20
Sapotaceae	Pouteria guianensis Aubl.	ZOO	SDT	8.91
Sapotaceae	Pouteria macahensis T.D.Penn.	ZOO	SDT	10.00
Sapotaceae	Pouteria macrophylla (Lam.) Eyma	ZOO	SDT	49.89
Sapotaceae	Pouteria microstrigosa T.D.Penn.	ZOO	SDT	11.00
Sapotaceae	Pouteria oblanceolata Pires	ZOO	P	15.00
Sapotaceae	Pouteria pachycalyx T.D.Penn.	ZOO	SDT	16.71
Sapotaceae	Pouteria psammophila (Mart.) Radlk.	ZOO	SDT	13.13
Sapotaceae	Pouteria reticulata (Engl.) Eyma	ZOO	SDT	8.04
Sapotaceae	Pouteria sp1	ZOO	SDT	16.15
Sapotaceae	Pouteria sp2	ZOO	SDT	16.15
Sapotaceae	Pouteria sp3	ZOO	SDT	16.15
Sapotaceae	Pouteria sp4	ZOO	SDT	16.15

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Sapotaceae	Pouteria venosa subsp. amazonica T.D.Penn.	ZOO	SDT	43.60
Sapotaceae	Pradosia lactescens (Vell.) Radlk.	ZOO	SDT	13.49
Schoepfiaceae	Schoepfia brasiliensis A.DC.	ZOO	SDT	3.00
Simaroubaceae	Homalolepis cedron (Planch.) Devecchi & Pirani	ZOO	SDT	39.16
Simaroubaceae	Homalolepis subcymosa (A.St.-Hil. & Tul.) Devecchi & Pirani	ZOO	P	5.62
Simaroubaceae	Simarouba amara Aubl.	ZOO	P	8.01
Siparunaceae	Siparuna reginae (Tul.) A.DC.	ZOO	SDT	2.31
Solanaceae	Solanum pseudoquina A.St.-Hil.	ZOO	P	3.30
Solanaceae	Solanum sooretamum Carvalho	ZOO	P	2.44
Trigoniaceae	Trigoniodendron spiritusanctense E.F.Guim. & Miguel	NZOO	SDT	13.00
Ulmaceae	Ampelocera glabra Kuhlm.	ZOO	P	7.82
Unidentified	Unidentified sp1	NA	NA	NA
Unidentified	Unidentified sp2	NA	NA	NA
Unidentified	Unidentified sp3	NA	NA	NA
Unidentified	Unidentified sp4	NA	NA	NA
Unidentified	Unidentified sp5	NA	NA	NA
Unidentified	Unidentified sp6	NA	NA	NA
Unidentified	Unidentified sp7	NA	NA	NA
Unidentified	Unidentified sp8	NA	NA	NA
Unidentified	Unidentified sp9	NA	NA	NA
Unidentified	Unidentified sp10	NA	NA	NA
Urticaceae	Cecropia hololeuca Miq.	ZOO	P	0.98
Urticaceae	Cecropia pachystachya Trécul.	ZOO	P	0.61
Urticaceae	Coussapoa curranii S.F.Blake	ZOO	SDT	6.00
Urticaceae	Coussapoa microcarpa (Schott) Rizzini	ZOO	SDT	1.20
Urticaceae	Pourouma mollis Trécul	ZOO	P	10.78
Urticaceae	Pourouma velutina Mart. ex Miq.	ZOO	P	0.50
Verbenaceae	Aegiphila verticillata Vell.	ZOO	P	3.00

Family	**Species**	**Dispersal Syndrome**	**Regeneration Strategy**	**Seed Diameter (mm)**
Violacaeae	Amphirrhox longifolia (A.St.-Hil.) Spreng.	ZOO	SDT	13.10
Violaceae	Paypayrola blanchetiana Tul.	ZOO	SDT	10.00
Violaceae	Rinorea bahiensis (Moric.) Kuntze	ZOO	SDT	4.03
Violaceae	Rinorea sp1	ZOO	SDT	6.00
Vochysiaceae	Qualea jundiahy Warm.	NZOO	SDT	7.78
Vochysiaceae	Qualea magna Kuhlm.	NZOO	SDT	8.00
Vochysiaceae	Vochysia angelica M.C.Vianna & Fontella	NZOO	P	5.71
Vochysiaceae	Vochysia riedeliana Stafleu	NZOO	P	7.50

Table S4 Correlation matrices among landscape attributes measured in four landscape sizes (concentric buffers ranging from 400 m to 3200 m-radius) in three Atlantic forest regions (R1, *n* = 9; R2, *n* = 18; R3, *n* = 8; total of 35 permanent sample plots). We show the coefficient of correlation (r), with significant values indicated with * (p < 0.05). MO = Matrix Openness, PD = Patch Density

	Region 1		**Region 2**		**Region 3**		**All regions combined**	
400 m	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**
MO	1	-	1	-	1	-	1	-
PD	0.12	1	0.54*	1	0.97*	1	0.7*	1
800 m	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**
MO	1	-	1	-	1	-	1	-
PD	0.69*	1	0.6*	1	0.91*	1	0.65*	1
1600 m	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**
MO	1	-	1	-	1	-	1	-
PD	0.21	1	0.56*	1	0.87*	1	0.47*	1
3200 m	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**	**MO**	**PD**
MO	1	-	1	-	1	-	1	-
PD	0.43	1	0.48*	1	0.97*	1	0.59*	1

Table S5 Pairwise correlation matrices among forest attributes in three Atlantic forest regions (R1, *n* = 9; R2, *n* = 18; R3, *n* = 8; all regions combined, *n* = 35). We show the coefficient of correlation (r), with significant values indicated with * ($p < 0.05$). BA = stand basal area, H_{MAX} = maximal stem height, SH = structural heterogeneity, SR = species richness, SD = Simpson diversity index, FR = functional richness, AD_{CWM} = community weighted-mean animal dispersal, ST_{CWM} = community weighted-mean shade tolerance, SS_{CWM} = community weighted-mean seed size

FOREST ATTRIBUTES									
Region 1									
	BA	**H_{MAX}**	**SH**	**SR**	**SD**	**FR**	**AD_{CWM}**	**ST_{CWM}**	**SS_{CWM}**
BA	1	-	-	-	-	-	-	-	-
H_{MAX}	0.59*	1	-	-	-	-	-	-	-
SH	0.84*	0.77*	1	-	-	-	-	-	-
SR	-0.48	-0.87*	-0.73*	1	-	-	-	-	-
SD	-0.18	-0.69*	-0.38	0.73*	1	-	-	-	-
FR	-0.44	-0.9*	-0.73*	0.86*	0.83*	1	-	-	-
AD_{CWM}	-0.46	-0.8*	-0.58	0.9*	0.79*	0.74*	1	-	-
ST_{CWM}	-0.22	-0.02	-0.19	<0.001	-0.44	-0.26	0.13	1	-
SS_{CWM}	-0.47	-0.52	-0.59*	0.24	0.02	0.47	0.12	0.25	1
Region 2									
	BA	**H_{MAX}**	**SH**	**SR**	**SD**	**FR**	**AD_{CWM}**	**ST_{CWM}**	**SS_{CWM}**
BA	1	-	-	-	-	-	-	-	-
H_{MAX}	0.81*	1	-	-	-	-	-	-	-
SH	0.92*	0.88*	1	-	-	-	-	-	-
SR	0.58*	0.62*	0.55*	1	-	-	-	-	-
SD	0.47*	0.41*	0.38	0.85*	1	-	-	-	-
FR	0.6*	0.67*	0.58*	0.81*	0.72*	1	-	-	-
AD_{CWM}	-0.28	-0.34	-0.35	0.02	0.16	-0.08	1	-	-
ST_{CWM}	0.62*	0.4	0.52*	0.34	0.27	-0.03	-0.19	1	-
SS_{CWM}	0.61*	0.34	0.53*	0.18	0.31	0.2	0.13	0.51*	1
Region 3									
	BA	**H_{MAX}**	**SH**	**SR**	**SD**	**FR**	**AD_{CWM}**	**ST_{CWM}**	**SS_{CWM}**
BA	1	-	-	-	-	-	-	-	-

H_{MAX}	0.95*	1	-	-	-	-	-	-	-
SH	0.91*	0.97*	1	-	-	-	-	-	-
SR	0.77*	0.74*	0.74*	1	-	-	-	-	-
SD	0.79*	0.69*	0.71*	0.96*	1	-	-	-	-
FR	0.72*	0.73*	0.71*	0.94*	0.91*	1	-	-	-
AD_{CWM}	-0.39	-0.26	-0.15	-0.05	-0.12	-0.12	1	-	-
ST_{CWM}	0.68*	0.68*	0.56	0.71*	0.59	0.58	-0.17	1	-
SS_{CWM}	0.71*	0.78*	0.71*	0.74*	0.59	0.6	0.02	0.94*	1
All regions combined									
	BA	**H_{MAX}**	**SH**	**SR**	**SD**	**FR**	**AD_{CWM}**	**ST_{CWM}**	**SS_{CWM}**
BA	1	-	-	-	-	-	-	-	-
H_{MAX}	0.73*	1	-	-	-	-	-	-	-
SH	0.86*	0.89*	1	-	-	-	-	-	-
SR	0.57*	0.66*	0.62*	1	-	-	-	-	-
SD	0.38*	0.49*	0.44*	0.85*	1	-	-	-	-
FR	0.39*	0.59*	0.54*	0.81*	0.74*	1	-	-	-
AD_{CWM}	-0.38*	-0.34*	-0.4*	<0.001	0.14	-0.04	1	-	-
ST_{CWM}	0.61*	0.6*	0.65*	0.56*	0.39*	0.19	-0.24	1	-
SS_{CWM}	0.16	0.21	0.32	0.15	0.17	0.23	0.07	0.43*	1

IV. CAPÍTULO II

FOREST SUCCESSION AND EDAPHIC FACTORS DRIVE CARBON STOCK AND FUNCTIONAL VULNERABILITY IN BRAZILIAN ATLANTIC RAINFORESTS

Abstract

The success of the successional process of second-growth tropical forests is important for the effectiveness of restoration and climate change mitigation projects, as a major part of tropical forest landscapes is covered by these forests. So, to ensure this success we need to understand how vulnerable these forests are in terms of functioning and services (i.e., capacity to store carbon). Here we used a trait-based approach in 27 0.1 ha second-growth forest plots to determine how stand age, landscape structure (matrix openness, patch density), seasonal water availability (climatic water deficit), and soil properties (sum of base, nitrogen, organic carbon and clay contents) predict aboveground carbon stock and functional composition, redundancy, and vulnerability in Brazilian Atlantic forests. We focused on three carbon-related species traits: maximum stem diameter, maximum stem height and species-specific stem wood density, which were treated as categorical variables; and we classified species as carbon-dominant (upper forest stratum) vs. non-carbon dominant (regenerating forest stratum) based on their relative contribution to carbon storage. Overall, we found that predictors had contrasting effects on these two groups. Stand age was the main driver of carbon stock in the upper forest stratum, whereas soil nitrogen and organic carbon were the main drivers of carbon stock in the regenerating stratum. Soil nitrogen, clay content, landscape deforestation and fragmentation had positive effects on carbon-dominant species growth, whereas water stress, soil organic carbon promoted non-carbon dominant species growth. Finally, succession and soil properties were the main drivers of functional redundancy and vulnerability of the regenerating forest stratum. Our findings advances our understanding of the mechanisms that drive carbon stock and functional composition in Brazilian Atlantic forests. This knowledge is crucial for predicting and managing the impacts of environmental changes on ecosystem functioning and services, and designing of effective forest restoration and mitigation strategies adapted to local site conditions.

Keywords: Climate change, Forest age, Landscape structure, Soil properties, Large trees, Wood density

1 Introduction

Tropical forests are carbon hotspots, accounting for around 68% of global forest carbon stocks, stored in the biomass of tree communities (Lewis et al. 2015; Hubau et al. 2020) and therefore crucial to climate change mitigation efforts (Myers et al. 2000; Bonan 2008; Beer et al. 2010). They play a key role in nature-based solutions that are mostly based on restoration (i.e. remove emissions that are already present in the atmosphere) and carbon avoidance projects (i.e. protect forests to avoid potential emissions), whereas both can be part of REDD+ mechanism (Mackey et al. 2020). Given the varying degrees of human impacts on forests, tropical landscapes can consist of forest areas at different successional stages, including old-growth forests, secondary forests resulting from clear-cutting, exploited forests, and burned forests (Ribeiro et al. 2009; Souza et al. 2020; Safar et al. 2022). Despite their differing conditions, each of these forest types can provide essential ecosystem services. For example, intact tropical old-growth forests are known to store large amounts of carbon and, therefore, they can be important potential carbon sources if disturbed (e.g., deforestation, fire and logging), while second-growth forests (forests regenerating after ceasing human impacts) are known to have higher carbon sequestration rates thus acting as efficient carbon sinks (Bongers et al. 2015; Poorter et al. 2016). Hence, promoting the conservation of tropical forests and ensuring the success of the successional process are important steps for maintaining the functioning of ecosystems (i.e., capacity to sequester and store carbon) and, therefore, for the effectiveness of mitigating climate change (Magnago et al. 2015a; Chazdon et al. 2016; Safar et al. 2020). To ensure this success, we need to improve restoration and carbon mitigation projects, thus this study aims to understand how vulnerable these forests are in terms of carbon storage capacity and which factors predict the stability of the functions provided by second-growth forests and their vulnerability to future disturbances.

The importance of tropical second-growth forests for biodiversity and carbon conservation has been increasingly recognized in recent years (Bongers et al. 2015). These forests cover about a third of the Neotropical forest landscapes (Chazdon et al. 2016) and have shown the potential to recover biodiversity and carbon stocks as natural regeneration progresses (Poorter et al. 2016; Lennox et al. 2018; Rozendaal et al. 2019; Safar et al. 2020). Thus, allowing these forests to regenerate naturally (i.e. a passive restoration approach) under favorable ecological and social conditions (Chazdon and Guariguata 2016; Crouzeilles et al. 2017) can be a more effective and lower cost approach to meet globally agreed targets for conserving biodiversity and mitigating climate change (Chazdon et al. 2016; Poorter et al. 2016; Busch et al. 2019). The outcomes of natural regeneration are generally uncertain, because the process depends on the species return, which is determined by the functional traits/strategies they possess and the constraints imposed by dispersal limitation (e.g., landscape context) and environmental filtering (e.g., soil and climate) (Boukili and Chazdon 2017; Le Bagousse-Pinguet et al. 2017; Toledo et al. 2018; Werden et al. 2018; Poorter et al. 2019).

A trait-based approach can better quantify and predict human-driven impacts (Laliberté et al. 2010; Mouillot et al. 2013; Laughlin 2014), as the degree to which the loss of an individual species impacts the ecosystem depends on whether there are other species within the community that perform similar functions (i.e. functional redundancy). The loss of any functional group (i.e. a collection of species from different taxonomic groups that share similar, if not identical, roles in the ecosystem, Lavorel and Garnier, 2002) can likely result in loss of some ecosystem functions and increase the vulnerability of ecosystem functioning to future disturbances (Biggs et al. 2020). Thus, an ecosystem functioning is expected to be less vulnerable when having high functional redundancy and response trait diversity (i.e., variety of species responses to environmental pressures), because the loss of any species is buffered against the loss of an individual species (Elmqvist et al. 2003; Mori et al. 2013). Thus, in the context of climate change mitigation, the return of species that contribute the most to carbon storage, such as large tree species (Slik et al. 2013) and hardwood species (Phillips et al. 2019), is essential for restoring forest functioning and conserving terrestrial carbon. Understanding the relationships between abiotic and anthropogenic drivers and tree species can help predict changes in ecosystem functioning and identify vulnerable ecosystems (Lohbeck et al. 2015; Poorter et al. 2016; Ouyang et al. 2019).

To better understand the conditions that might influence the vulnerability of tropical forests and improve restoration strategies, it is important to investigate the local and regional context that make the functions performed by species more vulnerable. Several studies have shown that succession (Chazdon 2014), landscape structure (Collins et al. 2017; Matos et al. 2017; San-José et al. 2019; Safar et al. 2022), seasonality in water availability (Becknell et al. 2012; Poorter et al. 2016, 2019), and soil properties (Pinho et al. 2018; Toledo et al. 2018; Werden et al. 2018) are stronger determinants of forest community composition and functioning. Yet, the extent to which these parameters affect the functional vulnerability in tropical forests is not well understood (but see Laliberté et al. 2010; Guo et al. 2020). Here we used a trait-based approach to identify the drivers of carbon storage stability in tropical forests and its vulnerability to future environmental changes. To obtain a wider generalization we did so for 27 second-growth forests of different ages distributed in three different regions within different landscape and edaphoclimatic contexts.

We ask how forest age, landscape structure, water availability, and soil properties drive the carbon stock, functional composition, redundancy and vulnerability of carbon-dominant and non-carbon dominant species in second-growth Atlantic forests. Hence, we selected tree species carbon-related traits that are informative of ecosystem functioning (maximum stem diameter, maximum stem height and species-specific stem wood density). Based on these traits and the relative contribution of species to carbon storage, we classified tree species into carbon dominant and non-carbon dominant. Understanding the drivers of functional community assembly and vulnerability in these two groups can help develop effective strategies and policies to mitigate the negative impacts of environmental changes on forest ecosystems and ensure their sustainable management and conservation. We then discuss the implications of our findings for carbon conservation and mitigation in human-modified landscapes under global and local initiatives for ecological restoration.

2 Material and methods

2.1 Study regions

This study was conducted in Atlantic forest sites located within and nearby five Protected Areas in Brazil: the Reserva Biológica do Córrego Grande (RBCG, 1,504 ha), the Floresta Nacional do Rio Preto (FRP, 2,817 ha), the Parque Nacional do Pau Brasil (PNPB, 19,027 ha), the Reserva Particular do Patrimônio Natural Estação Veracel (RPPNEV, 6,069 ha) and the Parque Estadual da Serra do Conduru (PESC, 9,275 ha) (**Fig. 7**). The forest sites are distributed between the north of Espírito Santo and the south of Bahia States in three different regions that are part of one of the best preserved sub-regions of the Atlantic Forest Domain (Silva & Casteleti 2003), holding 18% of its original vegetation (Ribeiro et al. 2009), in a biome that has already lost about 88% of its original cover (Fundação SOS Mata Atlântica and INPE 2022).

The regions slightly differ in terms of vegetation type, climate, soil and landscape structure. The vegetation in the regions B and C is classified as Lowland Dense Ombrophilous Forest or coastal tableland forest, as it develops on the sedimentary plateaus of the Tertiary Barreiras Group within an average altitude of 5 to 100 meters (IBGE 2012). The vegetation in the region A is classified as Submontane Dense Ombrophilous Forest, formed within an average altitude of 50 to 600 meters and characterized by the presence of species that vary according to latitude, being composed mainly of tall phanerophytes (IBGE 2012). The climate vary from tropical wet and dry (“Aw”, Köppen classification), with mean annual temperature and rainfall of 24°C and ~1,270mm and a dry season from April to September (Souza and Resende 1999;

Ferreira et al. 2019), and tropical hot and humid ("Af") with mean annual temperature of 24°C and rainfall and above 1,400 mm, without a defined dry season (ICMBIO 2011; RPPN 2016). The predominant soil types are deep, acid, kaolinitic, highly weathered and nutrient-poor soil, ranging from Yellow to Red-Yellow Argisols (Ultisols) and Latosols (Oxisols) (Souza and Resende 1999; ICMBIO 2011; RPPN 2016). Regarding the landscape structure, native forest cover and matrix quality varied between the regions (see Table S1). Hence, these regions can provide important insights into which local conditions, such as forest age, soil properties, water availability and landscape structure may influence the vulnerability of second-growth forest in highly fragmented and diverse tropical forests.

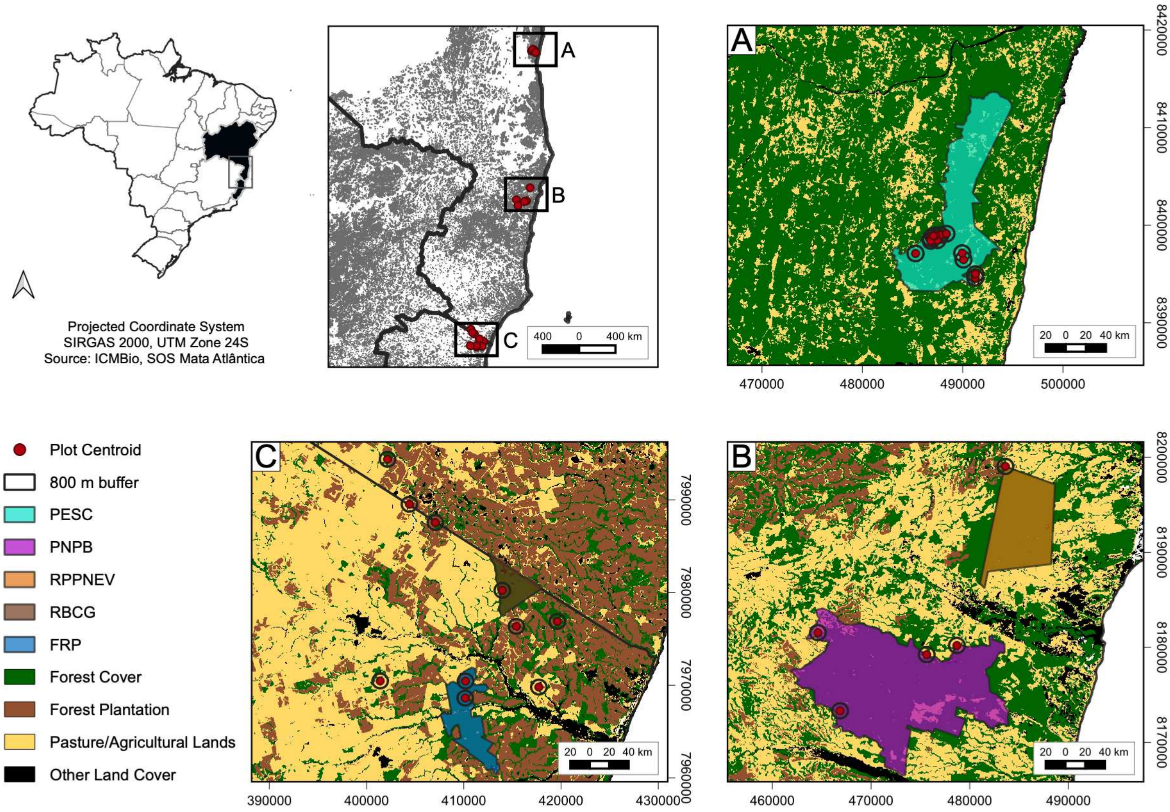

Fig. 7 Location of the 27 Atlantic rainforest plots distributed in southern Bahia State and northern Espírito Santo State, Brazil. The black circles represent the 800m buffer radius around each forest plot and the polygons represent the limits of the Protected Areas (PESC = Parque Estadual da Serra do Conduru, PNPB = Parque Nacional do Pau Brasil, RPPNEV = Reserva Particular do Patrimônio Natural Estação Veracel, RBCG = Reserva Biológica do Córrego Grande, and FRP = Floresta Nacional do Rio Preto). Land use and cover are derived from MapBiomas (https://mapbiomas.org/).

2.2 Permanent sample plots

We used data from 27 0.1 ha permanent sample plots of Atlantic forests that are recovering from different disturbances or past land uses, such as fire, clear-cutting and pasture (see Appendix Table S2). We acknowledge that the type of disturbance can influence forest regeneration, however, disturbances are very variable in highly fragmented and human-modified landscapes, and difficult to accurately quantify (see also Safar et al., 2022). Disturbance is here defined as any natural or anthropogenic event that causes the loss of forest coverage, affecting the structure, diversity and functioning of ecosystem. Henceforth these plots are referred to as second-growth, which varied in age from 10 to 40 years after disturbance or abandonment. Forest age was defined as the approximate time since the last disturbance (i.e., when disturbance ceased and succession started) or abandonment (i.e., when a land used for traditional agricultural activities was abandoned and left to regenerate naturally), and was determined based on Landsat images from Google Earth complemented with information from landowners and Protected Areas staff. Given the high number of plots across the Atlantic Forest Domain covering a large range of typical land-use types and intensities, we are confident that we provide realistic vulnerability assessments for second-growth Atlantic forests.

2.3 Forest inventory and carbon estimation

To capture local-scale variation, we described forest composition of each plot using a nested plot design. Each plot consisted of ten 10x10 m subplots established with a nearest distance between two neighboring subplots of 20 m. Following the recommendations by de Lima et al. (2015), for each plot all living woody trees and palms with a stem diameter at breast height (DBH at 1.3 m height) $\geq$ 4.8 cm were measured for their stem diameter and height, and identified to species. Liana species were not censused. The specimens nomenclature was verified using the database Flora do Brazil (Reflora), following the Angiosperm Phylogeny Group IV guidelines (APG IV 2016). In the 2.7 hectares sampled, we recorded 4,000 trees classified in 473 (morpho)species and 64 botanical families (see Table S3).

To obtain live plot aboveground carbon storage (AGC_{total}), we calculated the aboveground biomass of each individual tree (AGB_{tree}) using the *computeAGB* function from the R package 'BIOMASS' (Réjou-Méchain et al. 2017). This function adopts the allometric equation for moist forests from Chave et al., (2014), which takes into account the individual DBH, wood density and a site-specific "environmental stress factor" (*E*). We converted the AGB_{tree} into tree aboveground carbon storage (AGC_{tree}) by assuming that 50% of biomass is made up of carbon (Houghton et al. 2000). The AGC_{tree} was then summed to obtain live plot AGC_{total} (Mg ha^{-1}).

2.4 Edaphic and climatic factors

In each subplot, we collected one compound sample of topsoil (0-10 cm depth), totalizing 10 soil samples per plot. These samples were air-dried, sieved through a 2 mm sieve and sent for chemical and texture analysis at the Soil Laboratory of the Universidade Federal de Viçosa. Sum of base (SB, in cmolc/kg) was determined by summing the cations K, Ca, and Mg and used as an indicator of soil nutrient availability, soil total nitrogen (N, in %) was determined by the Kjeldahl method, soil organic carbon (SOC, in %) by the Walkley-Black method, and soil clay content (Clay, in %) by separating the samples into clay fractions (particles <0.002 mm diameter) using the pipette method. We combined the data collected in the ten subplots and obtained the average soil contents per plot.

Soil SB and N are indicators of nutrient availability which are a critical resource for plant growth (Davidson et al. 2004), while clay content (Silver et al. 2000; Osman 2013) and SOC (Blanco-Canqui et al. 2013) affect the ability of soils to retain water and nutrients, consequently also affecting plant development. Across plots, all soil predictors were moderately correlated (average Spearman's $r = 0.57$, $n = 27$; $p < 0.05$, Table S4), except for the sum of base and clay content ($r = 0.34$, $n = 27$; $p = 0.08$).

Climatic water deficit (CWD, in mm yr^{-1}) was obtained for each plot using the function *getBioclimParam* from the R package 'BIOMASS' (Réjou-Méchain et al. 2017) and it indicates the dry season intensity (i.e., seasonal drought stress). As water is essential for plant growth, the amount and timing of water availability can affect a plant's ability to photosynthesize, grow, and reproduce (Brando et al. 2008; Toledo et al. 2011). Across plots, CWD was strongly correlated with N and SOC (average Spearman's $r = 0.79$) but showed no significant correlation with SB and Clay (average Spearman's $r = 0.165$) (see Table S4).

2.5 Landscape structure

To determine how landscape structure drives functional composition, redundancy and vulnerability, we selected two landscape drivers: the matrix openness and patch density, and established a 800m circular landscape buffer (i.e., landscapes of 201 ha) from the center of each plot (see Crouzeilles & Curran 2016) (**Fig. 7**). We decided to use this buffer size because, based on our previous study (Safar et al. 2022), landscape openness does not have significant effects on forest attributes below a radius of 800m radius and because we observed buffer overlaps at larger scales (see Appendix Fig. S1). Matrix openness (MO) is the percentage of open area in the surrounding landscape covered by all land use and cover classes (e.g. grassland, agriculture, pasture, urban area, and water bodies) that are not natural forest formations (e.g. rainforest and savanna formation) or forest plantations (mainly *Eucalyptus* plantations). Matrix openness indicates the extent of deforestation or forest conversion towards other types of land use (i.e. forest loss) and high values indicate a more deforested landscape. Forest patch density (PD) relates to the degree of fragmentation and is the number of natural forest formation patches per ha (#/ha), without considering planted forests, since we are focusing only on seed sources. High values indicate a more fragmented landscape, however, this is not only a metric of forest fragmentation as it also indicates the amount of stepping stones in the landscape for forest-dependent animal and plant species. We refer to these metrics as "openness" as both refer to a more open, converted, and fragmented forest landscape. For each plot, we obtained matrix openness and forest patch density, which were strongly correlated (Spearman's $r = 0.72$, $n = 27$; $p < 0.05$, Table S4), using the R package 'landscapemetrics' (v.1.5.2) (Hesselbarth et al. 2021) and land use and cover maps freely available from the multi-disciplinary network MapBiomas (Collection 7, https://mapbiomas.org/), whose classification was based on Landsat images with a resolution of 30 m by 30 m (see Souza et al. 2020). We selected the maps referring to the year in which the plots were sampled (see Table S2 for details).

2.6 Functional composition

To understand how stand age, landscape, climatic and edaphic factors drive the functional composition of carbon-dominant and non-carbon dominant tree communities, we first combined per plot the data collected from the ten subplots and calculated for each plot the community functional composition based on three carbon-related attributes that are important for aboveground biomass and ecosystem processes (van der Sande et al. 2017b): maximum stem diameter (MD, cm), maximum stem height (MH, m), and species-specific wood density (WD, g/cm^{-3}). Stem diameter and height measures were taken at the field and species wood density ($g.cm^{-3}$) was obtained using the *getWoodDensity* function from the R package 'BIOMASS' (Réjou-Méchain et al. 2017), which uses the global wood density database (https://datadryad.org/stash/dataset/doi:10.5061/dryad.234). For species that we could not find information on wood density, we used the average of the genus or family.

Second, we separated the tree community in carbon-dominant vs. non-carbon dominant species. For that, we created functional entities (i.e., groups of species with same trait values, see Table S5), then compared among them the relative contribution of trees to carbon storage (see Fig. S2) and selected the entities with the greatest average relative contribution, which we called carbon-dominant trees. To create functional entities, we transformed the species attributes (MD, MH, WD) into categories or ordinal attributes (small x large; short x tall; softwood x hardwood). To classify species in size categories, we defined quartiles based on the distribution of maximum stem diameter and maximum stem height and used the average MD of the largest trees of all plots combined (10% upper quartile, that is, the trees that have size measurements within the upper quartile) as threshold for large trees (MD $\geq$ 23.76 cm) and the average MH of the tallest trees as threshold for tall trees (MH $\geq$ 16.04 m) (see Table S3). The method of quartiles provide a more accurate and representative view of the distribution of trees in a given area, avoiding false trends if there are extreme values or outliers present. We adopted this approach to avoid underestimating the presence of potential large and tall trees, as we are dealing with secondary forests where several species may not have reached their potential growth. For the wood density, all trees with WD $\geq$ 0.700 g.cm^{-3} were classified as hardwood trees (Santo-Silva et al. 2016) (see Table S3).

Species attributes were combined and functional entities created using the ‘mFD’ package (Magneville et al. 2022). In total, eight functional entities were computed (i.e., eight different combinations of Small/Large-Short/Tall-Softwood/Hardwood trees, see Table S5). Then, we tested for differences in the relative contribution to carbon storage among the functional entities by performing multiple-comparison post-hoc tests using the R package ‘emmeans’ (Lenth et al. 2021). We found that the functional entities formed by large and tall trees regardless of wood density (LTS, LTH) and by large, short and hardwood trees (LSH) store significantly more carbon per individual on average (Fig. S2). This group of carbon-dominant trees (CD), hereinafter referred to as upper forest stratum, comprises 53 species that together contribute 58% of the total carbon stock. The remaining functional entities make up the non-carbon dominant community (NCD), which represents and will be referred to as regenerating forest stratum, is composed of 420 species that contribute 42% of the carbon stock.

Third, we obtained for each plot the community functional composition given as community-weighted mean (CWM) maximal diameter (MD_{CWM}), maximal height (MH_{CWM}), and wood density (WD_{CWM}) (Table 3) for each carbon-dominant and non-carbon dominant tree community. The CWM describes the average trait values across all individuals in the community by weighing the trait value of a species by its proportional abundance in the plot. MD_{CWM} indicates the maximum stem diameter (centimeters, cm), MH_{CWM} indicates the maximum stem height (meters, m), and WD_{CWM} indicates the wood density (density, g.cm^{-3}).

CWM trait values were calculated for each plot based on species traits (MD, MH, WD) using the 'FD' package (Laliberté et al. 2015).

Table 3 The three species attributes with abbreviation, description, units, and an explanation of what they indicate.

Abbreviation	**Description**	**Units**	**Indicator of**
MD_{CWM}	Community-weighted maximum stem diameter	cm	Potential tree growth
MH_{CWM}	Community-weighted maximum stem height	m	Potential canopy development
WD_{CWM}	Community-weighted species-specific wood density	$g.cm^{-3}$	Volume growth

2.7 Functional Redundancy and Vulnerability

To assess how predictors affect the functional redundancy and vulnerability of second-growth Atlantic forests, we obtained the functional redundancy (FR) and functional vulnerability (FV) of carbon-dominant and non-carbon dominant tree communities. These metrics were computed using the functional entities obtained in the previous section and the 'mFD' package (Magneville et al. 2022). *FR* reflects the average number of species per functional entity, that is, the average number of species possessing similar functional traits that can perform similar ecosystem functions. *FV* reflects the proportion of functional entities with only one species (Mouillot et al. 2014), given in percentage, with higher values indicating greater vulnerability to environmental disturbances, and lower values indicating a lower risk of community collapse or loss of function.

2.8 Statistical Analyses

To determine how stand age, landscape, climatic and edaphic factors contributed to the prediction of (1) aboveground carbon storage, (2) functional composition (CWM trait values), (3) functional redundancy and (4) functional vulnerability of carbon-dominant and non-carbon dominant tree communities, we built generalized linear mixed models using the R package 'glmmTMB' (Brooks et al. 2023). We created two models for each relationship: one with forest age as the explanatory variable and another with the other predictors as explanatory variables, but both included interactions with the community type (carbon-dominant x non-carbon dominant) and the region where the plot is located as a random factor. We used the Gaussian (log) family to model continuous non-parametric data, which was assumed to have a log-normal distribution and we used beta distribution and a logit link to model proportion data (e.g., FV), which were bounded between 0 and 1. For the models with age as predictor, the parameters were modelled as a function of natural-logarithm transformed stand age to account for nonlinear responses over time. For the models with the other predictors, because there are many predictors and a relatively limited dataset of 27 second-growth forest plots, we started with a core model that included all seven predictors as fixed factors. Models were compared using Akaike's information criterion adjusted for small sample sizes (AICc) with the function *dredge* from R package 'MuMIn' (Bartoń 2020). We selected the best-supported model for each response variable, thus the model with $\Delta AIC_c \leq 4$ whose predictors have a correlation coefficient ≤ 0.6. All analyses were performed in R 4.2.2 (R Core Team 2022).

3 Results

Landscape structure, water availability and soil properties varied substantially across second-growth Atlantic forest plots. For example, the degree of deforestation (MO) varied from 1 to 87%, the degree of fragmentation (PD) varied 9-fold (from 0.5 to 4.49 number of patches/ha) and climatic water deficit (CWD) from -3.45 to -205.05 mm/yr. For the edaphic factors, soil SB varied 4.3-fold (from 1.16 to 4.95 cmolc/kg), N varied 4.2-fold (from 0.06 to 0.25%), C varied 5.6-fold (from 0.6 to 3.4%) and clay content varied 5.1-fold (from 7 to 36%).

The aboveground carbon stock varied considerably across plots, more than 7-fold (from 12.7 to 98.5 Mg C ha^{-1}), while the community MD varied from 19.4–31.2 cm, the community MH from 13–17 m, and the community WD from 0.53–0.67 g cm^{-3}, covering mainly medium-sized and softwood trees. The species were grouped into eight functional entities, but not all plots presented all species entities (see Table S5). The most representative functional entity (51.6%), in terms of number of species, was composed by small, short and softwood trees, while the least representative (1%) was composed by large, short and hardwood trees. The functional entities that together form the upper forest stratum (carbon-dominant trees), contributed 57% of the total carbon stock while accounting only for 11% of species community, whereas the regenerating forest stratum (non-carbon dominant species), accounted for 89% of species community and contributed 43% of the carbon stock.

How do stand age predicts tree carbon stock, functional composition, redundancy and vulnerability?

We assessed how different predictors drive 1) aboveground carbon storage, 2) functional composition, 3) functional redundancy and 4) functional vulnerability in second-growth Atlantic forests using GLMM. The GLMM results for stand age as predictor indicated that throughout forest succession, the aboveground carbon storage of upper forest stratum increased (**Fig. 8**a), and the functional redundancy of the regenerating forest stratum increased (**Fig. 8**e) while the vulnerability decreased (**Fig. 8**f). Although we found, across species communities, opposite effects of stand age on the proportion of large, tall, and dense wood trees, they were not significantly different from zero (**Fig. 8**b,c,d).

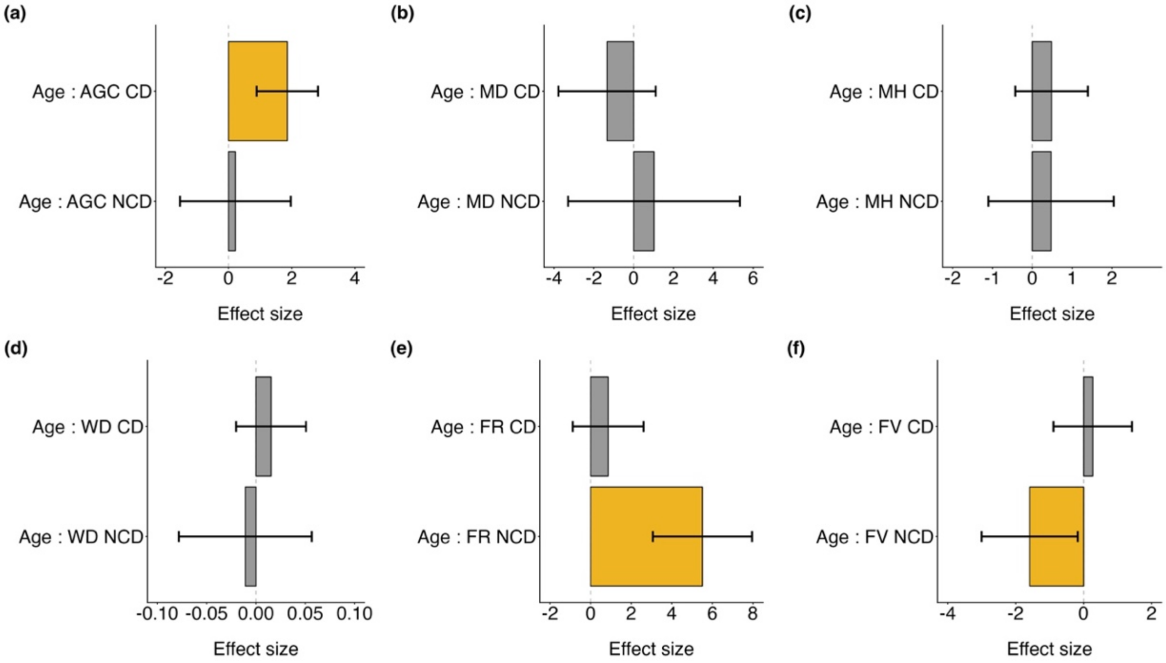

Fig. 8 The standardized effect size of stand age (predictor) on aboveground carbon stock, functional composition, redundancy and vulnerability. (**a**) Aboveground carbon stock (AGC), (**b**) community weighted-mean maximum diameter (MD), (**c**) community weighted mean-maximum height (MH), (**d**) community weighted-mean wood density (WD), (**e**) functional redundancy (FR) and (**f**) functional vulnerability (FV). The vertical bar indicates the mean standardized effect size of stand age on forest attributes and the error bars show standard errors for 95% confidence intervals of the mean parameter estimates. The yellow bar indicates that the effect size is significantly different from zero (non-overlap between confidence intervals and zero effect) and the gray bar indicates non-significant effects (overlap between confidence intervals and zero effect). See text for further details. CD = Carbon-Dominant trees, NCD = Non-Carbon Dominant trees.

How do tree carbon stock, functional composition, redundancy and vulnerability respond to landscape structure and edaphoclimatic factors?

The GLMM results of the best models with landscape structure, climatic water deficit and soil properties as predictors indicated that none of these predictors had significant effects on AGC, functional redundancy and functional vulnerability for the carbon-dominant community (**Fig. 9**a,e,f). In contrast, the carbon stock and the functional redundancy of non-carbon dominant trees increased with soil C and N content, while their functional vulnerability decreased (**Fig. 9**e,f).

Overall, the landscape structure, climatic water deficit and soil properties had opposite contrasting effects on carbon-dominant and non-carbon dominant tree communities. Increasing seasonal water availability, landscape deforestation and fragmentation drive a functional composition characterized by larger, taller and denser wooded carbon-dominant trees (**Fig. 9**b,c,d). On the contrary, more intense dry seasons and more forested landscape led to a non-carbon dominant community with bigger and denser-wooded trees (**Fig. 9**b,d). Furthermore, large and tall trees were positively affected by soil nitrogen and negatively affected by soil organic carbon (**Fig. 9**b,c). Clay content was a significant predictor of a functional composition characterized by large carbon-dominant trees (**Fig. 9**b). In contrast, increasing clay content had a influence on the size of non-carbon dominant trees (**Fig. 9**b,c).

4 Discussion

We assessed how different predictors (stand age, landscape structure, water availability, and soil properties) drive aboveground carbon stocks, functional composition, redundancy and vulnerability in second-growth Atlantic forests. We found that predictors had contrasting effects on carbon-dominant (i.e., upper forest stratum) and non-carbon dominant trees (i.e., regenerating forest stratum). Forest age and edaphic factors were the main drivers of functional redundancy and vulnerability of non-carbon dominant trees; whereas dry season length, soil nitrogen and soil carbon contents were the main predictors of carbon-dominant species growth. Here we will discuss how tree communities respond to local and regional drivers and end with the implications for climate change mitigation.

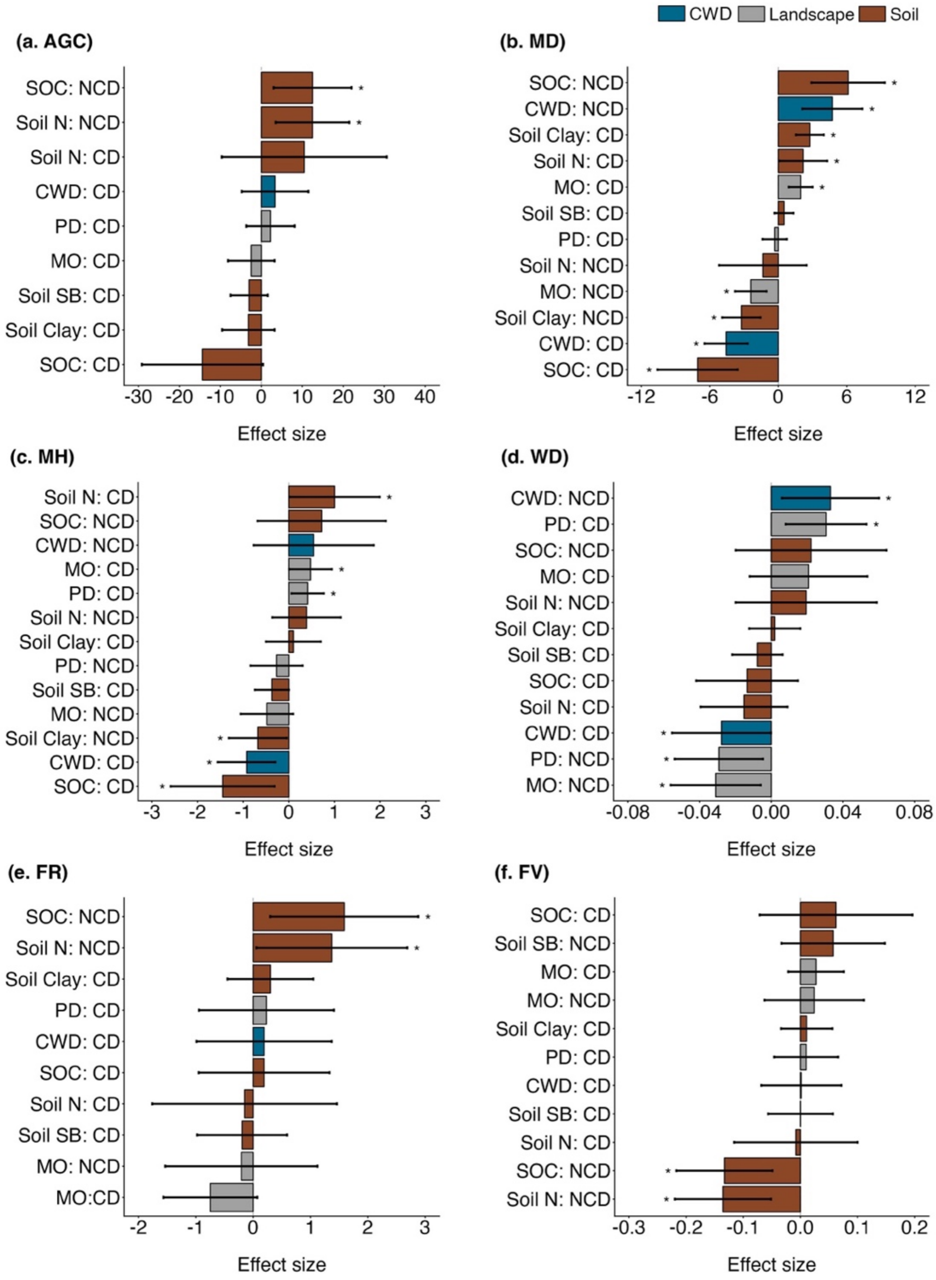

Fig. 9 Predictors of carbon stock, functional composition, redundancy and vulnerability. Standardized estimates of the coefficients from the best selected averaged models containing the effects of landscape structure, water availability and soil properties on aboveground carbon stock (**AGC**), community weighted-mean maximum diameter (**MD**), community weighted-mean maximum height (**MH**), community weighted-mean wood density (**WD**), functional redundancy (**FR**), and functional vulnerability (**FV**). The vertical bar indicates the mean standardized effect size of predictors (represented by different colors) on forest attributes and the error bars show standard errors for 95% confidence intervals of the mean parameter estimates. Predictors with significant effects ($p<0.05$) are shown with asterisks. Climatic water deficit was −1 transformed. See text for further details. CD = Carbon-Dominant trees, NCD = Non-Carbon Dominant trees, MO = Matrix Openness (%), PD = Patch Density (#/ha), CWD = Climatic Water Deficit (mm yr^{-1}), Soil SB = Sum of Bases (cmolc kg^{-1}), Soil N = Nitrogen (%), SOC = Soil Organic Carbon (%), Soil Clay = Soil Clay Content (%).

Succession and soil properties are the main drivers of aboveground carbon stock

We assessed how aboveground carbon storage is driven by successional status, landscape, water availability and soil properties. Our results indicate that the carbon stock of carbon-dominant and non-carbon dominant species had different responses to these predictors. We found that forest succession was the main driver of the carbon stock in the upper forest stratum (carbon-dominant species, **Fig. 8**a), whereas soil nitrogen and organic carbon were the main drivers of the carbon stock in the regenerating stratum (non-carbon dominant trees, **Fig. 9**a).

Standing tree carbon stock increased with stand age, as found in several other studies (Poorter et al. 2016; Jones et al. 2019; Safar et al. 2020). Although carbon stock of the regenerating stratum also tended to increase with stand age, the effects were only significantly for the upper stratum. This is probably because the upper stratum is exclusively made of large trees and mostly tall and hardwood trees (Fig. S2) which store more carbon (average $r= 0.57$, $p<0.05$, Table S6), and throughout forest succession those large-sized hard-wooded species are better competitors and tend to dominate the canopy (van Breugel et al. 2012; Poorter et al. 2019). Apart from stand age, we found no significant predictors for the carbon stock in the upper stratum. The lack of effects of soil properties on forest biomass was also found in phosphorus-depleted tropical forests (Soong et al., 2020), such as Atlantic forests, characterized by low phosphorous content due to its origin from pre-weathered sediments (Pavinato et al. 2020). Other factors than the ones we studied, such as soil phosphorous (van der Sande et al. 2017a; Waring et al. 2019), or topography and taxonomic identity (see Fotis et al., 2018; Rodrigues et al., 2023, 2019), might also influence carbon accumulation in carbon-dominant species.

The aboveground carbon stock of the regenerating stratum was mainly driven by soil nitrogen and organic carbon contents (**Fig. 9**a, see also (Sullivan et al. 2017). Nutrients are more limiting at earlier succession stages (Powers et al. 2015) and the use of these resources and biomass growth may vary depending on species traits (van der Sande et al., 2017a). For example, increasing nitrogen might contribute more to the productivity and carbon accumulation of early-successional species with fast-resource acquisitive strategies (Poorter and Remkes 1990) (Lohbeck et al. 2013; Poorter et al. 2019) that provide higher competitive ability on more fertile soils (Westoby et al. 2002). Yet, soil nitrogen did not drive the growth of species in the regenerating stratum (**Fig. 9**b,c), so we believe that the positive effect of soil nitrogen on AGC may be related to its effects on functional redundancy (**Fig. 9**e). Functional redundancy can contribute to ecosystem productivity by allowing for the compensation of species loss or reduced performance, once productivity tends to decline with plant species lost (Isbell et al. 2015), therefore ensuring the continuity of ecosystem processes and functions. Soil organic carbon, on the other hand, had positive effects not only on functional redundancy but also in the community MD (**Fig. 9**b,e). Soil carbon plays a vital role in maintaining soil structure, water-holding capacity, and nutrient availability (Blanco-Canqui et al. 2013), which are all important factors that affect plant growth and carbon accumulation. Therefore, we hypothesize that the combine effects of these strongly correlated soil properties (C and N, r=0.95, $p<0.05$, Table S4, see also Deng et al., 2013; Jones et al., 2019) on functional redundancy and community MD drives the aboveground carbon stock in the regenerating stratum.

Successional status was not a driver of functional composition

Overall, we found no successional changes in functional composition (**Fig. 8**b,c,d), probably because we are dealing with young secondary forests (≤40yr of succession), so significant differences in tree size and the expected replacement of softwood by hardwood trees (Poorter et al. 2019, 2021b) were not yet detected. However, landscape, seasonal water availability and soil properties showed contrasting effects on carbon-dominant and non-carbon dominant tree communities (**Fig. 9**), which will be discussed below.

Stands in highly fragmented and deforested landscapes can harbor carbon-dominant species

Increased landscape openness (deforestation and fragmentation) had opposite effects on upper and regenerating forest stratum species (**Fig. 9**b,c,d). This is probably explained by the local species pool and the edge effects expected to increase with habitat loss and fragmentation, such as higher wind disturbance and temperatures, and lower air and soil humidity (Arroyo-Rodríguez et al., 2017; Magnago et al., 2015), that impact plant establishment and performance. Most of the species that occupy the upper forest stratum in these young secondary forests are pioneer (42%), probably long-lived pioneer species, and early secondary species (39%), indicating that those are the ‘full-grown’ colonizers (Table S7). The positive effect of landscape openness in carbon-dominant species might be related to this dominance of pioneer species, which can be positively influenced by landscape fragmentation (Tabarelli et al. 2010; Magnago et al. 2014; Thier and Wesenberg 2016). In contrast, early and late secondary species in early stages of growth dominate the non-carbon dominant community (40% and 37%, respectively), which tend to be particularly sensitive to changes in environmental conditions and increased disturbances due to edge effects (Arroyo-Rodríguez et al. 2017). Our results show that second-growth Atlantic forests located in highly fragmented and deforested landscapes can harbor carbon-dominant species, highlighting the importance of these forests for climate change mitigation efforts.

Seasonal water availability predicts species growth and wood density

We found that the growth of species was driven by seasonal water availability (**Fig. 9**b,c,d), showing that stronger dry seasons can affect larger trees (Bennett et al. 2015). Drought stress, in general, reduce water availability for plant transpiration leading to reduced photosynthesis, and therefore, decreased carbon assimilation and reduced biomass production, ultimately affecting plant growth (Brando et al., 2008; Toledo et al., 2011). However, larger trees tend to be most impacted by drought stress (Nepstad et al. 2007; Saatchi et al. 2013) probably because of their greater water demand and longer hydraulic pathway. Furthermore, the negative effects of climatic water deficit on the growth of carbon dominant species might also be related to wood density and the successional stage of the studies plots. Reduced community WD range (from 0.45 to 0.75 g cm^{-3}) among the carbon-dominant species reflect a lower abundance of hard-wooded species in these forests, indicating the species in the upper stratum in early-mid successional Atlantic forests are mainly softwood, being more vulnerable to drought (Markesteijn et al. 2011; van der Sande et al. 2019). This results indicate that large tree species are more susceptible to climate change (Bennett et al. 2015).

In contrast, climatic water deficit had positive effects on community wood density, as reported in other neotropical forests (Poorter et al. 2019; Pyles et al. 2022), and on community MD for non-carbon dominant species (**Fig. 9**b,d). This indicate that water is not a limiting factor for the regenerating stratum in these forests. Stronger drier seasons are expected to favor hardwood species (Markesteijn et al. 2011), but this stratum is mainly characterized by softwood (community WD from 0.53 to 0.67 g cm^{-3}), so other traits rather than density wood might explain their positive relationship with climatic water deficit. For example, the species that compose the regenerating stratum might have resource acquisitive strategies, such as shallow and dense fine-root systems that could efficiently capture surface water (Raich et al. 2014), providing them with better competitive performance in drier conditions. Hence, further studies are needed to understand the relationship between regenerating stratum and water limitation.

Soil properties are the main drivers of species growth, but not of wood density

We found that the growth of carbon-dominant trees was positively affected by soil nitrogen and limited by soil organic carbon content (**Fig. 9**b,c), two strongly correlated soil properties (r=0.95, p<0.05, Table S4, see also Deng et al., 2013; Jones et al., 2019). These results show that stands with higher soil nitrogen sustained high tree growth, as expected as nitrogen is a key nutrient for plant growth (Davidson et al. 2004), whereas high levels of soil organic carbon limited plant growth, probably because soil organic carbon can affect the availability of nutrients (Blanco-Canqui et al. 2013). For example, in soils with high C:N ratios the nitrogen is likely immobilized within the microbial biomass, being less available for plant uptake (Laughlin et al. 2015). In contrast, we found that soil organic carbon promoted the growth of non-carbon dominant (community MD **Fig. 9**b), which might be related to its capacity to increase water retention in the soil (Blanco-Canqui et al. 2013), enhancing plant growth and productivity (Brando et al. 2008; Toledo et al. 2011). Future research should focus on understanding the complex interactions between SOC, plant communities, and soil fertility in these Atlantic forests.

Our results indicate that soil clay content influence the growth of tree species, showing opposite effects on carbon-dominant and non-carbon dominant species. The carbon-dominant community MD increased with soil clay content (**Fig. 9**b), suggesting that soils with higher clay content can sustain high tree growth (also see Toledo et al., 2018). More clayey soils have higher water retention capacity (Silver et al. 2000) and tend to avoid phosphorus losses from the ecosystem (Soong et al. 2020), a stronger limiting element for biomass growth (van der Sande et al. 2017a). However, this is not valid for the regenerating stratum as clay content limits plant growth (**Fig. 9**b,c), probably because high clay concentration can reduce the benefits from increased soil organic carbon, such as reduced soil compaction (Blanco-Canqui et al. 2013). In sum, our results show that the growth of carbon-dominant species and non-carbon dominant species in mainly affected by soil organic carbon and clay contents, probably related to their influence on soil compaction and water retention capacity.

Moreover, we found that soil properties were not predictors of community WD (**Fig. 9**d), indicating that nutrient availability is not a direct limiting factor for wood density (see also Arsić et al., 2021). This is because the formation of wood cells and the deposition of cell wall components are primarily determined by genetic and developmental processes that are relatively independent of nutrient availability, such as adult stature of the species and the regeneration light requirements (Poorter et al. 2010). Instead, wood density had been described to vary with environmental factors such as precipitation (**Fig. 9**d, also see Poorter et al., 2019; Pyles et al., 2022) and temperature (Wiemann and Williamson 2002).

Succession and soil properties are the main drivers of functional redundancy and vulnerability

We found that succession, soil nitrogen and organic carbon predict functional redundancy and vulnerability of the tree species in the regenerating forest stratum but not in the upper stratum. Functional redundancy in the regenerating stratum increased during succession (**Fig. 8**e), which might be linked to their high number of species (420 species, about 89% of total species richness) (Peterson et al. 1998) as it can increase the chance of including new species with redundant roles. Here we did not assess how taxonomic diversity change with stand age, although species richness in these second-growth Atlantic forest tend to increase throughout succession (see Safar et al., 2020), neither the effects of biodiversity on ecosystem vulnerability, so more research into the mechanism underlying the relationship between biodiversity-redundancy-vulnerability is needed.

Soil N and SOC drive higher functional redundancy in the regenerating stratum (**Fig. 9**e). The species composition in this lower stratum might be better adapted to soils richer in nitrogen and carbon probably due to other resource acquisitive strategies that we did not address in this study, such as deep or shallow and coarse or fine roots system (Raich et al. 2014), which allow them to be better compete in early stages of succession when nutrients are more limiting (Powers et al. 2015). Our results show that the region (C, **Fig. 7**) that presents higher soil N and SOC compared to the other regions (Fig. S3e,f) also presents the lower functional vulnerability (Fig. S4p,r), suggesting that these soil properties, along with succession, are the main drivers of regenerating stratum vulnerability.

The functional vulnerability of non-carbon dominant species, on the other hand, decreased with stand age, soil nitrogen and soil organic carbon contents. The overall decrease in vulnerability is likely due to increased functional redundancy ($r=-0.52$, $p<0.05$, Table S8), but also these non-carbon dominant species might show different and compensatory responses to environmental change (e.g., response traits diversity). An ecosystem functioning is expected to be less vulnerable to future disturbances when it presents higher functional redundancy, because the function is buffered by other species that perform similar functions (Biggs et al. 2020), and higher response diversity, which ensures that not all species from that particular group nor its functions will be lost after a disturbance (Elmqvist et al. 2003; Mori et al. 2013). So future studies could focus not only on effect traits (carbon stock) but response traits to better understand, quantify and predict the vulnerability of ecosystems functioning (Laliberté et al. 2010; Mouillot et al. 2013; Laughlin 2014).

Conversely, we found that the vulnerability of carbon-dominant species was not driven by any predictor (**Fig. 9**f). This means that most part of species/functions that disproportionally contributes for maintaining carbon stocks are resilient to the external agents addressed here and their vulnerability is not affected during forest succession. This suggest that the use of this group of species should be favored while planning and managing forest restoration.

Implications for carbon mitigation efforts

Here, we provided a comprehensive assessment of the main drivers of carbon stocks, functional composition and vulnerability of Brazilian Atlantic Forest with important implications for nature-based solutions to mitigate climate changes. Our study showed that even second-growth forest located in highly fragmented human-driven landscapes can contain important species for ecosystem functioning and carbon storage, offering potential opportunities for co-benefits under existing carbon markets. Also, we found that few carbon-dominant species (11% of total number of species) contributed 58% (28.9 Mg C ha^{-1}) of the total carbon stock while the non-carbon dominant species (89% of species community) contributed 42% (21.2 Mg C ha^{-1}), showing that these few large-sized species can play a more prominent role in forest carbon stock than those abundant smaller-sized species (see also Rodrigues et al., 2023; Slik et al., 2013). This also shows that the non-carbon dominant species matter for ecosystem functioning as their individuals dominate these forests (67% tree community) (Lohbeck et al. 2016). Yet, functional composition of carbon-dominant species can be particularly affected by water stress (**Fig. 9**b,c,d; see also Bennett et al., 2015), so based on the scenario of climate change in tropical forest predict severe droughts (IPCC 2023), we may expect potentially large shifts in the distribution of carbon-dominant trees. Hence, this climate dependence of tree community composition should be taken into account in restoration efforts to meet global commitments for forest restoration and climate change mitigation. Our findings suggest that it is crucial to carefully assess the site-specific conditions and select appropriate tree species that can thrive and sequester carbon efficiently in order to achieve effective carbon mitigation through reforestation efforts.

5. Conclusions

Here we provide a comprehensive picture of how stand age, landscape structure, seasonal water availability, and soil properties predict tree aboveground carbon stock, functional composition, redundancy and vulnerability in second-growth Atlantic forests. The successional status and edaphic factors were the main predictors of carbon stock and vulnerability in these forests, while resource availability, such as water and soil nitrogen and carbon, and soil texture were the main drivers of species growth. We also show that Atlantic forests located in highly fragmented and deforested landscapes can harbor carbon-dominant tree species, which were not vulnerable to the predictors studied here. This shows that these carbon-dominant species should be preferred in forest management and restoration efforts. Future research could focus on the role of other factors such as topography, soil phosphorous and matrix quality (e.g., different types of land uses) in predicting forest functional composition and vulnerability, and check for vulnerability thresholds. Our findings advances our understanding on the factors that drive carbon stock and vulnerability in second-growth Atlantic forests and highlight the importance of considering local site conditions to safeguard forest functioning and meet global commitments for forest restoration and climate change mitigation.

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Supplementary material (Appendix) for Safar et al.; Forest succession and edaphic factors drive carbon stock and functional vulnerability in Brazilian Atlantic rainforests.

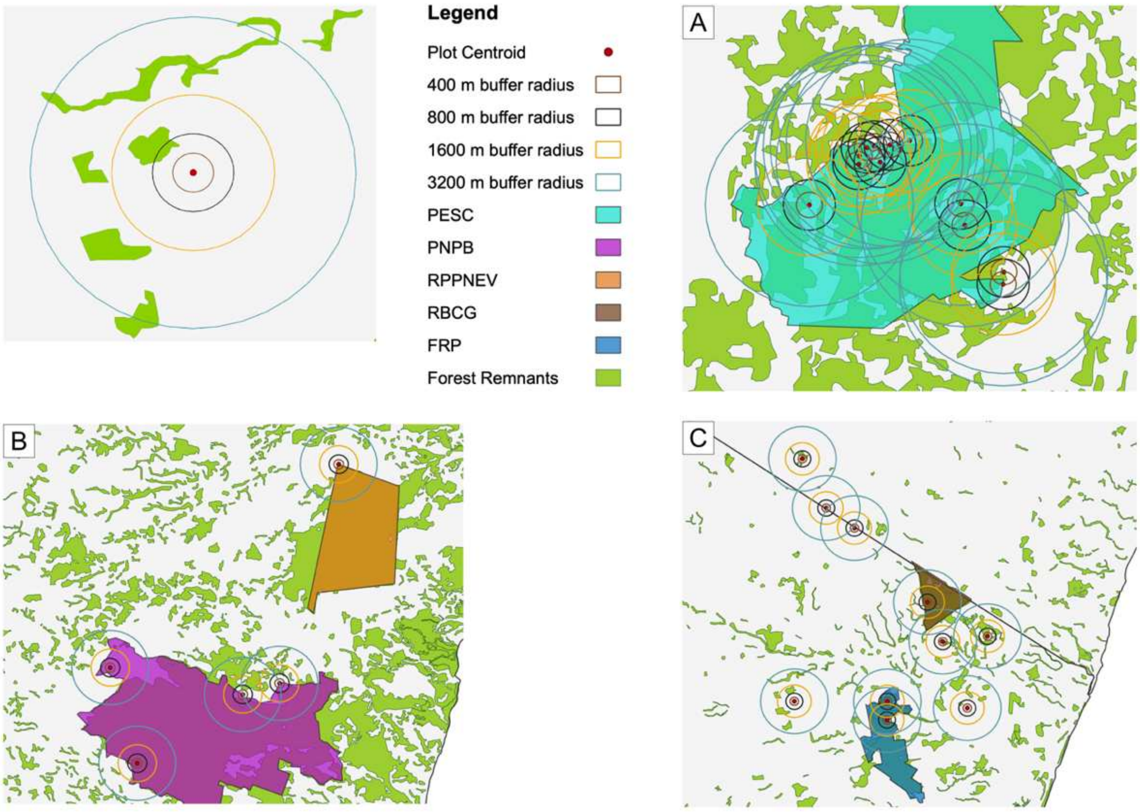

Fig. S1 Landscape buffer overlaps within each buffer size (400, 800, 1600 and 3200-m radius) around plot centroids in three Atlantic forest regions: A (*n* = 12), B (*n* = 5) and C (*n* = 10). Buffer overlaps are higher at larger scales (> 1600-m radius).

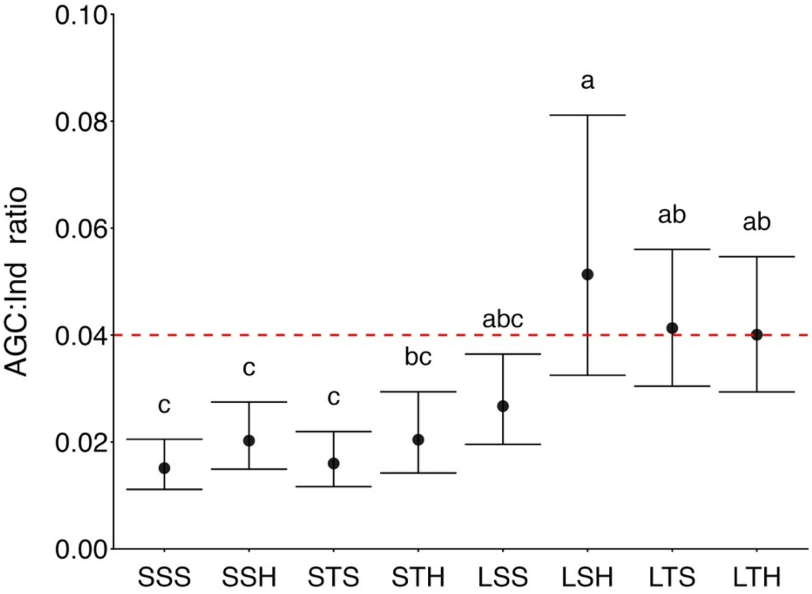

Fig. S2 Variation in the relative contribution of trees to carbon storage per functional entity. Data points represent the mean relative carbon contribution (Mg) within each functional entity and the whiskers indicate the 95% confidence interval. The replication unit used to calculated the means was the contribution per functional entity per plot (*n*=216; 8 functional entities x 27 plots). Differences in mean relative contribution between functional entities were tested using GLM models with natural-logarithm transformed AGC:Ind ratio and the package 'emmeans' (Lenth et al. 2021). Different lower case letters indicate significant differences between functional entity levels at $p < 0.05$. Red dashed line indicates the overall mean relative carbon contribution. SSS = Small, Short, Softwood; SSH = Small, Short, Hardwood; STS = Small, Tall, Softwood; STH = Small, Tall, Hardwood; LSS = Large, Short, Softwood; LSH = Large, Short, Hardwood; LTS = Large, Tall, Softwood; LTH = Large, Tall, Hardwood.

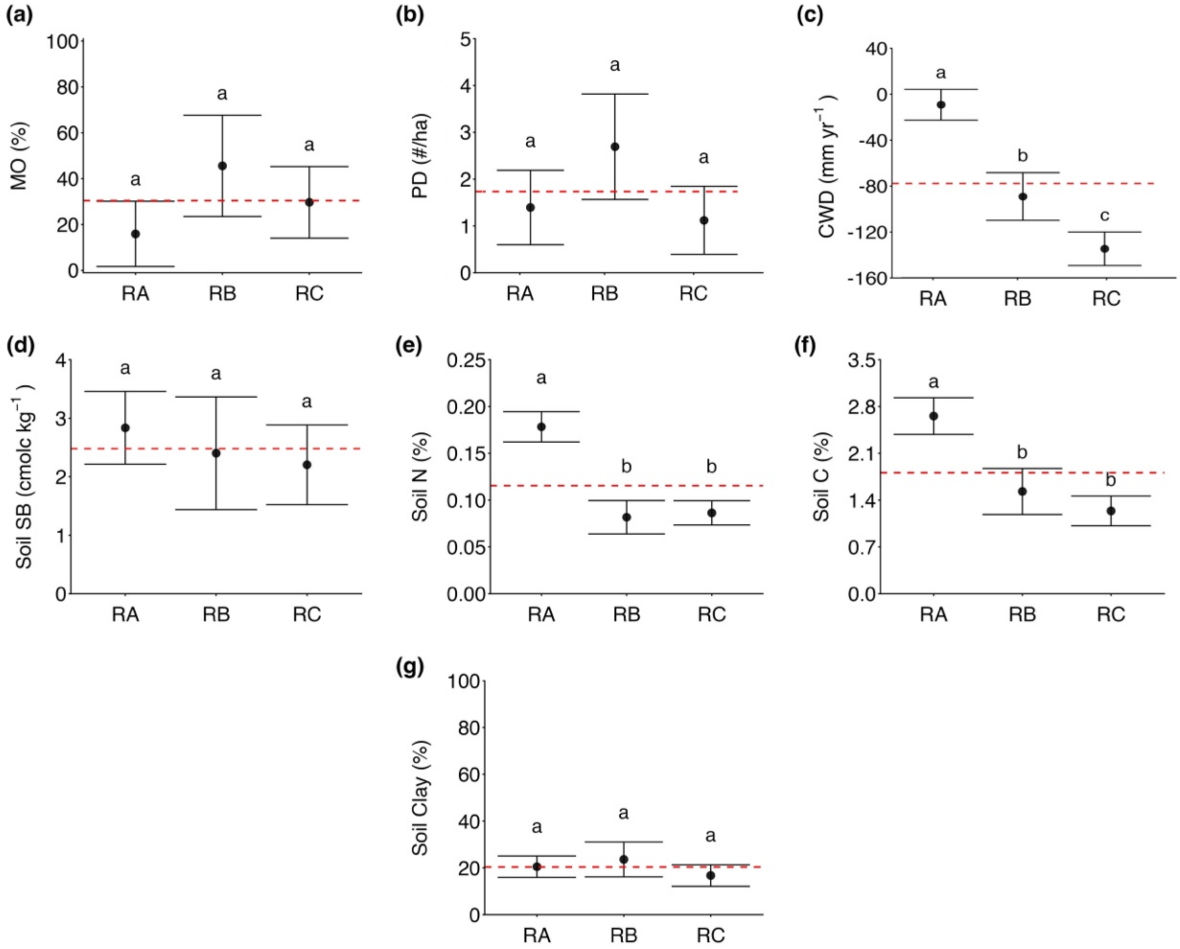

Fig. S3 Variation in the predictors across three different Atlantic forest regions (RA, RB, RC). (a) Matrix Openness, **(b)** Patch Density, **(c)** Climatic Water Deficit, **(d)** Sum of Bases (SB), **(e)** Soil Nitrogen, **(f)** Soil Organic Carbon, **(g)** Soil Clay Content. Data points represent the mean predictor values within each region (A, *n* = 12; B, *n* = 5, C, *n* =10) and the whiskers indicate the 95% confidence interval. Differences in predictor means between regions were tested using the package 'emmeans' (Lenth et al. 2021). Different lower case letters indicate significant differences between functional entity levels at $p < 0.05$. Red dashed line indicates the overall mean values.

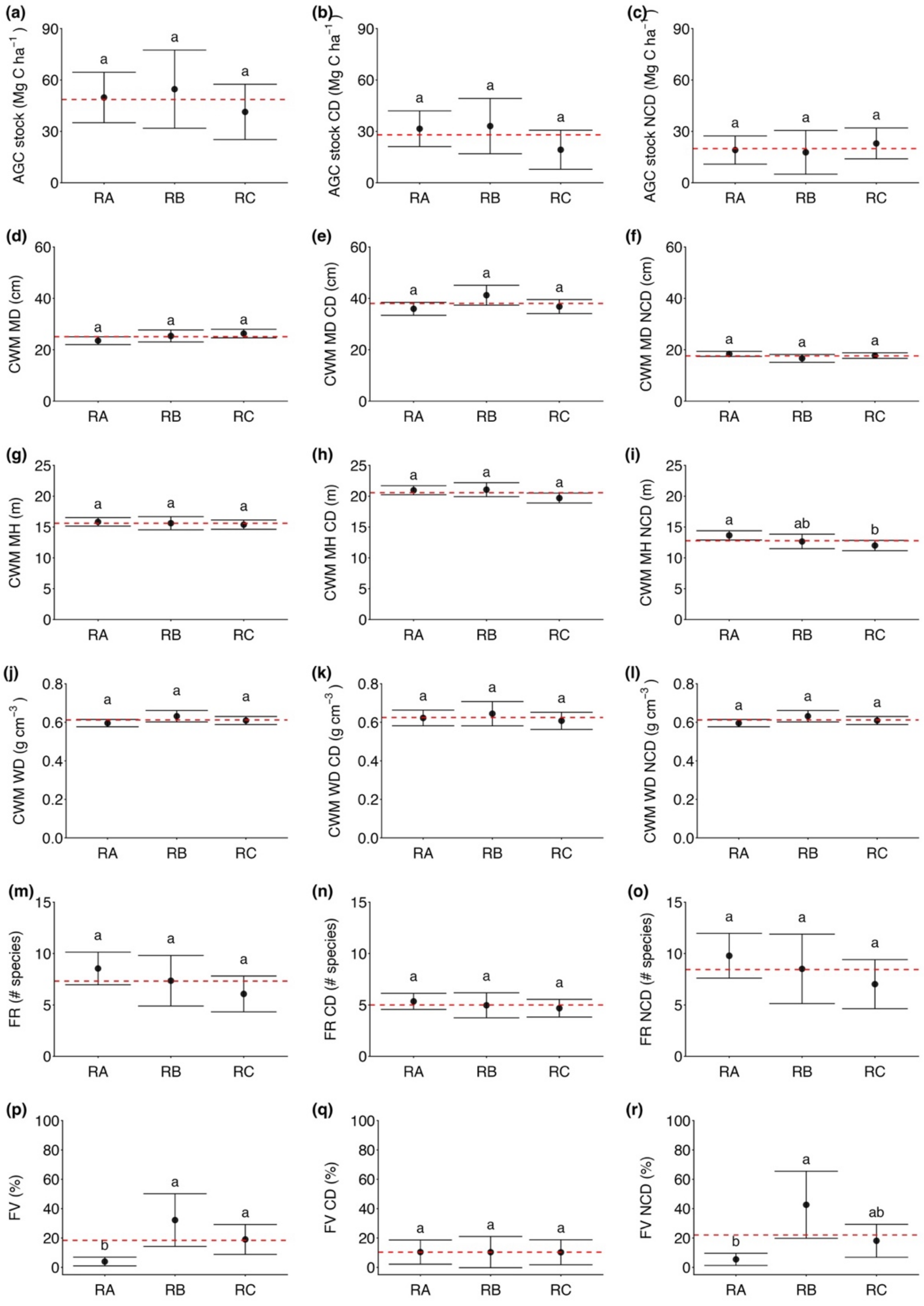

Fig. S4 Variation in the response variables across three different Atlantic forest regions. Data points represent the mean parameter values within each region (A, *n* = 12; B, *n* = 5, C, *n* =10) and the whiskers indicate the 95% confidence interval. Differences in forest attributes means between regions were tested using the package 'emmeans' (Lenth et al. 2021), beta regression distribution for the index variables (FV) and linear regression models for the parametric variables (AGC, MD_{CWM}, MH_{CWM}, WD_{CWM}, FR). Different lower case letters indicate significant differences between regions at $p < 0.05$. Red dashed line indicates the overall mean value. CD = Carbon-dominant tree community, NCD = Non-carbon dominant tree community, AGC = Aboveground Carbon Storage, CWM MD = community weighted-mean maximum stem diameter, CWM MH = community weighted-mean maximum stem height, CWM WD = community weighted-mean wood density, FR = Functional Redundancy, FV = Functional Vulnerability.

References

Lenth R V., Buerkner P, Herve M, et al (2021) Package ‘ emmeans ’: Estimated Marginal Means, aka Least-Squares Means. CRAN Repos.

Table S1 General characteristics of the three studied Atlantic forest regions of Brazil. The landscape metrics were measured in 500,000 hectares square landscapes encompassing all 27 second-growth forest plots.

Parameter	**Region A**	**Region B**	**Region C**
Land use and cover map (year-base)	2007	2020	2017
Altitude (m a.s.l.) [a]	124 - 243	73-114	28-86
Precipitation (mm/year) [a]	1931	1434	1268
Natural forest formation cover (%)	55.24	29.77	10.80
Natural non-forest formation cover (%) [b]	0.10	2.05	1.91
Forest plantation cover (%)	0.01	9.11	17.80
Pasture cover (%)	23.73	40.51	52.33
Agriculture cover (%)	0.01	1.01	2.55
Mosaic of uses cover (%)	9.49	8.8	8.62
Non-vegetated area cover (%) [c]	0.28	1.07	0.44
Water bodies (%) [d]	0.25	0.56	0.58
Open areas in the matrix (%) [e]	43.49	60.96	71.37
Matrix composition	Mainly natural forest formation mixed with cattle pasture	Heterogeneous but dominated by cattle pasture	Mainly cattle pasture and forest plantation
Density of natural forest patches (#/ha)	0.82	1.31	0.82
Maximal forest patch area (ha) [f]	251,578	31,707	3,224
Mean natural forest patch area (ha) [g]	137.40	22.71	13.24
Mean planted forest patch area (ha)	5.79	16.93	45.64
Mean pasture patch area (ha)	45.50	108.9	23.09
Mean distance to nearest forest patch (m)	138.4	123	203.6

[a] Altitude range based on the altitude of each plot centroid. All forest plots in both regions were located in lowland areas (< 600 m asl)

[b] All land cover classes that are natural formations but not forests, such as wetlands, grassland, salt flat, rocky outcrop, herbaceous sandbank vegetation and others. It does not include forest plantation

[c] Includes urban areas, mining, beach, dune and sand spot, and other non-vegetated areas

[d] Includes rivers, lakes, ocean, and aquaculture

[e] All land use and cover classes that are not natural forests (forest formation, savanna formation, mangrove, wooded sandbank vegetation) or forest plantations

[f] The minimum and maximum area of natural forest patches in hectares.

[g] Mean natural forest patch area and standard deviation

Table S2 Details of the 27 second-growth forest plots located in the Atlantic forest Domain. ES = Espírito Santo State; BA = Bahia State; RBCG = Reserva Biológica do Córrego Grande; FNRP = Floresta Nacional do Rio Preto; PNPB = Parque Nacional do Pau Brasil; RPPNEV = Reserva Particular do Patrimônio Natural Estação Veracel; PESC = Parque Estadual da Serra do Conduru.

Plot	**Stand Age (yr)**	**Disturbance type**	**Geographic Coordinates**	**Region**	**Location**	**Sampling period**
A3	28	fire	-18.3015, -39.8017	C	Close to RBCG	2017
A6	26	clearcut	-18.2001, -39.8802	C	Close to RBCG	2017
A7	29	fire	-18.2967, -39.7612	C	Close to RBCG	2017
A8	28	fire	-18.266, -39.8149	C	RBCG	2017
A9	14	pasture	-18.3608, -39.7793	C	Close to RBCG	2017
A11	28	fire	-18.3715, -39.8510	C	FNRP	2017
A12	28	fire	-18.3549, -39.8509	C	FNRP	2017
A13	20	clearcut	-18.3548, -39.9340	C	Close to FNRP	2017
A15	20	pasture	-18.1383, -39.9268	C	Close to RBCG	2017
A17	27	clearcut	-18.1822, -39.9055	C	Close to RBCG	2017
A19	22	fire	-16.4478, -39.3319	B	PNPB	2020
A20	18	fire	-16.4599, -39.1998	B	PNPB	2020
A21	26	fire	-16.2895, -39.1537	B	RPPNEV	2020
A24	24	fire	-16.4687, -39.2285	B	PNPB	2020
A25	17	fire	-16.5222, -39.3108	B	PNPB	2020

A56	40	Slash-and-burn. One rotation of manioc	-14.5048, -39.0922	A	PESC	2007
A57	25	Slash-and-burn. One rotation of manioc	-14.4987, -39.0934	A	PESC	2007
A58	10	Slash-and-burn. One rotation of manioc	-14.4990, -39.1366	A	PESC	2007
A59	10	Slash-and-burn. One rotation of manioc	-14.4819, -39.1136	A	PESC	2007
A60	10	Slash-and-burn. One rotation of manioc	-14.4868, -39.1164	A	PESC	2007
A61	40	Slash-and-burn. One rotation of manioc	-14.4807, -39.1080	A	PESC	2007
A62	40	Slash-and-burn. One rotation of manioc	-14.4823, -39.1181	A	PESC	2007
A63	10	Slash-and-burn. One rotation of manioc	-14.4851, -39.1224	A	PESC	2007
A64	40	Slash-and-burn. One rotation of manioc	-14.4874, -39.1225	A	PESC	2007
A65	25	Slash-and-burn. One rotation of manioc	-14.4827, -39.1201	A	PESC	2007
A66	25	Slash-and-burn. One rotation of manioc	-14.5216, -39.0813	A	PESC	2007
A67	25	Slash-and-burn. One rotation of manioc	-14.5181, -39.0811	A	PESC	2007

Table S3 List of 473 identified tree species recorded in the 27 second-growth forest plots located in northern Espírito Santo State and southern Bahia State, Brazil, and the traits used in this study. SSS = Small, Short, Softwood; SSH = Small, Short, Hardwood; STS = Small, Tall, Softwood; STH = Small, Tall, Hardwood; LSS = Large, Short, Softwood; LSH = Large, Short, Hardwood; LTS = Large, Tall, Softwood; LTH = Large, Tall, Hardwood.

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Achariaceae	*Carpotroche brasiliensis*	12.03	10.62	0.45	SSS
Anacardiaceae	*Astronium concinnum*	37.44	16.06	0.825	LTH
Anacardiaceae	*Astronium graveolens*	27.06	16.63	0.818	LTH
Anacardiaceae	*Schinus terebinthifolia*	10.5	9.8	0.82	SSH
Anacardiaceae	*Tapirira guianensis*	51.1	18.94	0.457	LTS
Anacardiaceae	*Thyrsodium spruceanum*	24.4	14.24	0.54	LSS
Annonaceae	*Annona acutiflora*	8.76	9	0.424	SSS
Annonaceae	*Annona bahiensis*	16.7	12	0.424	SSS
Annonaceae	*Annona cacans*	17.86	14.33	0.424	SSS
Annonaceae	*Annona dolabripetala*	30.88	19.29	0.424	LTS
Annonaceae	*Annona salzmannii*	30.5	15	0.424	LSS
Annonaceae	*Indet sp*	12	12	0.569	SSS
Annonaceae	*Duguetia bahiensis*	8.5	9	0.747	SSH
Annonaceae	*Duguetia chrysocarpa*	8.18	7.1	0.747	SSH
Annonaceae	*Guatteria australis*	16.74	13.14	0.555	SSS
Annonaceae	*Guatteria candolleana*	19.2	18	0.555	STS
Annonaceae	*Guatteria ferruginea*	9.77	10	0.555	SSS
Annonaceae	*Guatteria oligocarpa*	8.5	15	0.555	SSS
Annonaceae	*Guatteria pogonopus*	6	5	0.555	SSS
Annonaceae	*Guatteria sellowiana*	17.95	13.4	0.555	SSS
Annonaceae	*Guatteria sp*	11	16	0.555	SSS
Annonaceae	*Pseudoxandra spiritus-sancti*	5.25	6.36	0.37	SSS
Annonaceae	*Xylopia frutescens*	27.75	18.41	0.58	LTS
Annonaceae	*Xylopia ochrantha*	5.4	8	0.579	SSS
Apocynaceae	*Aspidosperma discolor*	24.2	19	0.758	LTH
Apocynaceae	*Aspidosperma pyricollum*	10.41	10.52	0.741	SSH
Apocynaceae	*Aspidosperma spruceanum*	11.9	18	0.753	STH

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Apocynaceae	*Aspidosperma thomasii*	18.2	15	0.741	SSH
Apocynaceae	*Forsteronia sp*	6.8	9	0.554	SSS
Apocynaceae	*Geissospermum laeve*	13.75	8	0.782	SSH
Apocynaceae	*Himatanthus bracteatus*	20.37	18	0.53	STS
Apocynaceae	*Lacmellea aculeata*	7.9	10	0.527	SSS
Apocynaceae	*Malouetia cestroides*	15.63	13.4	0.5	SSS
Apocynaceae	*Rauvolfia bahiensis*	5.5	2.5	0.505	SSS
Apocynaceae	*Rauvolfia capixabae*	12.96	11.91	0.505	SSS
Apocynaceae	*Tabernaemontana salzmannii*	15.5	12	0.462	SSS
Apocynaceae	*Tabernaemontana sp*	7	6	0.462	SSS
Aquifoliaceae	*Ilex theezans*	15.1	14	0.528	SSS
Araliaceae	*Didymopanax morototoni*	26.96	18	0.575	LTS
Arecaceae	*Allagoptera caudescens*	16.49	10	0.441	SSS
Arecaceae	*Astrocaryum aculeatissimum*	20.03	6.5	0.508	SSS
Arecaceae	*Attalea burretiana*	44.56	7	0.326	LSS
Arecaceae	*Attalea funifera*	25.5	15	0.326	LSS
Arecaceae	*Bactris ferruginea*	10.8	12	0.441	SSS
Arecaceae	*Elaeis guineensis*	47.75	22.51	0.441	LTS
Arecaceae	*Euterpe edulis*	9.4	12	0.407	SSS
Arecaceae	*Syagrus botryophora*	60	15	0.441	LSS
Asteraceae	*Baccharis calvescens*	9	4	0.505	SSS
Asteraceae	*Baccharis reticularia*	6.14	7.04	0.505	SSS
Asteraceae	*Vernonanthura divaricata*	22	15	0.54	SSS
Bignoniaceae	*Handroanthus chrysotrichus*	6.68	5.5	0.57	SSS
Bignoniaceae	*Handroanthus serratifolius*	11.62	10.99	0.57	SSS
Bignoniaceae	*Handroanthus sp*	9.74	9.45	0.57	SSS
Bignoniaceae	*Jacaranda macrantha*	6	7	0.395	SSS
Bignoniaceae	*Jacaranda puberula*	10.36	6.67	0.395	SSS
Bignoniaceae	*Sparattosperma leucanthum*	41.18	21.32	0.57	LTS
Bignoniaceae	*Tabebuia cassinoides*	21.5	20	0.768	STH
Bignoniaceae	*Tabebuia elliptica*	12	12	0.768	SSH
Boraginaceae	*Cordia ecalyculata*	24.5	18	0.487	LTS
Boraginaceae	*Cordia nodosa*	16.5	18	0.39	STS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Boraginaceae	*Cordia sellowiana*	11.9	8.5	0.487	SSS
Boraginaceae	*Cordia sp1*	14	12	0.487	SSS
Boraginaceae	*Cordia sp2*	14.3	13	0.487	SSS
Boraginaceae	*Cordia trichoclada*	5.47	6.55	0.487	SSS
Burseraceae	*Protium atlanticum*	6.46	7.5	0.554	SSS
Burseraceae	*Protium heptaphyllum subsp. heptaphyllum*	24.81	17.34	0.629	LTS
Burseraceae	*Protium icicariba*	26.8	15	0.554	LSS
Burseraceae	*Protium sp*	18.6	18	0.554	STS
Burseraceae	*Protium warmingianum*	28.01	22	0.554	LTS
Calophyllaceae	*Kielmeyera itacarensis*	18.4	12	0.673	SSS
Calophyllaceae	*Calophyllum brasiliense*	5.5	12	0.594	SSS
Cardiopteridaceae	*Citronella paniculata*	9.55	9.26	0.635	SSS
Caryocaraceae	*Caryocar edule*	8.63	7.5	0.693	SSS
Celastraceae	*Monteverdia cestrifolia*	6.84	7.53	0.745	SSH
Celastraceae	*Monteverdia distichophylla*	5.7	8	0.745	SSH
Celastraceae	*Monteverdia sp*	9	12	0.745	SSH
Chrysobalanaceae	*Indet sp*	24	19	0.783	LTH
Chrysobalanaceae	*Couepia impressa*	12	12	0.805	SSH
Chrysobalanaceae	*Couepia schottii*	9.55	9.28	0.805	SSH
Chrysobalanaceae	*Hirtella bahiensis*	12.2	12	0.796	SSH
Chrysobalanaceae	*Hirtella gracilipes*	5.1	8	0.796	SSH
Chrysobalanaceae	*Hirtella hebeclada*	5.19	8.5	0.796	SSH
Chrysobalanaceae	*Hirtella insignis*	7	5	0.796	SSH
Chrysobalanaceae	*Hirtella triandra*	12	10	0.71	SSH
Chrysobalanaceae	*Licania belemii*	18.5	18	0.829	STH
Chrysobalanaceae	*Licania kunthiana*	25.22	15.06	0.88	LSH
Chrysobalanaceae	*Licania lamentanda*	10.5	15	0.829	SSH
Chrysobalanaceae	*Licania littoralis*	11.9	12	0.829	SSH
Chrysobalanaceae	*Licania sp*	28.81	17.36	0.829	LTH
Chrysobalanaceae	*Parinari alvimii*	8.3	13	0.702	SSH
Chrysobalanaceae	*Parinari parvifolia*	29.7	18.25	0.702	LTH
Clusiaceae	*Garcinia gardneriana*	18.3	18	0.657	STS
Clusiaceae	*Garcinia macrophylla*	5.3	5	0.67	SSS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Clusiaceae	*Tovomita choisyana*	8.5	8	0.58	SSS
Clusiaceae	*Tovomita guianensis*	11.11	10.14	0.6	SSS
Clusiaceae	*Tovomita mangle*	17.1	15	0.695	SSS
Combretaceae	*Terminalia glabrescens*	11.9	10.56	0.682	SSS
Combretaceae	*Terminalia grandis*	16.5	14	0.682	SSS
Dichapetalaceae	*Stephanopodium blanchetianum*	6.6	9	0.64	SSS
Ebenaceae	*Diospyros lasiocalyx*	18.74	7	0.578	SSS
Elaeocarpaceae	*Sloanea garckeana*	7.14	7.76	0.786	SSH
Elaeocarpaceae	*Sloanea guianensis*	16.7	18	0.821	STH
Elaeocarpaceae	*Sloanea hirsuta*	6	8	0.786	SSH
Elaeocarpaceae	*Sloanea sinemariensis*	12.1	9	0.786	SSH
Erythropalaceae	*Heisteria ovata*	15.85	12.58	0.54	SSS
Erythropalaceae	*Heisteria perianthomega*	18.5	18	0.704	STH
Erythroxylaceae	*Erythroxylum sp*	5.5	5	0.71	SSH
Euphorbiaceae	*Actinostemon concolor*	16.5	10	0.52	SSS
Euphorbiaceae	*Alchornea glandulosa*	14.8	14	0.373	SSS
Euphorbiaceae	*Aparisthmium cordatum*	7.35	7.88	0.39	SSS
Euphorbiaceae	*Brasiliocroton mamoninha*	5.73	6.67	0.52	SSS
Euphorbiaceae	*Croton floribundus*	34	20	0.407	LTS
Euphorbiaceae	*Croton macrobothrys*	11	5	0.407	SSS
Euphorbiaceae	*Joannesia princeps*	44.24	21.47	0.39	LTS
Euphorbiaceae	*Mabea piriri*	11.7	13	0.598	SSS
Euphorbiaceae	*Pausandra morisiana*	8	8	0.59	SSS
Euphorbiaceae	*Sapium glandulosum*	6.68	7.44	0.415	SSS
Euphorbiaceae	*Senefeldera verticillata*	23.59	13	0.78	SSH
Euphorbiaceae	*Tetrorchidium rubrivenium*	10.5	10	0.52	SSS
Fabaceae	*Abarema turbinata*	10.7	12	0.585	SSS
Fabaceae	*Albizia pedicellaris*	41.54	21.16	0.532	LTS
Fabaceae	*Albizia polycephala*	26.32	9.54	0.532	LSS
Fabaceae	*Andira anthelmia*	6.31	7.31	0.754	SSH
Fabaceae	*Andira fraxinifolia*	16.92	8.5	0.754	SSH
Fabaceae	*Andira legalis*	10.5	15	0.754	SSH
Fabaceae	*Arapatiella psilophylla*	24.92	16.04	0.696	LTS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Fabaceae	*Bauhinia forficata*	14.16	8.4	0.6	SSS
Fabaceae	*Bauhinia ovata*	9.7	12	0.6	SSS
Fabaceae	*Centrolobium tomentosum*	7.61	8.12	0.58	SSS
Fabaceae	*Chamaecrista apoucouita*	16.9	12	0.924	SSH
Fabaceae	*Chamaecrista duartei*	30	18	0.904	LTH
Fabaceae	*Chamaecrista ensiformis*	37.47	8.5	0.904	LSH
Fabaceae	*Dialium guianense*	10.95	10.78	0.867	SSH
Fabaceae	*Dimorphandra jorgei*	12.1	10.67	0.774	SSH
Fabaceae	*Diplotropis incexis*	25.62	28	0.706	LTH
Fabaceae	*Indet sp1*	6.05	7.54	0.696	SSS
Fabaceae	*Indet sp3*	14	12	0.696	SSS
Fabaceae	*Indet sp4*	11.3	10	0.696	SSS
Fabaceae	*Indet sp5*	18.1	12	0.696	SSS
Fabaceae	*Goniorrhachis marginata*	10.28	7	0.696	SSS
Fabaceae	*Harleyodendron unifoliolatum*	11	9	0.696	SSS
Fabaceae	*Hymenolobium janeirense*	16.55	12.83	0.651	SSS
Fabaceae	*Inga blanchetiana*	7.5	13	0.581	SSS
Fabaceae	*Inga capitata*	8	10	0.592	SSS
Fabaceae	*Inga cylindrica*	46.1	22.3	0.581	LTS
Fabaceae	*Inga flagelliformis*	18.33	14.54	0.581	SSS
Fabaceae	*Inga hispida*	17.17	12.95	0.581	SSS
Fabaceae	*Inga laurina*	12.9	9	0.62	SSS
Fabaceae	*Inga pleiogyna*	5	3.5	0.581	SSS
Fabaceae	*Inga striata*	10.09	12	0.581	SSS
Fabaceae	*Inga subnuda subsp. subnuda*	22.92	14.56	0.581	SSS
Fabaceae	*Inga subnuda subsp. luschnathiana*	16	13	0.581	SSS
Fabaceae	*Inga tenuis*	5	6	0.581	SSS
Fabaceae	*Inga thibaudiana subsp. thibaudiana*	20.5	20	0.581	STS
Fabaceae	*Inga unica*	12.08	10.87	0.581	SSS
Fabaceae	*Lonchocarpus cultratus*	19.19	14.15	0.707	SSH
Fabaceae	*Machaerium fulvovenosum*	16.36	8	0.495	SSS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Fabaceae	*Machaerium ovalifolium*	12.57	10.9	0.495	SSS
Fabaceae	*Machaerium sp*	12.4	4.5	0.495	SSS
Fabaceae	*Macrolobium latifolium*	16	14	0.614	SSS
Fabaceae	*Melanoxylon brauna*	53.48	23.86	0.9	LTH
Fabaceae	*Moldenhawera blanchetiana*	5.1	14	0.696	SSS
Fabaceae	*Ormosia arborea*	9.33	8.06	0.608	SSS
Fabaceae	*Ormosia nitida*	12.73	11.02	0.608	SSS
Fabaceae	*Parapiptadenia pterosperma*	13.53	7.5	0.74	SSH
Fabaceae	*Parkia pendula*	10.5	13	0.521	SSS
Fabaceae	*Piptadenia paniculata*	16.94	12.99	0.747	SSH
Fabaceae	*Pterocarpus rohrii*	20.37	15.4	0.427	SSS
Fabaceae	*Swartzia apetala var. apetala*	11.46	10.36	0.842	SSH
Fabaceae	*Swartzia apetala var. glabra*	13.69	4.5	0.842	SSH
Fabaceae	*Swartzia euxylophora*	10.65	9.91	0.65	SSS
Fabaceae	*Swartzia flaemingii*	23.5	15	0.842	SSH
Fabaceae	*Swartzia linharensis*	19.37	14.01	0.842	SSH
Fabaceae	*Swartzia macrostachya*	6.5	8	0.842	SSH
Fabaceae	*Swartzia myrtifolia*	5	4	0.842	SSH
Fabaceae	*Swartzia reticulata*	15.4	18	0.842	STH
Fabaceae	*Swartzia simplex var. continentalis*	10.95	12	0.842	SSH
Fabaceae	*Swartzia sp*	22.25	12	0.842	SSH
Fabaceae	*Sweetia fruticosa*	8.46	8.52	0.68	SSS
Fabaceae	*Tachigali densiflora*	39.1	20	0.583	LTS
Fabaceae	*Vatairea heteroptera*	7.67	8	0.662	SSS
Fabaceae	*Zollernia ilicifolia*	23.78	15.97	1.05	LSH
Humiriaceae	*Humiriastrum dentatum*	5.63	6.68	0.69	SSS
Humiriaceae	*Humiriastrum sp*	5.5	4	0.69	SSS
Hypericaceae	*Vismia guianensis*	36	25	0.475	LTS
Hypericaceae	*Vismia latifolia*	13	12	0.43	SSS
Hypericaceae	*Vismia martiana*	17.79	13.33	0.464	SSS
Lacistemataceae	*Lacistema aggregatum*	11.17	10.17	0.51	SSS
Lacistemataceae	*Lacistema robustum*	14.7	14	0.514	SSS
Lamiaceae	*Aegiphila integrifolia*	7	10	0.86	SSH

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Lamiaceae	*Vitex orinocensis*	19.7	18	0.527	STS
Lauraceae	*Aniba firmula*	17.84	13.33	0.593	SSS
Lauraceae	*Aniba intermedia*	8.4	17	0.593	STS
Lauraceae	*Aniba sp*	5.86	6.88	0.593	SSS
Lauraceae	*Endlicheria glomerata*	9.42	9.18	0.501	SSS
Lauraceae	*Endlicheria paniculata*	10.2	14	0.682	SSS
Lauraceae	*Endlicheria sp*	5.7	9	0.5	SSS
Lauraceae	*Indet sp2*	5.57	9	0.558	SSS
Lauraceae	*Indet sp3*	6.3	7	0.558	SSS
Lauraceae	*Indet sp6*	7	12	0.558	SSS
Lauraceae	*Licaria bahiana*	12	8	0.773	SSH
Lauraceae	*Licaria guianensis*	19.09	13.85	0.748	SSH
Lauraceae	*Ocotea beulahiae*	11.55	10.38	0.519	SSS
Lauraceae	*Ocotea cernua*	5.2	6	0.32	SSS
Lauraceae	*Ocotea confertiflora*	8.44	7.35	0.519	SSS
Lauraceae	*Ocotea daphnifolia*	5.1	9	0.519	SSS
Lauraceae	*Ocotea deflexa*	8.3	15	0.519	SSS
Lauraceae	*Ocotea divaricata*	17.52	13.32	0.519	SSS
Lauraceae	*Ocotea glauca*	6.3	9	0.519	SSS
Lauraceae	*Ocotea glomerata*	12	12	0.508	SSS
Lauraceae	*Ocotea indecora*	29.2	18	0.519	LTS
Lauraceae	*Ocotea kostermanniana*	16.6	15	0.519	SSS
Lauraceae	*Ocotea lancifolia*	5.8	13	0.519	SSS
Lauraceae	*Ocotea longifolia*	28.2	14	0.519	LSS
Lauraceae	*Ocotea mosenii*	16.7	12.89	0.519	SSS
Lauraceae	*Ocotea neesiana*	12.69	11	0.55	SSS
Lauraceae	*Ocotea nitida*	5.91	16	0.519	SSS
Lauraceae	*Ocotea notata*	6.5	12	0.519	SSS
Lauraceae	*Ocotea nutans*	11	14	0.519	SSS
Lauraceae	*Ocotea pluridomatiata*	19.68	14.14	0.519	SSS
Lauraceae	*Ocotea prolifera*	8.65	6	0.519	SSS
Lauraceae	*Ocotea puberula*	13.6	16	0.455	SSS
Lauraceae	*Ocotea sp3*	16.52	12.57	0.519	SSS
Lauraceae	*Ocotea sp5*	5.1	8	0.519	SSS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Lauraceae	*Ocotea sp6*	9.5	12	0.519	SSS
Lauraceae	*Ocotea spectabilis*	6.75	7.47	0.519	SSS
Lauraceae	*Ocotea velutina*	7.96	8.21	0.519	SSS
Lauraceae	*Persea caesia*	11.6	14	0.451	SSS
Lauraceae	*Rhodostemonodaphne sp*	15	18	0.395	STS
Lecythidaceae	*Cariniana estrellensis*	14.64	11.82	0.565	SSS
Lecythidaceae	*Cariniana legalis*	6.14	3	0.483	SSS
Lecythidaceae	*Cariniana parvifolia*	7.42	7	0.548	SSS
Lecythidaceae	*Couratari macrosperma*	17.1	12.92	0.67	SSS
Lecythidaceae	*Eschweilera ovata*	75.12	27.97	0.9	LTH
Lecythidaceae	*Lecythis lanceolata*	15.13	12.25	0.817	SSH
Lecythidaceae	*Lecythis lurida*	18	20	0.83	STH
Lecythidaceae	*Lecythis pisonis*	10.5	10	0.852	SSH
Lecythidaceae	*Lecythis sp*	15.57	12.36	0.817	SSH
Linaceae	*Roucheria columbiana*	10.2	13	0.77	SSH
Malpighiaceae	*Byrsonima crispa*	22.3	15.15	0.58	SSS
Malpighiaceae	*Byrsonima sericea*	28.55	18.5	0.629	LTS
Malpighiaceae	*Byrsonima sp*	7	9	0.629	SSS
Malpighiaceae	*Byrsonima stipulacea*	32.87	15.5	0.709	LSH
Malvaceae	*Apeiba albiflora*	9.5	12	0.239	SSS
Malvaceae	*Apeiba tibourbou*	15.5	12	0.2	SSS
Malvaceae	*Eriotheca globosa*	25.7	18	0.41	LTS
Malvaceae	*Eriotheca macrophylla*	27.1	22	0.441	LTS
Malvaceae	*Hydrogaster trinervis*	9.1	9.7	0.437	SSS
Malvaceae	*Luehea mediterranea*	46.45	22.65	0.507	LTS
Malvaceae	*Pachira endecaphylla*	9.39	9	0.49	SSS
Malvaceae	*Pavonia morii*	6.5	8	0.437	SSS
Malvaceae	*Pseudobombax majus*	43	15	0.293	LSS
Malvaceae	*Sterculia excelsa*	17.63	13	0.51	SSS
Melastomataceae	*Henriettea succosa*	32.5	12.12	0.69	LSS
Melastomataceae	*Miconia cinnamomifolia*	24.22	14.05	0.623	LSS
Melastomataceae	*Miconia lurida*	30.8	18	0.623	LTS
Melastomataceae	*Miconia mirabilis*	17.3	10	0.603	SSS
Melastomataceae	*Miconia prasina*	6.97	7.62	0.71	SSH

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Melastomataceae	*Miconia pyrifolia*	19	15	0.623	SSS
Melastomataceae	*Tibouchina sp*	23.5	20	0.624	STS
Meliaceae	*Cedrela odorata*	6.5	8	0.427	SSS
Meliaceae	*Guarea blanchetii*	5.1	4	0.632	SSS
Meliaceae	*Guarea guidonia*	10.7	12	0.548	SSS
Meliaceae	*Trichilia lepidota subsp. schumanniana*	16.2	14	0.651	SSS
Meliaceae	*Trichilia ramalhoi*	9.8	10	0.651	SSS
Meliaceae	*Trichilia sp*	6.2	12	0.651	SSS
Metteniusaceae	*Emmotum nitens*	28.01	18.27	0.7265	LTH
Monimiaceae	*Mollinedia lamprophylla*	5.16	6.34	0.665	SSS
Moraceae	*Brosimum glaucum*	15.49	12.44	0.658	SSS
Moraceae	*Brosimum glaziovii*	20.68	12	0.658	SSS
Moraceae	*Brosimum guianense*	11	20	0.844	STH
Moraceae	*Brosimum rubescens*	20.5	20	0.825	STH
Moraceae	*Clarisia ilicifolia*	6.98	4.5	0.53	SSS
Moraceae	*Clarisia racemosa*	7.16	8	0.585	SSS
Moraceae	*Ficus arpazusa*	6.5	8	0.396	SSS
Moraceae	*Ficus bahiensis*	11.7	10	0.396	SSS
Moraceae	*Ficus gomelleira*	56.98	24.55	0.396	LTS
Moraceae	*Ficus pulchella*	27.31	16.87	0.396	LTS
Moraceae	*Ficus sp1*	7.92	8.28	0.396	SSS
Moraceae	*Ficus sp2*	32.5	15	0.396	LSS
Moraceae	*Helicostylis tomentosa*	9.5	14	0.627	SSS
Moraceae	*Sorocea guilleminiana*	20.37	10.46	0.578	SSS
Myristicaceae	*Virola gardneri*	15.82	14	0.45	SSS
Myristicaceae	*Virola officinalis*	34.12	14.38	0.478	LSS
Myrtaceae	*Campomanesia guazumifolia*	30.81	17.82	0.73	LTH
Myrtaceae	*Campomanesia lineatifolia*	19.75	14.25	0.73	SSH
Myrtaceae	*Campomanesia sp*	13.5	13	0.73	SSH
Myrtaceae	*Eugenia ayacuchae*	5.3	6	0.722	SSH
Myrtaceae	*Eugenia beaurepairiana*	11.25	7	0.722	SSH
Myrtaceae	*Eugenia fusca*	7.19	6.5	0.722	SSH
Myrtaceae	*Eugenia itacarensis*	9.5	12.5	0.722	SSH

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Myrtaceae	*Eugenia longifolia*	7.2	12.5	0.722	SSH
Myrtaceae	*Eugenia macrosperma*	8.91	5	0.722	SSH
Myrtaceae	*Eugenia mandioccensis*	6.5	9	0.722	SSH
Myrtaceae	*Eugenia melanogyna*	8.28	8.48	0.722	SSH
Myrtaceae	*Eugenia pisiformis*	12.73	8	0.722	SSH
Myrtaceae	*Eugenia platyphylla*	10.28	9.67	0.722	SSH
Myrtaceae	*Eugenia pruniformis*	9	10	0.722	SSH
Myrtaceae	*Eugenia sp2*	14.53	9	0.722	SSH
Myrtaceae	*Eugenia sp5*	7.5	10	0.722	SSH
Myrtaceae	*Eugenia zuccarinii*	10.5	12	0.722	SSH
Myrtaceae	*Myrcia amazonica*	14.3	11.66	0.82	SSH
Myrtaceae	*Myrcia amplexicaulis*	7.2	14	0.807	SSH
Myrtaceae	*Myrcia excoriata*	20.2	14	0.807	SSH
Myrtaceae	*Myrcia gigantea*	7.8	14	0.807	SSH
Myrtaceae	*Myrcia grandifolia*	6.72	7.45	0.807	SSH
Myrtaceae	*Myrcia loranthifolia*	11	14	0.807	SSH
Myrtaceae	*Myrcia neoblanchetiana*	14.8	18	0.807	STH
Myrtaceae	*Myrcia neoregeliana*	6.5	12	0.807	SSH
Myrtaceae	*Myrcia pubiflora*	10.9	12	0.807	SSH
Myrtaceae	*Myrcia pubipetala*	9.6	10	0.807	SSH
Myrtaceae	*Myrcia racemosa*	8.3	13	0.807	SSH
Myrtaceae	*Myrcia sp2*	5.5	6	0.807	SSH
Myrtaceae	*Myrcia sp3*	6.8	8	0.807	SSH
Myrtaceae	*Myrcia sp4*	5.7	12	0.807	SSH
Myrtaceae	*Myrcia sp5*	5.2	8	0.807	SSH
Myrtaceae	*Myrcia sp6*	7.5	10	0.807	SSH
Myrtaceae	*Myrcia sp7*	5.8	8	0.807	SSH
Myrtaceae	*Myrcia sp8*	5	5	0.807	SSH
Myrtaceae	*Myrcia splendens*	21	16	0.8	SSH
Myrtaceae	*Myrcia sucrei*	5.57	6	0.807	SSH
Myrtaceae	*Myrcia vittoriana*	8.98	9.62	0.807	SSH
Myrtaceae	*Myrciaria cuspidata*	6.5	10	0.658	SSS
Myrtaceae	*Myrciaria sp*	11.5	12	0.658	SSS
Myrtaceae	*Indet sp12*	10.3	10	0.748	SSH

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Myrtaceae	*Indet sp14*	14.5	10	0.748	SSH
Myrtaceae	*Indet sp16*	14.4	18	0.748	STH
Myrtaceae	*Indet sp17*	6.3	8	0.748	SSH
Myrtaceae	*Indet sp2*	6.49	8	0.748	SSH
Myrtaceae	*Indet sp23*	9.1	9	0.748	SSH
Myrtaceae	*Indet sp29*	10	10	0.748	SSH
Myrtaceae	*Indet sp30*	30.6	18	0.748	LTH
Myrtaceae	*Plinia callosa*	5	6	0.748	SSH
Myrtaceae	*Plinia spiciflora*	15	10	0.748	SSH
Myrtaceae	*Psidium guineense*	7.29	7.5	0.685	SSS
Nyctaginaceae	*Guapira laxiflora*	13	13	0.492	SSS
Nyctaginaceae	*Guapira nitida*	19.7	13	0.492	SSS
Nyctaginaceae	*Guapira noxia*	19.74	7	0.492	SSS
Nyctaginaceae	*Guapira obtusata*	26	15	0.492	LSS
Nyctaginaceae	*Guapira opposita*	18.5	20	0.492	STS
Nyctaginaceae	*Neea floribunda*	6.62	12	0.62	SSS
Nyctaginaceae	*Neea hirsuta*	19.5	15	0.694	SSS
Nyctaginaceae	*Neea macrophylla*	6.2	13	0.694	SSS
Nyctaginaceae	*Nyctaginaceae sp*	11	9	0.496	SSS
Ochnaceae	*Elvasia sp.1*	6.94	7.67	0.765	SSH
Ochnaceae	*Elvasia sp.2*	16.31	12.67	0.765	SSH
Ochnaceae	*Ouratea gigantophylla*	19.5	15	0.774	SSH
Ochnaceae	*Ouratea sp*	8	8	0.774	SSH
Peraceae	*Chaetocarpus myrsinites*	28.2	19	0.805	LTH
Peraceae	*Pera glabrata*	29.71	18.25	0.67	LTS
Peraceae	*Pera heteranthera*	22.94	15.66	0.666	SSS
Peraceae	*Pera sp*	5.19	7.5	0.666	SSS
Peraceae	*Pogonophora schomburgkiana*	28.61	25	0.833	LTH
Phyllanthaceae	*Amanoa guianensis*	6.2	12	0.843	SSH
Phyllanthaceae	*Discocarpus pedicellatus*	8.4	10	0.616	SSS
Phyllanthaceae	*Discocarpus sp*	5.5	8	0.616	SSS
Phyllanthaceae	*Hyeronima oblonga*	19.5	14	0.616	SSS
Phyllanthaceae	*Margaritaria nobilis*	21.1	15	0.484	SSS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Picramniaceae	*Picramnia ciliata*	6	3.5	0.422	SSS
Polygalaceae	*Acanthocladus pulcherrimus*	7.8	6	0.687	SSS
Polygonaceae	*Coccoloba alnifolia*	18.7	15	0.568	SSS
Polygonaceae	*Coccoloba arborescens*	14	13	0.568	SSS
Primulaceae	*Cybianthus amplus*	11.4	10	0.593	SSS
Primulaceae	*Cybianthus oblongifolius*	5.4	9	0.593	SSS
Primulaceae	*Myrsine coriacea*	9.07	9.05	0.49	SSS
Primulaceae	*Myrsine gardneriana*	5	10	0.49	SSS
Primulaceae	*Myrsine guianensis*	13.21	11.23	0.49	SSS
Proteaceae	*Panopsis sp*	9.2	10	0.512	SSS
Proteaceae	*Roupala montana*	63.66	25.96	0.73	LTH
Proteaceae	*Roupala montana var. brasiliensis*	33.3	21	0.73	LTH
Quiinaceae	*Lacunaria crenata subsp. decastyla*	7.83	8.79	0.807	SSH
Rubiaceae	*Alibertia baiana*	11	12	0.683	SSS
Rubiaceae	*Alibertia sp*	9	4	0.683	SSS
Rubiaceae	*Alseis floribunda*	14.5	13	0.85	SSH
Rubiaceae	*Alseis involuta*	6.05	6.99	0.75	SSH
Rubiaceae	*Alseis sp*	8.1	8	0.75	SSH
Rubiaceae	*Amaioua intermedia var. brasiliana*	17.22	13.08	0.625	SSS
Rubiaceae	*Amaioua pilosa*	9.2	13	0.625	SSS
Rubiaceae	*Bathysa sp*	10.82	9.97	0.62	SSS
Rubiaceae	*Coussarea contracta*	13	12	0.61	SSS
Rubiaceae	*Coussarea sp*	18.5	14	0.61	SSS
Rubiaceae	*Coutarea hexandra*	21.5	12	0.6	SSS
Rubiaceae	*Faramea sp*	10.3	8	0.62	SSS
Rubiaceae	*Ferdinandusa guainiae*	5.51	7.04	0.725	SSH
Rubiaceae	*Guettarda angelica*	12.67	8	0.707	SSH
Rubiaceae	*Guettarda grazielae*	27.2	16	0.707	LSH
Rubiaceae	*Guettarda viburnoides*	10.1	14	0.707	SSH
Rubiaceae	*Ixora brevifolia*	13.37	11.3	0.62	SSS
Rubiaceae	*Palicourea divaricata*	25.5	15	0.55	LSS
Rubiaceae	*Palicourea sessilis*	22.3	12	0.55	SSS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Rubiaceae	*Psychotria carthagenensis*	17.63	13.26	0.52	SSS
Rubiaceae	*Psychotria pedunculosa*	8.2	10	0.52	SSS
Rubiaceae	*Randia armata*	8	9	0.69	SSS
Rubiaceae	*Indet sp1*	5.3	8	0.62	SSS
Rubiaceae	*Indet sp2*	5.2	6	0.62	SSS
Rubiaceae	*Rudgea sp*	10	12	0.62	SSS
Rubiaceae	*Schizocalyx cuspidatus*	7.2	8	0.62	SSS
Rubiaceae	*Simira alba*	6.97	8.18	0.675	SSS
Rubiaceae	*Tocoyena brasiliensis*	7.93	9	0.62	SSS
Rubiaceae	*Tocoyena formosa*	10.5	8	0.62	SSS
Rutaceae	*Dictyoloma vandellianum*	22.7	13.77	0.699	SSS
Rutaceae	*Hortia brasiliana*	16.3	15	0.842	SSH
Rutaceae	*Neoraputia alba*	5.41	4	0.699	SSS
Rutaceae	*Rauia nodosa*	6.77	7	0.699	SSS
Rutaceae	*Zanthoxylum nemorale*	19	14	0.586	SSS
Rutaceae	*Zanthoxylum rhoifolium*	16.8	15	0.493	SSS
Rutaceae	*Zanthoxylum sp*	8.5	10	0.586	SSS
Salicaceae	*Banara brasiliensis*	13.21	11.33	0.606	SSS
Salicaceae	*Casearia bahiensis*	9.2	12	0.678	SSS
Salicaceae	*Casearia commersoniana*	21.2	18	0.678	STS
Salicaceae	*Casearia oblongifolia*	8.69	7.61	0.678	SSS
Salicaceae	*Casearia sp. nov.1*	15.37	5	0.678	SSS
Salicaceae	*Casearia sp. nov.2*	5.79	6.8	0.678	SSS
Salicaceae	*Casearia sp1*	21.06	8.5	0.678	SSS
Salicaceae	*Casearia sylvestris*	14	18	0.68	STS
Salicaceae	*Xylosma prockia*	9.5	14	0.785	SSH
Sapindaceae	*Allophylus edulis*	35.55	11.5	0.435	LSS
Sapindaceae	*Allophylus petiolulatus*	13.53	11.42	0.435	SSS
Sapindaceae	*Allophylus puberulus*	5.8	9	0.435	SSS
Sapindaceae	*Allophylus sp*	8.5	8	0.435	SSS
Sapindaceae	*Cupania emarginata*	21.14	15.83	0.619	SSS
Sapindaceae	*Cupania rugosa*	10.98	10.15	0.619	SSS
Sapindaceae	*Cupania scrobiculata*	30.06	18.36	0.628	LTS
Sapindaceae	*Cupania sp*	12.7	16	0.619	SSS

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Sapindaceae	*Pseudima frutescens*	11.59	10.49	0.8	SSH
Sapindaceae	*Talisia cupularis*	6	7	0.803	SSH
Sapindaceae	*Talisia sp*	6.5	9	0.803	SSH
Sapotaceae	*Chrysophyllum januariense*	9.03	8	0.768	SSH
Sapotaceae	*Chrysophyllum lucentifolium subsp. lucentifolium*	6.53	6.82	0.787	SSH
Sapotaceae	*Chrysophyllum splendens*	29.3	17.66	0.768	LTH
Sapotaceae	*Diploon cuspidatum*	12.2	16	0.85	SSH
Sapotaceae	*Ecclinusa ramiflora*	10.97	12	0.655	SSS
Sapotaceae	*Manilkara bella*	6.68	7.42	0.84	SSH
Sapotaceae	*Manilkara longifolia*	18.5	18	0.84	STH
Sapotaceae	*Manilkara maxima*	23	18	0.84	STH
Sapotaceae	*Manilkara salzmannii*	53.48	23.86	0.84	LTH
Sapotaceae	*Micropholis crassipedicellata*	8.5	8.69	0.657	SSS
Sapotaceae	*Micropholis gardneriana*	8.28	6.4	0.657	SSS
Sapotaceae	*Micropholis guyanensis*	7.5	5	0.657	SSS
Sapotaceae	*Pouteria bangii*	16.14	12	0.758	SSH
Sapotaceae	*Pouteria bilocularis*	5.3	6	0.708	SSH
Sapotaceae	*Pouteria butyrocarpa*	10	13	0.758	SSH
Sapotaceae	*Pouteria gardneriana*	5.19	6.31	0.758	SSH
Sapotaceae	*Pouteria grandiflora*	14	10	0.758	SSH
Sapotaceae	*Pouteria guianensis*	8.93	14	0.93	SSH
Sapotaceae	*Pouteria macahensis*	9.18	9.11	0.758	SSH
Sapotaceae	*Pouteria macrophylla*	6.21	5	0.737	SSH
Sapotaceae	*Pouteria pachycalyx*	7.86	8.89	0.76	SSH
Sapotaceae	*Pouteria procera*	5.2	8	0.758	SSH
Sapotaceae	*Pouteria reticulata*	7.5	10	0.876	SSH
Sapotaceae	*Pouteria sp1*	27.06	16.78	0.758	LTH
Sapotaceae	*Pouteria sp6*	12	13	0.758	SSH
Sapotaceae	*Pouteria sp7*	20.5	15	0.758	SSH
Sapotaceae	*Pouteria torta*	17.1	19	0.769	STH
Sapotaceae	*Pouteria venosa subsp. amazonica*	12.25	12	0.92	SSH
Sapotaceae	*Pradosia lactescens*	11.89	10.55	0.724	SSH

Family	**Species**	**Maximal diameter (cm)**	**Maximal Height (m)**	**Wood Density (g cm^{-3})**	**Functional Entities**
Schoepfiaceae	*Schoepfia brasiliensis*	12.96	11.09	0.723	SSH
Simaroubaceae	*Homalolepis cedron*	6.21	7.09	0.425	SSS
Simaroubaceae	*Simarouba amara*	24.06	18	0.378	LTS
Siparunaceae	*Siparuna guianensis*	6.5	10	0.662	SSS
Siparunaceae	*Siparuna reginae*	11.2	10.93	0.662	SSS
Solanaceae	*Solanum pseudoquina*	5.6	5.5	0.28	SSS
Solanaceae	*Solanum sooretamum*	6.97	8	0.28	SSS
Solanaceae	*Solanum swartzianum*	8	10	0.28	SSS
Thymelaeaceae	*Daphnopsis granulosa*	6	8	0.458	SSS
Urticaceae	*Cecropia pachystachya*	11.3	12	0.308	SSS
Urticaceae	*Pourouma mollis*	14.4	14	0.39	SSS
Violaceae	*Paypayrola blanchetiana*	7.3	12	0.606	SSS
Violaceae	*Rinorea bahiensis*	27.25	8	0.683	LSS
Violaceae	*Rinorea guianensis*	15.5	8	0.78	SSH
Vochysiaceae	*Vochysia acuminata*	15.5	14	0.444	SSS
Vochysiaceae	*Vochysia angelica*	18.72	13	0.444	SSS
Vochysiaceae	*Vochysia riedeliana*	32.3	19	0.444	LTS

Table S4 Correlation matrices among the predictors calculated for the 27 permanent sample plots in Brazilian Atlantic rainforest. We show the Spearman's coefficient of correlation (r), with significant values indicated with * ($p < 0.05$). MO = Matrix Openness, PD = Patch Density, CWD = Climatic Water Deficit, SB = Soil Sum of Bases, N = Soil Nitrogen, SOC = Soil Organic Carbon, Clay = Soil Clay content.

	Predictors							
	Age	**MO**	**PD**	**CWD**	**SB**	**N**	**SOC**	**Clay**
Age	1							
MO	**-0.46***	1						
PD	**-0.4***	**0.72***	1					
CWD	0.03	0.08	0.12	1				
SB	0.02	0.08	-0.31	-0.15	1			
N	0.15	-0.13	-0.37	**-0.78***	**0.47***	1		
SOC	0.11	-0.07	-0.34	**-0.8***	**0.52***	**0.95***	1	
Clay	0.05	0.14	-0.03	-0.22	0.34	**0.42***	**0.47***	1

Table S5 Number of species within each functional entity (i.e., group of species with same trait values) found in the 27 second-growth forest plots located in northern Espírito Santo State and southern Bahia State, Brazil. The functional entities were built based on the combination of species traits (maximum stem diameter, maximum stem height and wood density). SSS = Small, Short, Softwood; SSH = Small, Short, Hardwood; STS = Small, Tall, Softwood; STH = Small, Tall, Hardwood; LSS = Large, Short, Softwood; LSH = Large, Short, Hardwood; LTS = Large, Tall, Softwood; LTH = Large, Tall, Hardwood.

Plot	**SSS**	**SSH**	**STS**	**STH**	**LSS**	**LSH**	**LTS**	**LTH**	**Number of functional entities**
A3	19	6	1	4	1	0	11	4	7
A6	11	8	1	4	2	1	7	1	8
A7	26	13	0	3	1	2	8	2	7
A8	33	10	0	3	1	1	12	3	7
A9	8	3	1	2	1	1	4	2	8
A11	19	10	0	6	3	1	7	5	7
A12	26	11	0	4	1	0	7	3	6
A13	14	7	1	2	1	0	7	2	7
A15	13	5	1	3	0	0	5	1	6
A17	9	3	0	2	0	2	10	2	6
A19	35	10	1	9	1	2	8	5	8
A20	12	8	1	3	1	0	5	0	6
A21	23	9	1	5	1	1	11	3	8
A24	23	15	0	4	1	2	7	2	7
A25	27	11	1	4	1	0	10	5	7
A56	35	20	2	5	6	0	11	7	7
A57	25	7	5	3	7	0	9	4	7

Plot	**SSS**	**SSH**	**STS**	**STH**	**LSS**	**LSH**	**LTS**	**LTH**	**Number of functional entities**
A58	10	3	0	2	3	0	10	1	6
A59	13	7	2	4	4	0	4	1	7
A60	16	2	1	2	3	0	9	1	7
A61	32	12	5	8	11	0	11	6	7
A62	23	11	2	3	5	0	7	5	7
A63	9	2	0	0	2	0	5	2	5
A64	36	24	8	8	6	2	8	7	8
A65	32	28	4	4	7	0	10	5	7
A66	26	15	3	6	5	1	10	2	8
A67	36	13	2	4	4	2	8	4	8
Total number of species	**244**	**132**	**13**	**14**	**17**	**5**	**28**	**20**	

Table S6 Pairwise correlation matrices among the carbon storage, maximum diameter, maximum height and wood density of 473 tree species recorded in 27 second-growth forest plots in Brazilian Atlantic rainforests. We show Spearman's correlation coefficient (r), with (*) indicating significant values ($p < 0.05$).

Species Attributes				
	Aboveground C storage	**Maximum Diameter**	**Maximum Height**	**Wood Density**
Aboveground C storage	1			
Maximum Diameter	**0.89***	1		
Maximum Height	**0.66***	**0.76***	1	
Wood Density	**0.15***	-0.06	0.005	1

Table S7 Number of species (S) and individuals (Abund) of pioneer, early-successional and late-successional species within each functional entity found in 27 second-growth forest plots. SSS = Small, Short, Softwood; SSH = Small, Short, Hardwood; STS = Small, Tall, Softwood; STH = Small, Tall, Hardwood; LSS = Large, Short, Softwood; LSH = Large, Short, Hardwood; LTS = Large, Tall, Softwood; LTH = Large, Tall, Hardwood; CD = carbon-dominant species; NCD = non-carbon dominant species.

Functional Entity	**Carbon dominance**	**Pioneer**		**Early-successional**		**Late-successional**	
		S	**Abund**	**S**	**Abund**	**S**	**Abund**
SSS	NCD	78	437	68	545	98	414
SSH	NCD	31	88	27	107	74	239
STS	NCD	3	46	5	131	5	147
STH	NCD	4	29	2	3	8	57
LSS	NCD	1	13	12	289	4	118
LTS	CD	11	549	14	366	3	16
LSH	CD	2	8	1	2	2	13
LTH	CD	3	6	6	156	11	221
			Total				
SSS, SSH, STS, STH, LSS	NCD	117	613	114	1075	189	975
LTS, LSH, LTH	CD	16	563	21	524	16	250

Table S8 Pairwise correlation matrices among aboveground carbon storage, forest functional composition (CWM trait values), redundancy and vulnerability in 27 second-growth forest plots. AGC = Aboveground Carbon Storage, MD_{CWM} = community weighted-mean maximum stem diameter, MH_{CWM} = community weighted-mean maximum stem height, WD_{CWM} = community weighted-mean wood density, FR = Functional Redundancy, FV = Functional Vulnerability. We show Spearman's correlation coefficient (r), with (*) indicating significant values ($p < 0.05$).

	Response Variables					
	AGC	**MD_{CWM}**	**MH_{CWM}**	**WD_{CWM}**	**FR**	**FV**
AGC	1					
MD_{CWM}	-0.005	1				
MH_{CWM}	0.25	**0.45 ***	1			
WD_{CWM}	-0.009	0.13	0.14	1		
FR	**0.52 ***	**-0.68 ***	-0.22	-0.08	1	
FV	-0.32	**0.40 ***	0.03	0.16	**-0.52 ***	1

V. CONCLUSÕES GERAIS

A partir dos resultados dos dois capítulos podemos concluir que:

(i) A maioria dos atributos florestais foi afetada negativamente pela perda de cobertura florestal e pelo grau de fragmentação (i.e., abertura da paisagem), mas a magnitude dos efeitos variou com o atributo da paisagem, atributo da floresta e região (i.e., contexto da paisagem). Os efeitos do desmatamento foram muito mais fortes do que os da fragmentação e, em geral, a abertura da paisagem afetou negativamente e mais fortemente a estrutura da floresta e as espécies dispersas por animais, enquanto teve efeitos opostos na diversidade e no tamanho das sementes entre as diferentes regiões. Além disso, a abertura da paisagem afetou a estrutura da floresta na maioria das escalas espaciais, enquanto as espécies dispersas por animais foram afetadas nas escalas maiores e o tamanho das sementes em escalas pequenas.

(ii) O status sucessional e os fatores edáficos foram os principais preditores de estoque de carbono e vulnerabilidade em florestas Atlânticas secundárias, enquanto a disponibilidade de recursos, como água e nitrogênio e carbono do solo, e a textura do solo foram os principais impulsionadores do crescimento das espécies. Contudo, os efeitos dos preditores foram contrastantes entre as espécies do estrato florestal superior e do estrato regenerante (ou seja, espécies dominantes em carbono e espécies não dominantes em carbono, respectivamente).

Como considerações finais, destacamos a importância das florestas tropicais para a conservação da biodiversidade e funcionamento dos ecossistemas. Nossos resultados avançam nossa compreensão dos mecanismos que impulsionam a estrutura, diversidade, composição funcional e estoque de carbono nas florestas atlânticas brasileiras, contribuindo para a prevenção e gerenciamento dos impactos das mudanças no uso da terra e mudanças climáticas no funcionamento e provisionamento de serviços ecossistêmicos. No geral, nossas descobertas destacam a importância de avaliar adequadamente o contexto da paisagem ao redor das áreas destinadas à conservação e reflorestamento, e elaborar estratégias eficazes de restauração florestal adaptadas às condições locais, a fim de orientar o manejo de paisagens fragmentadas para salvaguardar a estrutura, diversidade e funcionamento da floresta.

VI. GENERAL CONCLUSIONS

From the results of the two chapters we can conclude that:

(i) Most forest attributes were negatively affected by the loss of forest cover and the degree of fragmentation (i.e., landscape openness), but the magnitude of the effects varied with the landscape attribute, forest attribute, and region (i.e. landscape context). The effects of deforestation were much stronger than those of fragmentation and overall; landscape openness affected negatively and more strongly forest structure and animal-dispersed species, whereas it had opposite effects on diversity and seed size across different regions. Finally, landscape openness affected forest structure at most spatial scales, animal-dispersed species at larger scales and seed size at small scales.

(ii) The successional status and edaphic factors were the main predictors of carbon stock and vulnerability in second-growth Atlantic forests, while resource availability, such as water and soil nitrogen and carbon, and soil texture were the main drivers of species growth. Yet, these predictors had contrasting effects on upper and regeneration forest stratum species (i.e. carbon-dominant and non-carbon dominant species, respectively).

As final considerations, we emphasize the importance of tropical forests for the conservation of biodiversity and the functioning of ecosystems. Our results advance our understanding of the mechanisms that drive structure, diversity, functional composition and carbon stock in Brazilian Atlantic forests, contributing to the prevention and management of the impacts of land use and climate changes on the functioning and provision of ecosystem services. Overall, our findings highlight the importance of properly assessing the landscape context surrounding areas targeted for conservation and reforestation, and designing effective forest restoration strategies adapted to local site conditions in order to guide the management of fragmented landscapes to safeguard forest structure, diversity and functioning.